THE VERTICAL DISTRIBUTION
OF THE SIPHONOPHORES COLLECTED DURING THE
SOND CRUISE, 1965

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(Text-figs. 1–13)

The siphonophores obtained from the day and night series of horizontal hauls made using a 10 ft Isaacs–Kidd mid-water trawl (IKMT) and a 1 m² ring net (N113), off Fuerteventura in the Canary Islands, have been identified. Because of the low numbers found in some hauls and the possibility that there was some 'hold-up' of material in the nets themselves, the samples from the oblique parts of the IKMT hauls were also examined for siphonophores. A total of 64 species were identified of which there were 51 calycophoran, 12 physonect and 1 cystonect species.

The vertical distributions of most of the calycophoran species have been considered in detail, and, where sufficient numbers were present, their diurnal variations analysed. The overall vertical distributions of the physonect species have been compared but because of the difficulty in relating the individual pieces found in the samples to the number of animals present, no attempts were made to analyse quantitatively any of these data. The possible effects on the results on the timing of the hauls and the absence of the catch-dividing bucket in the shallowest ones are discussed in detail for certain species.

INTRODUCTION

In many of the more general studies on marine zooplankton the part played by siphonophores is frequently ignored or only given a cursory mention. However, their ecological importance is far from insignificant. In this context we are indebted to the late Mr A. K. Totton whose publications have done much to draw attention to the siphonophores and the part which they play in the zooplankton community. His synopsis of the siphonophores (Totton, 1965) is a masterly work from which any student of this fascinating group can derive much benefit.

Some more recent studies show the important part which siphonophores play in the zooplankton community. Boucher & Thiriot (1972) in their study of the top 200 m of water in the western Mediterranean found that, although the ostracods and copepods numerically contributed over 95% of the total population, within the macroplankton group the siphonophores represented from 45 to 67% of the total. Grice & Hart (1962) found that in the region between New York and Bermuda the siphonophores in the epizooplankton were numerically not very important but if their displacement volume was considered then they represented between 0·9 and 17·7% of the total. These latter studies were continued in the Sargasso Sea by Deevey (1971) and Deevey & Brooks (1971). In the former paper it was found that the coelenterates, of which the siphonophores contributed the majority, numerically represented about 3% of the zooplankton organisms found in the top 500 m of water. Again this is a small percentage but if the dry weight and displacement volume percentages were considered then the siphonophores

accounted for 8·1 and 17·7% respectively. In the latter paper the water column down to 2000 m was considered, in four equal zones. In the top 500 m, the siphonophores were numerically the fourth most important group, after the copepods, ostracods and tunicates, but only accounted for 2·4% of the total population, while below 500 m they represented only about 1%. Grice & Hart (1962) found that siphonophores were more common in oceanic than neretic waters and concluded that in the former they would be very important in the zooplankton, especially because of their predatory nature, even if this was not immediately apparent from their numbers.

The lack of information on siphonophores probably results from the technical difficulties inherent in any quantitative study. They are, for instance, difficult to separate completely from the samples because of the smallness of many of their parts and their transparency. Moreover the specimens are very fragile and tend to break up into numerous parts, some of which may then be lost in the nets. It is, therefore, often impossible to obtain a reliable quantitative estimate of the catch.

There is rather little information available on the vertical distribution of siphonophores. Most of the records of the geographical distribution of the species come from the major expeditions, with samples usually having been obtained by open nets fished over wide depth ranges. Thus Haeckel (1888) described 30 species from the 'Challenger' Expedition collections; Lens & van Riemsdijk (1908) 32 from the 'Siboga' Expedition; Bigelow (1911b) 48 from the 'Albatross' collections (several expeditions); and Moser (1925) 57 from the 'Gauss' German South Polar Expedition. These are important works in the history of the study of siphonophores but it was not until the work of Bigelow & Sears (1937) that any attempt was made at an understanding of their depth distribution and seasonal variations. Even though almost all of the 'Thor' collections were made with open Young fish Trawls, Bigelow & Sears discuss various methods of overcoming the problems which arise from contamination of the samples during the oblique parts of the hauls. The information which can be gained from this work is limited because of the corrections which had to be applied to the data, but it is possible to establish the upper depth limit of any given species and to make some estimate of its peak depth and lower limit.

The 'Meteor' cruise of 1925–7 used closing nets fished over various depth ranges down to 3500 m, and the siphonophores from the collections are listed by Leloup (1934). Depth and geographical distributions were discussed by Leloup & Hentschel (1935), but since the stations were all in different localities in the Atlantic Ocean from 20° N to 60° S, any conclusions which may be reached on vertical distributions must be qualified by the latitude differences. Totton (1941, 1954) similarly gives depth data for all his specimens, many of which were isolated from closing net samples, but the stations were in widely differing localities and so the information can only give a general guide to vertical distribution patterns.

More recent investigations do allow some more precise conclusions to be reached on the depth distributions of siphonophores. Moore (1949, 1953) gives a detailed account of the population of zooplankton in the waters of Bermuda and in the Florida current, down to a depth of 300 m. He also studied the diurnal migrations of siphonophores and their reactions to variations in temperature and illumination. Apart from the fact that he was

dealing with only a limited population, his analysis of the depth distribution patterns of epipelagic siphonophores has not been surpassed to date. Other papers which deal with this subject include those of Patriti. He studied the seasonal changes and distribution of siphonophores: (a) in the top 25–50 m of water in the Gulfs of Marseille and Gabes (Tunisia) (Patriti, 1964, 1969); (b) in the Gulf of Gascogne down to 4000 m (Patriti, 1965a, b; 1966); and (c) in hauls down to 1200 m in a region near Madagascar (Patriti, 1970). Stepanyants (1970) studied the siphonophores from nets at differing depths at several stations in the North Pacific, but the information was not sufficient to establish any depth distribution patterns. Siphonophores have also been included in some other general studies of the vertical distribution of zooplankton, such as that by Hure (1955) who worked in the Adriatic, and by Alvarino (1967) in the Pacific.

The present study is a further contribution to a series of papers (Angel, 1969; Clarke, 1969; Baker, 1970; Foxton, 1970a, b; Badcock, 1970; Roe, 1972a, b, c, d; Angel & Fasham, 1973) which are concerned with an investigation of the diurnal depth variations in the zooplankton population off Fuerteventura, Canary Islands, during the 'Discovery' SOND cruise in 1965. The cruise itself and the hydrology of the area is described by Currie, Boden & Kampa (1969), and details of the nets used in the biological sampling programme are given by Foxton (1969), who also discusses some of the advantages and disadvantages of such a programme.

MATERIAL AND METHODS

The major part of the biological sampling programme undertaken during the SOND cruise consisted of two series of day and night hauls carried out using a modified Indian Ocean Standard 1 m² ring net (N113) and a 10 ft Isaacs–Kidd mid-water trawl (IKMT), both fitted with catch-dividing buckets. These nets were described in detail by Foxton (1969), who also discussed some of the problems associated with the sampling methods. Further to this, the problems associated with the interpretation of the results from the N113 series of hauls were discussed in detail by Angel (1969) and Roe (1972a). This latter author stressed points which will be frequently referred to in this paper, concerning (a) the timing of these hauls, and (b) the absence of the catch-dividing bucket in the shallowest hauls which resulted in a change in the minimum mesh size of the N113 net. These points will not be discussed further here but reference should be made to the afore-mentioned papers. A list of the N113 horizontal hauls and their times are given by Angel (1969).

Similarly, the timings of the IKMT hauls were thought to be of importance in any attempt at an understanding of the depth distribution of some of the siphonophore species discussed here. A summary of these hauls with their times has not previously been published and so is given in Appendix III. There was no change in the minimum mesh-size of the IKMT net when the catch-dividing bucket was removed for the shallowest hauls, and so in these cases the results should not have been affected. In addition to a study of the siphonophores caught during the horizontal part of each haul, the oblique or shallow catches for the IKMT series were also examined. The significance of the data which can be derived from these oblique hauls was discussed by Badcock (1970), but also many of the catches of the rarer siphonophore species were derived entirely from these hauls. Foxton (1970a) also discussed the limitations of the sampling procedure from the point of view of the capture of decapods, but it is to be hoped that the effects which he noted concerning the 'hold-up' of specimens in the net, as well as their active swimming, may not apply to such an extent in the case of the siphonopores. However, there were definite indications of some degree of 'hold-up' as exemplified by some of the catches of the diphyid, *Chelophyes appendiculata*, where large numbers of specimens were found in the samples from the oblique parts of the hauls.

Badcock (1970) has made the point that the N113 and IKMT series of hauls are by no means replicates, because of the differences in the sizes of the net openings and of the mesh size. There are several other factors which will affect any analysis of the relative retention powers of each net,

not least of which is the difference in the speed at which the nets were towed. The IKMT nets were towed at an average of 2·8 knots (Appendix III), while the N113 nets, because of their finer mesh, were only towed at *ca.* 1·9 knots. This and other factors will be discussed in more detail later.

Initially the larger pieces of siphonophores were sorted from the samples obtained during the horizontal hauls of both the IKMT and N113 nets. A preliminary identification of these pieces was then made by the late Mr A. K. Totton. The smaller pieces were then isolated from the residues and identified along with all those separated from the oblique hauls. In addition the siphonophores present in a series of 36 neuston net samples were examined. This neuston net series, the 'Star' (St. 5802), was carried out over a 6 hr period at night and, although the samples are limited, they do give some indication of which siphonophore species ascend right into the surface layers at night. In all the samples from the SOND collections attention was mainly paid to the asexual polygastric stages which were present. The numbers of specimens of the eudoxid, sexual stage are small and so only brief mention of them is made in the text.

RESULTS AND DISCUSSION

ORDER SIPHONOPHORA

The order Siphonophora is divided into three sub-orders based mainly on the presence or absence of an apical aboral pneumatophore or float, and of nectophores or swimming bells. These sub-orders are the Cystonectae Haeckel, 1887, which have a pneumatophore but no nectophores; the Physonectae Haeckel, 1888, which usually have both a pneumatophore and one or more nectophores; and the Calycophorae Leuckart, 1854, which do not possess a pneumatophore but have one or more nectophores present. As Totton (1965) points out, this classification is not based on the sexual, adult medusoid stage but on the asexual, larval nurse-carriers. However, these latter individuals are by far the more dominant siphonophore form in the zooplankton and are the ones which are mainly considered in this paper. Each particular sub-order presents its own problems for any quantitative study of their vertical distribution and abundance, and these will be discussed separately in each section.

SUB-ORDER CYSTONECTAE HAECKEL, 1887

This sub-order contains only five recognized species from three genera, of which the best known is the pleustonic siphonophore *Physalia physalis* (L.) 1758, the 'Portuguese Man O'War'. No specimens were found in the SOND neuston net samples but the species was undoubtedly present in the area.

Rhizophysa filiformis (Forskål, 1775)

A single specimen was taken in a N113H day haul at 150 m (5716 (7)). The species appears to be difficult to catch in a net due to its ability to retract its stem quickly from any point of contact. More frequently it attaches itself to lines such as those used in long-lining and specimens up to 15 + m long have been caught in this way. Our knowledge of the geographical and depth distribution of this species is limited, but Bigelow & Sears (1937) consider it to be a warm water species usually found at the surface although occasionally at considerable depths.

A young specimen of *Rhizophysa ?eysenhardti* Gegenbauer, 1859, was found in one neuston net sample (St. 5802 (12)).

SUB-ORDER PHYSONECTAE HAECKEL, 1888

The Physonectae are characterized by the presence of an apical pneumatophore and nectophores. The neotenous family *Athorybiidae* Huxley, 1859, contains two species, one of which does not develop any nectophores while the other develops only one. In general it is very difficult to assess the vertical distribution pattern of any physonect species as they are rarely taken intact in a trawl net. The specimens are very fragile and easily become broken up in the net, while, in the case of the long-stemmed forms, the stem may easily be severed and only part of the animal caught. It is doubtful whether a prolonged study of those intact animals which can be collected by hand would alleviate the situation, for, although a relationship might be established for the average number of bracts, nectophores, etc., per adult individual, the likely differential loss of these in the net would confuse the situation. Thus the presence of only one nectophore in a sample would indicate the presence of at least one specimen of that species at that depth, but so also would, in most cases, the presence of forty. A similar argument, but on a much larger scale, applies to the presence of bracts, as some species may have up to 400 or more. The number of pneumatophores present would be the best indicator, as there is only one per individual, if it was not for the fact that they are so easily lost in the net.

For these reasons the depth distributions of the physonect species taken during the SOND cruise are not shown in any quantitative manner. The horizontal hauls of both nets in which fragments of each species were caught, together with the actual number of nectophores, bracts, etc., are listed in Appendix I, and reference should be made to Appendix III and Angel (1969) for the depths and timings of these hauls. (The depths referred to in the text are the mean depths for the relevant hauls.) Whenever it has been found necessary to refer to the catches in the oblique hauls, the station data for these are given in the text, but otherwise the data for these catches have not been included.

Family Apolemiidae

Apolemia uvaria (Lesueur, ?1811)

Fragments of this species were found in three hauls from widely differing depths. Nineteen nectophores and some stem pieces occurred in a N113H night haul at 910 m, and two nectophores plus stem pieces at 350 m in an IKMT day haul. The oblique IKMT night haul (5793 (3), 340–0 m) also contained three nectophores. The only conclusion which can thus be reached is that *A. uvaria* is not common at Fuerteventura but does exist over a wide depth range.

Apolemia uvaria is not well documented in the literature and it was not taken during any of the major oceanographic expeditions of this century. Leloup (1955) considered the species to be common in both the Atlantic and Indian Oceans, as well as in the Mediterranean, and to have a wide depth distribution. The findings of Fraser (1961, 1967) showed that the species was not only present in the oceanic warm-water fauna, but also in the colder waters of the North Sea, thus indicating a fairly wide temperature tolerance.

Family Agalmidae

Agalma okeni (Sars, 1846) Fewkes, 1880

One almost complete specimen was caught at 570 m in a N113H day haul, and a single juvenile nectophore appeared in a similar haul at 215 m. Nine badly damaged nectophores of an *Agalma* sp. were found at 350 m in an IKMT day haul, while an IKMT oblique haul (5811 (2), 475–0 m) contained two bracts. This species is known to be widely distributed in the warmer waters of the three Great Oceans, but there is very little information on its depth distribution. Bigelow (1911*b*) found the species to occur mainly at the surface with occasional specimens down to 600 m, while Totton (1954) found it almost exclusively in the top 100 m. It is possible that the paucity of specimens found in the present collections is connected with the insufficiency of sampling in the surface waters.

Halistemma rubrum (Vogt, 1852)

This species was very common at Fuerteventura, being found in 51 out of the 76 horizontal N113 and IKMT hauls, and at all depths from 40 to 940 m, but it was not present in the deepest hauls of either series. Fragments of specimens were also found in several of the neuston net samples. As was discussed at the beginning of this section, the fact that some hauls contained considerably more nectophores or bracts than others does not necessarily mean that more specimens were present, and so it is not meaningful to analyse the data (Appendix I) quantitatively.

Totton (1954) discussed the presence in the Indian and Atlantic Oceans of small nectophores and bracts which closely resembled the Mediterranean form of this species, on which the original description was based. They do, however, differ in certain aspects and Totton divided his specimens into 'e' and 'f' types, the latter being somewhat more compressed in the abaxial–adaxial plane and having a more conspicuous mouth-plate. It appears that the majority of the specimens taken during the SOND cruise are of the 'e' type. In some of the younger nectophores an additional ridge connecting the more ostial vertico-lateral and apico-lateral ridges, close to the ostium, was present. This was not described by Totton (1954) but does become very indistinct in the older nectophores. I am, at present, in the slow process of reviewing the whole of the genus *Halistemma* and it is possible that these *H. rubrum* types may have to be raised to subspecific or even specific level when enough material is available for a critical study. It should be noted that Totton (1965), in his monograph, abandoned the use of the genus *Stephanomia* and reclassified *S. rubra* as *H. rubrum*. A discussion of this point is given in Totton (1954). Two juvenile specimens of *H. rubrum* were found in the N113H night haul at 150 m. It has not been possible yet to make any detailed comparison with the equivalent stage in the Mediterranean form and, as it is not really within the context of this present paper, any discussion on these specimens will be reserved for a later paper.

Halistemma rubrum is quite well documented in the literature and is known to be common in the warmer waters of the three Great Oceans and in the Mediterranean. There are, however, few data on its depth distribution. Bigelow & Sears (1937) did not

record the species, while Alvarino (1967) described it as mesopelagic occurring by day between 250 and 300 m, although absent from her night hauls. Thus the present data which indicate a wide depth distribution for the species considerably enhance our knowledge.

?Nectalia loligo Haeckel, 1888

Single nectophores were found in the horizontal and oblique parts of an IKMT day haul, at depths of 810–(675) m and 675–0 m. It is likely that the latter nectophore resulted from a 'hold-up' in the net, and that both came from a single specimen caught during the horizontal part of the haul.

The identification of this species is based on a comparison with nectophores of *Nectalia loligo* taken off Bermuda (Totton, 1936). There have been very few previous records of this 'species', whose validity has frequently been doubted. Haeckel (1888) originally described the species from a complete(?) specimen taken at the surface off Lanzerote, Canary Islands. Chun (1897) reported another specimen from a similar locality (Orotava), and two others from the 'Plankton Expedition'. Moser (1925) found one almost complete specimen and parts of four others in the 'Gauss' collections, while Totton (1936) found parts of eleven specimens from Beebe stations off Bermuda. All these findings, and two by Leloup (1955) are restricted to various localities in the Atlantic Ocean, and the only others are a complete specimen described by Bigelow (1911*b*) southwest of the Galapagos Islands and some undescribed fragments found by Alvarino (1963) in the Pacific Ocean.

Totton, as quoted by Leloup (1955), considered that the Bigelow (1911*b*) specimen, at least, was not of a valid species but represented a juvenile stage in the development of a large physonect. Recently many complete or semi-complete specimens of *Nectalia*-like siphonophores have been caught and it is hoped to be able to review the validity of *Nectalia loligo* as a species when these specimens have been fully examined. However, it appears most probable that the species is not a valid one, but that the specimens described as it are the juvenile stages of at least two physonects, almost certainly of the genus *Halistemma*, one of which is still to be described.

Marrus orthocanna (Kramp, 1942)

Twenty-two nectophores, 71 bracts and several stem pieces with associated gastrozooids, etc., probably representing an almost complete specimen, were found in a N113H night haul at 720 m. This species appears to have been recorded previously only at six stations; three in Baffin Bay (Kramp, 1942), two to the northwest of Scotland (Fraser, 1961, 1967) and one in the Chukchi Sea on the other side of the Arctic Basin (Stepanyants, 1967). There are two doubtful records, discussed by Kramp, from the Robeson Channel region north of Baffin Bay, and the distribution given in Totton & Fraser (1955), for the Barents and Norwegian Seas, is a supposition based on the earlier results.

This present record thus considerably extends the geographical distribution of *Marrus orthocanna* southwards. The previous most southerly record was at 55° N. This species has also been found in some samples from 18° N, 25° W ('Discovery' St. 7089) in the 500–800 m range. Stepanyants (1967) considered this species to be a high Arctic form,

usually found at temperatures around 0 °C and at depths of 300–2000 m. It is thus rather surprising to find this species at 18° and 28° N in temperatures of up to 9·2 °C. Since, however, the number of records for *M. orthocanna* are so few it is difficult to draw any firm conclusions as to its geographical or depth distribution, but it does appear to be wider than was previously suspected. It is interesting to conjecture that the occurrence of this species may indicate the presence of waters of Arctic origin at Fuerteventura.

Marrus orthocannoides Totton, 1954

A single nectophore of this rare species was found in an IKMT oblique haul (5811 (2)) from 475 m to the surface. There appears to be only one other certain record, that of Totton (1954) who described the new species from some loose nectophores, bracts and stems separated from a single haul in the western tropical Indian Ocean. The depth range of this haul (1400–700 m) indicated a temperature range of 4·85–8·35 °C, whereas the range covered by the present record was 11·5–22 °C. Alvarino (1964) lists this species amongst those found during the MONSOON Expedition (1960–3) in the Indian Ocean but in her review (Alvarino, 1971) she includes under *Marrus orthocannoides* the records of Fraser (1961, 1967) and Kramp (1942) which actually are for *M. orthocanna*. There is thus some confusion of the species here although the Indian Ocean specimen is more likely to be *M. orthocannoides* than *M. orthocanna*. However, the present record for the Canary Islands not only indicates a much wider temperature tolerance for the former species, but also represents an entirely new geographical locality for it.

Nanomia bijuga (Chiaje, 1841)

Twelve nectophores of this species were found in a N113H day haul at 40 m, and two other nectophores and a bract in a similar night haul at 100 m. Totton (1965) states that the species is common in the Mediterranean, and I have seen it at Villefranche-sur-Mer, but Bigelow & Sears (1937) did not observe it. It is possible that *Nanomia bijuga* is a neritic form whereas most of Bigelow and Sear's hauls were carried out in deep water. However, Stepanyants (1967) has reviewed its world-wide distribution as being common in the warmer waters of all three Great Oceans at superficial depths down to a maximum of 600 m. The results of Alvarino (1971) indicate it to be mainly a new surface form and the present results agree with this.

Physonect 'C', nov.sp.

A total of 65 nectophores, 63 bracts and one or two denuded stem fragments of a new small species of physonect were isolated from 14 hauls at depths ranging from 660 to 950 m, the majority being in the 750–800 m range. Most of the fragments are in poor condition and I am awaiting some better material before undertaking a description of the species.

Family ?Pyrostephidae ?Agalmidae

Bargmannia elongata Totton, 1954

The exact systematic position of this species is in doubt as it is only known from its nectophores. No associated stem fragments or bracts could be found with the necto-

phores which were recorded in seventeen hauls between 360 and 950 m. The greatest concentration of nectophores was in hauls between 500 and 625 m although, as discussed earlier, this does not necessarily indicate a peak in the distribution pattern. A total of 237 nectophores were found.

It is surprising that this species, which is common both in this SOND collection and in later 'Discovery' collections, has been recorded so little in the past. It was originally described by Totton (1954) from material collected at 13 stations, 4 in the Indian Ocean and 9 in the Atlantic, while Leloup (1955) mentioned a single nectophore found at a station south-west of the Azores. Stepanyants (1967, 1970) has recorded this species from four stations in the North Pacific and concluded that it was a bathypelagic form. Alvarino (1971) has found the species at several localities in the Pacific Ocean. The present results add considerably to our knowledge of *Bargmannia elongata* in that the Canary Island region is a new locality for this species and the depth distribution data are the most comprehensive yet. These latter results indicate that the species is more meso-pelagic than bathypelagic, as suggested by Stepanyants (1967), but no definite conclusions can be reached as only the water column down to 1000 m was studied.

Family Physophoridae

Physophora hydrostatica Forskål, 1775

Pieces of this short-stemmed physonect were found in five horizontal hauls, and the oblique parts of three of these also contained some fragments. This probably indicates some hold-up in the net until after the catch-dividing bucket had operated. Four of the horizontal hauls were at depths of 250 m or less, while the fifth was from a depth of 950 m. This latter N113H haul contained twenty nectophores, which probably represents more than one specimen as there are normally only about twelve nectophores per animal. Fragments of specimens were also found in three other IKMT oblique hauls. A stem and pneumatophore together with two detached nectophores were isolated from one of the neuston net samples (St. 5802 (23)).

This species is very well documented in the literature although most of the captures have been either at the surface or in open nets. Totton (1965) concludes that the species is cosmopolitan, occurring quite frequently in all the great oceans and the Mediterranean, and over a temperature range of 3–21·1 °C. Bigelow & Sears (1937) reviewed the previous records for its depth distribution and concluded, for the Mediterranean, that it usually occurred at the surface, with nectophores, probably detached ones, appearing at depths down to 800 m. Kielhorn (1952) found the species at the surface, and Alvarino (1967) found it in a haul between 350 and 250 m. Stepanyants (1967) concludes that it is generally found in the upper 200 m but occasionally down to 900 m. In general, the SOND specimens are from the shallower waters but the large numbers of nectophores found at 950 m would seem to indicate the presence of living specimens at that depth and not just detached nectophores.

Family Athorybiidae

Melophysa melo (Quoy & Gaimard, 1827)

One (?) nectophore and six bracts of this species were found in an IKMT horizontal haul at 50 m, while an oblique IKMT haul (5798 (3)) from 160 m to the surface contained three (?) nectophores and nine bracts. Since it appears that *Melophysa melo* has only one functional nectophore at any instant, it would be possible to make some quantitative estimates with this species. However, with à total of four specimens, all that can be concluded is that *M. melo* is an epipelagic form.

There is not a great deal of information on this species and much of it is confused as *Melophysa melo* has often been mistaken for a closely related species, *Athorybia rosacea*. Bigelow (1931) considered it to be cosmopolitan in the warmer seas. The earlier records were from the Mediterranean, Straits of Gibraltar and Canary Islands, but subsequently it has been found in the South Atlantic, Pacific and Indian Oceans. Totton (1965) reviews the more recent sparse records.

Family Forskaliidae

Forskalia edwardsii Köllicker, 1853

Eight nectophores and a stem fragment were found in four hauls at depths ranging from 660 m to the surface, although three of these were shallower than 290 m. As Totton (1954) states, 'very little advance has been made in our meagre knowledge of species of *Forskalia* since Bedot (1893), who was familiar with living Mediterranean forms, reviewed the genus'. The present information can do little to enhance our knowledge. Totton (1954) found the species to have a wide depth distribution in the Indian Ocean, namely from 1650 m to the surface, while in the Red Sea he found it only in the top 250 m. The present records seem to indicate a fairly shallow existence for this species, and I would like here to include a record for twelve nectophores, nine bracts and a stem fragment including the pneumatophore isolated from a haul (St. 7856 (73)) at 250 m from a locality close by (30° N, 23° W).

SUB-ORDER CALYCOPHORAE

The six families of the Calycophorae, of which five are represented in SOND collections, each exhibit their own range of difficulties when any consideration of their depth distribution pattern on a quantitative basis is attempted. For example, the hippopodiid and some of the prayid species have several nectophores comprising their asexual forms, which are generally referred to as the polygastric stage in calycophorans. This fact, as was the case with the physonect species, makes difficult any attempt to assess the actual number of specimens present. However, as will be discussed in the relevant sections, the majority of calycophoran species are comprised of only one or two distinguishable nectophores and in these cases some quantitative estimates of the numbers of specimens present at various depths is possible.

In addition to these asexual, polygastric forms of each species there are the eudoxid, sexual stages, which carry the gonophores. These are quite often encountered in the plankton, but the attention which has been paid to them varies with the individual

species. The presence of any eudoxids of a species in the SOND collection is noted but where numbers are low they have generally been disregarded for the purpose of any quantitative study.

The vertical distributions of the predominant parts of the polygastric and eudoxid stages of the calycophoran species for the horizontal hauls of the N113 and IKMT day and night series are given in Tables 1–2, and 3–4 respectively. The station data for the minor elements comprising these stages are either given in the text or are listed in Appendix II. Also listed in this Appendix are the data for the specimens of the rarer species, etc., found in the oblique haul samples. For the commoner species, histograms have been drawn which show the percentage of the total population of that species present at the mean depth of each of the hauls. Usually the day and night distribution patterns have been directly compared but where only a few specimens were present, and where there was no apparent diurnal variation, the results for the day and night hauls have been combined to give a general picture for the vertical distribution of the species. These methods of data presentation have been briefly discussed by Foxton (1970a).

Family Prayidae

Sub-family Amphicaryoninae

The prayids are a diverse family with a multiplicity of forms, but generally characterized by the presence in the nectophores of a relatively large proportion of mesoglea. These animals are slow swimming and the mesoglea must aid in flotation. The amphicaryonines differ from the other two sub-families in that the larval nectophore is retained as the functional one, while the single definitive, heteromorphic nectophore is much reduced or vestigial. The commonest species, *Amphicaryon acaule*, has this latter nectophore almost completely enclosed by the former and so the animal is usually found intact. Even so, the occurrence of either of the nectophores will indicate the presence of the polygastric phase and should enable quantitative estimates of the depth distributions of these species to be made.

Amphicaryon acaule Chun, 1888

A total of 157 whole polygastric stages, plus 39 vestigial and 47 larval loose nectophores were isolated from the SOND collections. The majority of specimens occurred in the IKMT hauls and the depth distributions of these, by day and night, are compared in Fig. 1 A. The number of individuals present at each depth was calculated as the number of complete polygastrics plus the larger number of either the vestigial or larval loose nectophores. This number of individuals is tabulated in Tables 2 and 4 for the N113 and IKMT series of hauls respectively. A list of the actual numbers of vestigial and larval nectophores, or the intact individuals, for these horizontal series is given in Appendix II.

There is a great disparity between the numbers found during the day (93) and night (27) series. During the day, the peak distribution level was at 250 (57·0%), with 75·5% of the population occurring between 200 and 250 m. There was a marked diurnal migration so that at night 55·6% of the population was found at 70 m. It is probable that the majority of the population had in fact migrated to a level shallower than 70 m but, because of the insufficiency of sampling in these surface layers, it was not accounted for.

The species did not, however, appear right at the surface as no specimens were found in the neuston net samples. There appears, then, to be a diurnal migration of at least 200 m, which is considerable when the swimming power of these animals is considered. It is to be hoped that the diurnal migration of this species into the shallower waters will be gauged more accurately when some more recent 'Discovery' collections are analysed.
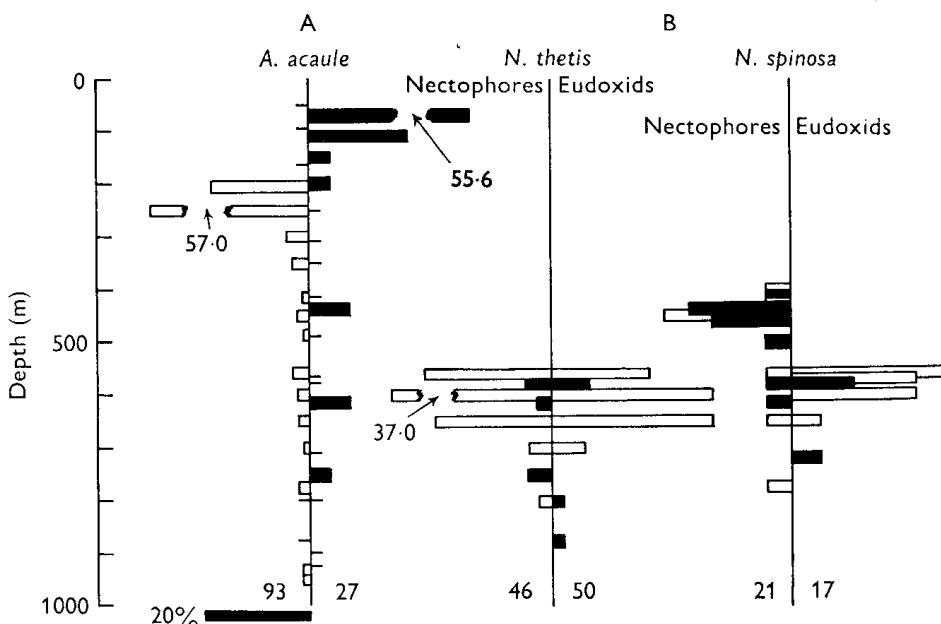

Fig. 1A. The depth distribution of the polygastric stage of *Amphicaryon acaule* (IKMT data) by day (outlined) and by night (blackened). The number beneath each histogram is the total number of specimens of the growth stage being considered, by day or by night, and the values plotted are the percentages of this total. B. The depth distribution of the nectophores and eudoxids of *Nectopyramis thetis* (IKMT data) and *N. spinosa* (IKMT + N113 data). The total number of specimens of each stage is given beneath the histogram and the values plotted are the percentage of this total. The individual day (outlined) and night (blackened) hauls are distinguished.

Although 78·4 % of the total number of animals were found in the top 250 m of water, individual specimens were found down to 950 m. As they were found in almost all the IKMT day hauls, their presence in the deeper hauls was considered to be due to contamination as the net passed through the shallower waters. Bigelow & Sears (1937) considered that *Amphicaryon acaule* had a wide vertical distribution which extended down to at least 450–500 m, and upwards to 40–50 m but not actually rising to the surface. However, the 'Thor' data were insufficient to show whether there was any level of maximum abundance. Moore (1949) found that there was a seasonal period of maximum abundance for this species in the vicinity of Bermuda, and that in general 80 m was its mean day level. This level is defined as that depth above which 50 % of those individuals occurring in the top 300 m are found in the daytime. He also noted a tendency for diurnal migrations with a day–night range of 77 m, and obtained similar results from the Florida Current region (Moore, 1953) where the mean day level was 92 m. Other individual records indicate the presence of *A. acaule* at depths anywhere between 600 m and the surface.

Amphicaryon acaule is a well-known species and has a wide geographical distribution in the warmer waters of the three Great Oceans and the Mediterranean, generally within the limits 40° N to 40° S. Fraser (1967) has, however, found it close to the surface at 60° 12′ N, 7° 40′ W, while Leloup (1933, 1955) has previously recorded it from the vicinity of the Canary Islands.

Amphicaryon ernesti Totton, 1954

One complete specimen of the polygastric stage was found in an IKMT horizontal haul (5798 (3)) at 250 m. There have been several reports of findings of this species since it was originally described twenty years ago, but it still remains a relatively rare siphonophore. Totton (1954) reported its presence from stations in the Atlantic, south of the Cape Verde Islands, from the Indian Ocean and the Red Sea. Alvarino (1971) has found the species in both the Atlantic and Pacific Oceans, while Patriti (1970) reported it from the Indian Ocean. This present record is thus the most northerly for the Atlantic Ocean. Nearly all the previous records have come from non-closing shallow nets which indicate that it is most often found in the top 150–250 m of water. This is in agreement with the present single record at 250 m.

Maresearsia praeclara Totton, 1954

A large larval nectophore of *Maresearsia praeclara* was found in each of the samples from two IKMT horizontal hauls at 415 m (5796 (3)) and 450 m (5793 (2)). The oblique part associated with the former haul also contained a complete polygastric specimen, while another oblique haul (5811 (2)) from 475–0 m contained the separated nectophores of a further specimen. This latter oblique haul transversed the depths of the horizontal hauls and so it is likely that at Fuerteventura this very rare species is localized in the 400–475 m depth range.

There are only five previous records for this species, four in the Atlantic and one from off Zanzibar in the Indian Ocean (Totton, 1954). Stepanyants (1967) described a new species, *Maresearsia sphaera*, from a single specimen caught in the Sea of Okhotsk (North-west Pacific) but her description and figures do not easily distinguish it from *M. praeclara*. Since so little is known about this genus I am inclined to think that the minor differences proposed by Stepanyants are insufficient to separate the species and that they are probably synonymous.

The previous depth distribution records for *Maresearsia praeclara* are contradictory and indicate that the species has been found at all depths between 1828 m and the surface. None of the depth data from the specimens caught in closing nets agrees with the present findings.

Sub-family Prayinae

The prayines are a small but diverse group of siphonophores comprising about ten species characterized by the shape of their somatocysts and the course of the radial canals in the nectosac. The polygastric stages of the two common genera, *Rosacea* and *Praya*, are comprised of two definitive nectophores, but these can be added to or replaced by several reserve nectophores. Thus although the differences between the two types of

nectophores are fairly obvious in the *Praya* species and should enable their distinction, is is more difficult in the case of the *Rosacea* species, particularly as they are often badly damaged and preserved. It is, therefore, possible to make some quantitative estimates of the numbers of individuals so long as it is recognized that the population may be over-estimated if there are reserve bells present.

Praya dubia (Quoy & Gaimard (1833), 1834)

This species was represented in the SOND collections mainly by the bracts of the eudoxid, sexual stage, and only a few nectophores were found. From a total of 21 hauls, 147 eudoxid bracts and 16 nectophores were isolated and some gonophores of either *Praya dubia* or *P. reticulata* were noted. The depth distributions of the nectophores and eudoxid bracts in the horizontal series of the two nets are given in Tables 2 and 4. The nectophores were generally in very bad condition. Since the number of eudoxids normally associated with a polygastric individual probably varies greatly it is impossible to say from how many animals they were derived. All the fragments, apart from one eudoxid bract, were found in the 450–750 m range, with a peak between 550 and 750 m.

Most of the earlier records for this species come from the Pacific Ocean (Bigelow, 1911*b*, 1931; Moser, 1925), but Fraser (1967) has found the species in the Hebrides and Faroes region off Scotland, and Totton (1965) quotes occurrences at several Atlantic 'Discovery' stations. Moore (1949) mentions that several nectophores of a *Praya* sp. were found off Bermuda, but gives no depth distribution data. There are thus very few records of this species and it would appear to be rare. However, more recent preliminary investigations of 'Discovery' material from the North-east Atlantic from between 11° and 60° N indicate that this is not the case.

The depth records given by Totton (1965), although mainly for non-closing nets, indicate that *Praya dubia* is usually found at depths less than 480 m, with a concentration in the 200–350 m range. This is slightly shallower than the present results but until one knows and understands more about the effects of latitude, time of day, season, etc., on the depth distribution of any siphonophore species, it is difficult to compare these results.

Praya reticulata (Bigelow, 1911)

Altogether, 12 nectophores and 40 eudoxid bracts of *P. reticulata* were recovered from 1 oblique haul (415–0 m 1n, 1 e.b.) and 3 horizontal hauls at widely differing depths (205, 600 and 900 m). The previous records for the species, as reviewed by Stepanyants (1967), are mostly from the Pacific Ocean, and there are only two records for the Atlantic Ocean for an area off the African Coast between the equator and 10° S (Totton, 1965). However, as with *Praya dubia*, more recent observations have shown that this species is certainly not uncommon in the Atlantic. Tho presence of *P. reticulata* at Fuerteventura considerably enlarges the known geographical distribution of the species, but the depth records merely indicate that it can be found over a wide depth range.

Rosacea spp.

It is not easy, with poorly preserved and damaged nectophores, to separate the two widely known species of *Rosacea*, *R. cymbiformis* (Chiaje, 1822) and *R. plicata* sensu

Bigelow, 1911. The third species, *R. villafrancae* Carré, 1969, is little known and so far restricted to a very small area of the Mediderranean. Totton (1954) states that 'I have found outside the Mediterranean – in the Atlantic, Indian and Antarctic Seas – many rosacean nectophores all of which, except a few of *Rosacea cymbiformis*, appear to belong to one species, *R. plicata*'. Indeed the majority of records of this genus are for *R. plicata*, although the synonomy has often been confused (see Alvarino, 1971). Leloup & Hentschel (1935), however, found *R. cymbiformis* at several localities in the Atlantic, and Leloup (1933, 1955) found it in the Bay of Biscay and Azores regions. Bigelow & Sears (1937) found *R. cymbiformis* to be more common than *R. plicata* in the Mediterranean.

The presence of eudoxid bracts of *Rosaceae cymbiformis* in the SOND collections establishes that this species is present in the Canary Island region, although they may have originated from Mediterranean water carried out into the Atlantic.

In the SOND material 188 nectophores were isolated together with 51 eudoxid bracts of *Rosacea cymbiformis* and four unidentifiable ones. The depth distributions of the nectophores are given in Tables 2 and 4, and the stations where the *R. cymbiformis* bracts were found are listed in Appendix II. The four unidentified eudoxids were all taken in IKMT oblique hauls and are not listed here. From the evidence of these bracts it would appear that *R. cymbiformis* is the dominant species in this region although the state of the nectophores was insufficient for any proper speciation of them. The depth distribution of the specimens was very confused, fragments being found at almost every depth from 85 to 900 m, but not in the shallowest hauls. There was no well-defined maximum. This also seems to apply to previous records where both species have been found at depths ranging from 2400 m to the surface. Bigelow & Sears (1937) considered that *R. cymbiformis* was generally found at depths greater than 100 m and preferred temperatures of less than 20 °C. Totton (1954) confirmed this for *R. plicata* in the Indian Ocean.

Desmophyes annectens Haeckel, 1888

This is a very rare species which has only been recorded twice this century. Seven nectophores of this species were isolated from an IKMT night haul (5806 (3)) at 200 m. They probably represent one specimen, for it is known that as well as the two definitive nectophores several reserve ones can be present. The species appears to have been noted originally by Blainville (1834) who called it *Praya diphyes* and it was under this name that Vogt (1854) gave a detailed description of it. Vogt recorded that it was not uncommon around Nice but it was not until recently that it was again noted in this vicinity. C. Carré (personal communication) has observed specimens captured in the Rade de Villefranche on several occasions.

Hardy & Gunther (1935) recorded this species from five stations in the South Georgia region which indicates, along with the few other records, that *Desmophyes annectens* is a widespread, eurythermal but very rare species and the present single record can serve at least to extend our knowledge of its geographical distribution.

Sub-family Nectopyramidinae

The Nectopyramidinae are described by Totton (1965) as 'a small group of four aberrant prayines, the nectophores of which instead of being smoothly rounded bear

ridges, angles and serrations'. Totton has concluded, because of their shape, the course of the somatocyst and the fact that the nectophores are usually taken singly, that the species have retained their larval nectophores as the functional ones. There are four species, all of the genus *Nectopyramis*, and all of which were found in the SOND collections.

Because of the rarity of these species, the depth distributions of the nectophores and eudoxids of each species found in the two horizontal series of hauls are given in Tables 2 and 4, and included in Appendix II is a list of the specimens found in the IKMT oblique hauls.

Nectopyramis diomedeae Bigelow, 1911

Four polygastric nectophores and four eudoxids were found in two horizontal hauls, at 660 and 720 m, and in three oblique hauls, from 800, 700 and 650 m to the surface. The oblique hauls thus approximately span the depths of the horizontal hauls, and indicate that the species is most likely to be found in the 650–750 m depth region.

Up to the time of Totton's (1965) synopsis there had only been definite records for sixteen polygastric and twenty-seven eudoxid stages of *Nectopyramis diomedeae*, and so the present records considerably increase our knowledge of the species. Fraser (1961, 1967) and Alvarino (1964, 1967) found specimens at six localities but do not state which stage was identified. Stepanyants (1967) records eudoxids from two stations in the Arctic Basin and Bering Sea, and also describes the polygastric stage which she may have found. Although the records are so few the geographical distribution is very wide. Bigelow (1911*b*, 1913, 1931), Alvarino (1964, 1967) and Stepanyants (1967) found specimens in the Pacific and Arctic regions; Totton (1954) found Indian Ocean specimens and some from the Antarctic regions of the Atlantic Ocean. Other Atlantic specimens were found by Totton (1936) off Bermuda, by Fraser (1961, 1967) off Ireland and the Faroe Isles, and by Totton (1965) in the Bay of Biscay. The distribution is now extended to include the Canary Islands region.

Totton (1954) concluded from the previous records that the depth distribution of *Nectopyramis diomedeae* was probably in the range 650–1600+ m. Alvarino (1967) found her specimens between 410 and 775 m, and the 650–750 m range at Fuerteventura is very similar. I have found the species in samples from greater depths and in this context I would like to include a record for a very large polygastric specimen caught at 'Discovery' St. 7803 (7) (17° 47′ N, 25° 11′ W; 20 February 1972) from a depth of 2000–1500 m. The specimen was diamond-shaped and measured 5·0 cm across and 6·5 cm from base to apex. This is considerably larger than any previous specimen which Totton (1965) quotes as having a maximum length of 4·5 cm.

Nectopyramis natans (Bigelow, 1911)

Three polygastric stages and six eudoxids, four of which still had the asexual special nectophore attached, were found in seven samples. Only three of the samples came from horizontal hauls, at 780, 900 and 950 m, while the rest came from oblique hauls from 500, 650, 675, and 800 m to the surface.

Like *Nectopyramis diomedeae* the records for this rare species are few, but spread over

a wide geographical area. There have only been three previous records for the polygastric stage, two from the Atlantic (Totton, 1954) and one from the North-west Pacific (Stepanyants, 1967). Alvarino (1964, 1967) in recording this species again did not state which stage was caught. The two Atlantic specimens were taken at depths of 2480–2580 m and 750–0 m, while the SOND specimens were caught at 950, 900 and 500–0 m. The polygastric stage thus appears to be generally bathypelagic, but with only six specimens it is difficult to draw any firm conclusions.

In the case of the eudoxid stage, there are ten previous, definite records, of which seven are from the Pacific, two in the Indian and only one in the Atlantic Ocean. There are only two depth records for the eudoxids at 800–1000 m and 1650–950 m (Totton, 1954), which is slightly deeper than the SOND specimens, but again the information is very inadequate. The occurrence at Fuerteventura of both stages of *Nectopyramis natans* has thus extended their ranges into the northern part of the Atlantic Ocean up to 28° N.

Nectopyramis spinosa Sears, 1952

Nectopyramis spinosa is the only one of the four nectopyramidines which develops a second definitive nectophore. This latter one, unlike the amphicaryonines, appears to have a functional nectosac, while the larval nectophore has a vestigial one. The nectophores have never been found attached, apart from the observations by Totton (1965) of the presence of a very early growth stage of the definitive nectophore within the hydroecium of the larval one. It would thus appear that the larval one is caducous, but whether it remains alive or not after the detachment of the definitive nectophore is not certain.

Seventeen of the horizontal hauls and three of the oblique ones contained a total of five definitive functional nectophores, eighteen larval ones and twenty-two eudoxids. Two of the functional nectophores and five of the eudoxids were found in the oblique hauls, but the depth distributions of the others are shown in Fig. 1B. There was little difference between the day and night distributions of either stage and so the results are shown as a comparison of the overall depth distributions of the nectophores and eudoxids found in both series of hauls. The functional nectophores were found at 400 and 650 m in day hauls and at 500 m in one night haul. Approximately equal numbers of the larval nectophores were found during the day and night (8:10), but considerably more eudoxid stages were present in the day hauls (14:3). As the day/night vertical distributions were almost identical it is difficult to explain this latter anomaly by variations in the timing of the haul (cf. *Chelophyes appendiculata*). The interesting feature of the results, however, is that the peak of the depth distribution for the larval nectophores (66·7%) is between 435 and 460 m, while that for the eudoxids (88·2%) is in the 560–600 m range. Because of the insufficiency of numbers it is impossible to assess the significance of this observation. However, it remains an interesting feature, especially as the nectophores and eudoxids of *Nectopyramis thetis* are found at the same depth.

There have only been records for five definitive and nine larval nectophores in the literature, and the eudoxid phase has never previously been found separated from the polygastric individual. However, like the other species of *Nectopyramis*, the records for *N. spinosa* are from various parts of the three Great Oceans, varying from 60° N in the

Atlantic to 58° S in the Indian Ocean. The specimens from the 'DANA' cruise (Sears, 1952) were caught in the nets fished with 1000–3000 m of wire out, while Totton (1954) found specimens at depths between 250 and 2400 m. However, most of these latter hauls covered the range of depth distribution found at Fuerteventura. The SOND collections have thus not only considerably increased the numbers of known specimens of each stage of this rare nectopyramidine, and extended its geographical distribution to the Canary Islands, but have also contributed information on its depth distribution.

Nectopyramis thetis Bigelow, 1911

Nectopyramis thetis is the best known of the four Nectopyramis species and in the SOND collections 77 nectophores of the polygastric stage, and 118 eudoxids, some with the special nectophore still attached, were isolated. There was very little difference between the day and night distributions of either stage, and so the depth distributions of the nectophores and eudoxids are directly compared in Fig. 1B, for the specimens derived from the IKMT horizontal hauls. There is a considerable discrepancy between the numbers of nectophores (41:5) and eudoxids (43:7) found in the day and night hauls. This is difficult to explain unless it is connected with some slight diurnal variation which, because of the timing of the hauls, resulted in the species being missed at a particular depth. This is probably unlikely, but will be discussed in more detail with regard to some other siphonophore species.

The peak depth distributions of the nectophores and eudoxids of Nectopyramis thetis are almost identical, with 89·2% of the former and 90·0% of the latter being found between 560 and 650 m. The specimens caught in the N113H hauls are also concentrated in the 570–660 m range, and have an overall depth range of 570 to 800 m.

Although the species has been reported by several authors the number of specimens actually caught is very small and the present collection probably quadruples the total. Most of the records are from the Atlantic Ocean with a few from the Indian (Totton, 1954) and Pacific Oceans (Alvarino, 1967; Stepanyants, 1967). Leloup (1932, 1933, 1936, 1955) has found this species in the Azores and Canary Islands regions and Bigelow (1911a), Bigelow & Sears (1937) and Patriti (1965) have found it in the Bay of Biscay. Nectopyramis thetis is thus quite well known in the North-east Atlantic as far north as 63° N (Fraser, 1961). Most of the previous specimens were caught in non-closing nets, but Totton (1954) quotes figures for nine closing nets which range from depths of 2800–2300 m to 100–250 m. However, most of the depths at least cover part of the depth range for N. thetis found at Fuerteventura, the latter being the most detailed and comprehensive so far.

Family Hippopodiidae

The hippopodiids, a small family of calycophoran siphonophores, comprises only five closely related species which are conventionally split into two genera although they are probably congeneric. The polygastric individuals of each species are made up of several definitive nectophores, anything up to about sixteen in Vogtia spinosa. Except in the case of Hippopodius hippopus, it is not known whether there is a precise number of nectophores present in the mature polygastric of each species, or whether this number is

variable. In the four *Vogtia* species the nectophores are loosely attached to the stem and so are rarely found as complete animals.

In the case of *Hippopodius hippopus* the nectophores fit more closely together so that complete or semi-complete specimens are often caught. One is also able to refer to the excellent study of the post-larval development of this species made by D. Carré (1968). She has found that the development of new nectophores continues in the post-larva until there are eight, and then, as a new one is produced, the oldest becomes caducous, and so this number is maintained. I have confirmed this with some specimens caught during a recent 'Discovery' cruise, but have found that sometimes the oldest nectophore is retained until the newest is quite well developed. Moore (1949) arrived at a figure of thirteen nectophores per 'colony', which must have resulted in a considerable under-estimation of the number of individuals present. The fact that the oldest nectophore is caducous raises another problem in that it is not known how long it remains alive and buoyant after dropping off, and thus how often it is likely to be found in the samples. If they do become included in any quantitative estimate then they would lead to an over-estimation of the population.

Since there appears to be a definite number of nectophores per individual, at least for *Hippopodius hippopus*, and preliminary observations indicate the same for the *Vogtia* species, and since the fishing conditions were theoretically identical in almost all cases, it was considered that a direct comparison of the numbers of nectophores found at each depth, although not quantitative in respect of the number of individuals, should approxi-mate to a true representation of their depth distribution. Thus the depth distributions of the nectophores found in the samples from the horizontal series of hauls of the N113 and IKMT nets are given in Tables 2 and 4 respectively.

Hippopodius hippopus (Forskål, 1776)

The day and night depth distributions of the nectophores of *Hippopodius hippopus* found in the IKMT and N113 horizontal hauls are compared in Fig. 2. A comparison of the total numbers of nectophore found in the two-day series shows that there were about ten times as many in the IKMT as in the N113 hauls. Whether this is a true com-parison of the relative filtering efficiencies of the two nets is not known.

While the day and night totals for N113 captures agree fairly closely, there is a wide discrepancy between those for the IKMT series. In addition the mean day levels indicated by the results for each series are vastly different, being *ca.* 85 m for the N113 net and 240–250 m for the IKMT one. It is possible that the term 'mean day level' is not meaningful and that these differences in daytime depth distribution could, at least in part, be caused by the timing of the hauls (see Angel (1969) and Appendix III). In my interpretation many of the siphonophores which undertake diurnal migrations move only slowly so that a vertical migration of 100 or 200 m would take a considerable time. If the vertical migration is a slow process then the so-called 'mean day level' will be constantly changing during the day. It is possible that as soon as a siphonophore species reaches its maximum daytime depth it immediately reverses its migration and begins to ascend in such a way that it never actually remains at one depth for any length of time.

In the case of *Hippopodius hippopus* it appears that the maximum depth to which the

animal migrates during the day is in the 250–300 m range. The three IKMT hauls at 205, 250 and 300 m were all carried out at approximately the same time in mid-afternoon and the peak of the population occurred at 250 m with some animals at 300 m. If it is supposed that the bulk of the population has already begun to migrate upwards and is passing through the 250 m band at that time then the specimens caught at 300 m were probably taken early on in the haul right at the beginning of the migration.
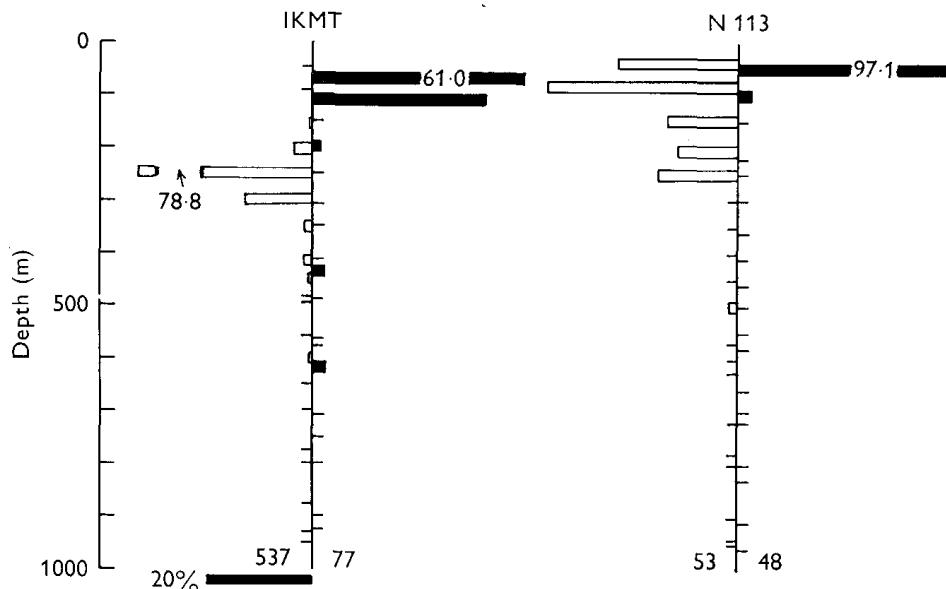
Fig. 2. The depth distribution of nectophores of *Hippopodius hippopus* as shown by the IKMT and N113 net captures, plotted as in Fig. 1 A.

In the case of the N113 day hauls, both the 250 and 300 m hauls were carried out much earlier in the day, when possibly the population was still slowly moving downwards but had not yet reached that depth. This is supported by the fact that the population peak in these hauls is found at 85 m. This haul was carried out only 1–2 h after sunrise and clearly the population is only just beginning to move down through this depth. However the proportionally large number of nectophores found in the shallowest day haul at 40 m is difficult to explain on this basis as the haul was carried out in the late afternoon. However, although the percentage is high at this depth, it consists of only twelve nectophores which probably represent two individuals, and the similarly timed IKMT day haul at 50 m contained no nectophores. One further point is that, because of the timing of the deeper hauls, the bulk of the population of *Hippopodius hippopus* was probably not fished and so the total population in the N113 series of nets may have been underestimated. This would then make the shallowest result much less significant. As Roe (1972a) has pointed out, the shallowest N113 hauls were carried out without the presence of the catch-dividing bucket (CDB) which may have resulted in the net being more efficient at capturing small animals (because the mesh size after the CDB was in fact larger than the net itself). Whether this would have any effect on the capture of this particular species is not known.

In the case of the N113 night series of hauls, the population of *Hippopodius hippopus* was found almost entirely in the shallowest haul at 50 m, although it should again be noted that this was the haul where the catch-dividing bucket was not used. Similarly, almost all of the IKMT night population was found in the 70 and 110 m hauls and it is possible that, at the time of these hauls, the bulk of the population was at a depth shallower than 70 m. If so, this would help to explain the large discrepancy in the numbers of nectophores found in the IKMT day and night hauls. In the case of the N113 hauls it is suggested that the day population has been underestimated, because of the timing of the hauls, and this probably also applies to the night population. However, the large number of nectophores found in the shallowest haul at 50 m is possibly representative as it was carried out very late in the night, only 2 h before the day haul at 85 m, and both of these hauls indicate the gradual descent of the population through the water column.

Thus, the results for the depth distribution of *Hippopodius hippopus* are complex and misleading. It is concluded that during the day the bulk of the population gradually migrates downwards to about 300 m before ascending again at night into the waters shallower than *ca.* 50 m, although it did not appear in the neuston net samples. Like *Amphicaryon acaule* this sort of range of diurnal migration is large for such poorly swimming animals.

Hippopodius hippopus is widely known from the three Great Oceans and the Mediterranean Sea. The available information on its depth distribution is, however, very inconclusive. Bigelow (1911*a*) found it to be present between 91 and 456 m in the Bay of Biscay, while Bigelow & Sears (1937) found its maximum abundance in the Mediterranean to be in the upper 200 m. Leloup & Hentschel (1935) found it at all depths down to 800 m in the South Atlantic Ocean. The most detailed information on the depth distribution of *H. hippopus* is that given by Moore (1949) who found a mean day level at 140 m, with a spread of 160 m. In the Florida Current (Moore, 1953) he found a mean day level at 110 m and a day–night vertical migration with a range of 50 m.

Vogtia glabra Bigelow, 1918

The day and night depth distributions of the nectophores of *Vogtia glabra* found in both the IKMT and N113 horizontal hauls are shown in Fig. 3. The N113 results indicate a wide distribution of the species in the water column from 40 to 950 m, although there were only isolated finds below 630 m, with no particular population maxima. The numbers of nectophores found by day and by night also match up moderately well. Similarly in the IKMT hauls the species was found in almost all the hauls from 50 to 950 m but there appeared to be a daytime maximum at 560–600 m and a vertical migration at night to 415–435 m. There is, however, a large discrepancy between the numbers of nectophores found by day and night, and it is postulated that, assuming this diurnal migration to be real, the timing of the night hauls resulted in the bulk of the population being missed.

Vogtia glabra is one of the commonest species at Fuerteventura and was found in 62 out of the 76 horizontal hauls. The total number of nectophores found was about four times that for *Hippopodius hippopus*, but it is not clear what the average number of nectophores per individual is in the case of *V. glabra*. The maximum number per individual

which I have observed is ten but since the animal is fragile this is probably an under-estimate.

Vogtia glabra is quite well documented in the literature especially in the Atlantic Ocean, and Leloup (1933, 1936, 1955) has found it in the region of the Canary Islands. Bigelow & Sears (1937) considered the species to be bathypelagic in the Mediterranean, occurring at depths below 400 m, but never common, while Totton (1954) quotes depth figures from 1000 m to close to the surface. The present results also indicate a wide distribution but with the majority of the population to be found in the 400–600 m depth range.
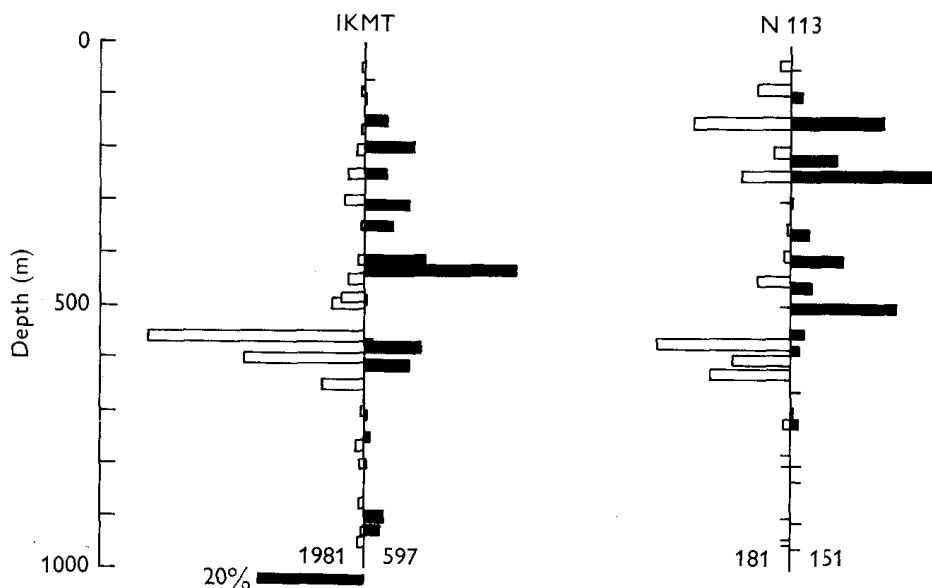
Fig. 3. The depth distribution of nectophores of *Vogtia glabra* as shown by the IKMT and N113 net captures, plotted as in Fig. 1A.

Vogtia spinosa Kefferstein & Ehlers, 1861

The depth distribution of the nectophores found in the IKMT horizontal hauls is shown in Fig. 4. Although nectophores were found at virtually all the depths from 95 to 950 m, there were fairly clear population maxima. By day 63·7 % of the population was found between 415 and 450 m, and by night 63·4 % was found in a virtually identical depth range (415–435 m). There is, however, a twofold discrepancy in the numbers of nectophores between the day and night hauls. If there is no diurnal migration then it is difficult to postulate that the population was not sampled properly and so this difference remains unexplained.

Moser (1925) and Leloup (1933) have both taken *Vogtia spinosa* in the vicinity of the Canary Islands, and it was quite common in the present collections. Information on the depth distribution is sparse, but Bigelow and Sears (1937) considered it to be bathypelagic, occurring at depths greater than 300–400 m. Bigelow (1911a) found it between 273 and 455 m in the Bay of Biscay and this agrees with the present results which indicate a fairly narrow band of maximum population between 350 and 450 m.
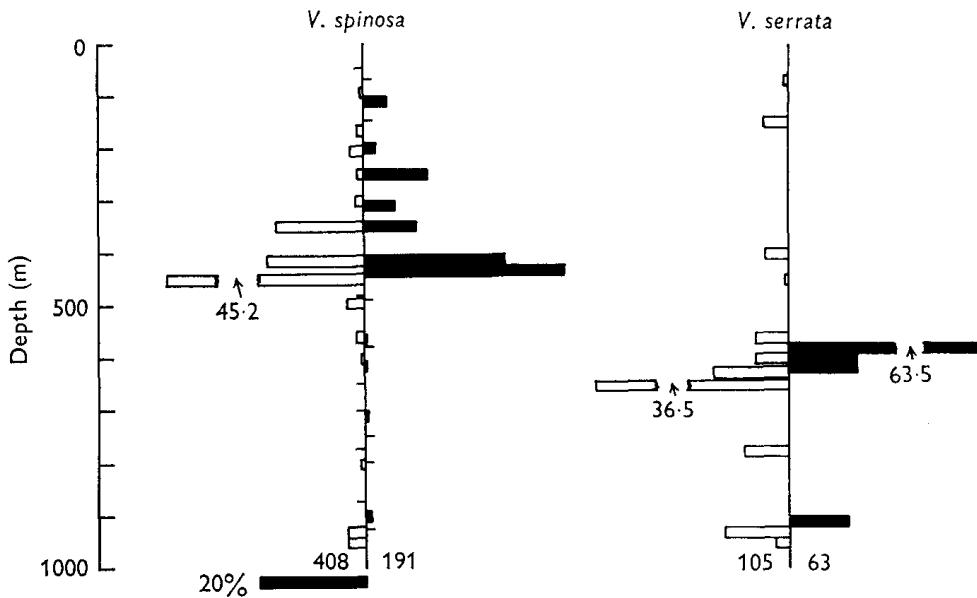
Fig. 4. The depth distributions of nectophores of *Vogtia spinosa* (IKMT data)
and *V. serrata* (IKMT + N113 data), plotted as in Fig. 1 A.

Vogtia serrata (Moser, 1925)

A total of 359 nectophores of this species were isolated, of which 167 were found in horizontal hauls. The numbers found in both the IKMT and N113 net have been combined without any correction for differences in the filtering characteristics of the two nets, and the resulting depth distributions by day and night are shown in Fig. 4. The species is clearly bathypelagic with the majority of the population being found between 560 and 650 m. The results indicate a slight diurnal migration but this may simply be due to the lack of hauls in the 615–660 m range at night.

Moser (1925) and Leloup (1933) have both found *Vogtia serrata* in the region of the Canary Islands and the former author concluded that it was a bathypelagic species which occasionally appeared at the surface. Bigelow & Sears (1937) found the species at two stations in the Bays of Cadiz and Biscay at 1066 and 2900 m, while Fraser (1961, 1967) found it at depths between 800 m and the surface at stations up to 59° N. Although the present data seem to considerably enhance our knowledge on the depth distribution of *V. serrata* more information is still required.

Vogtia pentacantha Köllicker, 1853

At Fuerteventura 115 nectophores of *Vogtia pentacantha* were isolated from twelve hauls, eight of which were horizontal ones. However, much of the material was in a bad condition and so some of the identifications may be open to doubt. The material was found in hauls ranging from 150 to 660 m, with the majority in the deeper hauls. Bigelow & Sears (1937) considered the species to be an uncommon midwater form which had a wide depth distribution. Most of their records for it were in hauls between 400 and 1000 m, with a peak at 666–933 m, but with a second population close to the surface.

Hippopodiidae – General Discussion

Since the species within this family are so closely related, and probably congeneric, it is of interest to note the stratification which exists in their depth distributions. *Hippopodius hippopus* is mainly found by day in the 250 m depth range but undertakes a substantial migration into the subsurface layers at night. It is the shallowest living of the five species and *Vogtia spinosa* has a deeper distribution, occurring between 350 and 450 m by day but with some indication of a migration at night up to about 250 m and thus to occupy the daytime peak level of *H. hippopus*. Below these two species, *Vogtia glabra* is found at a depth of between 560 and 600 m, as indicated by the IKMT results, with the possibility of an upward migration at night with a range of about 100 m. Finally *V. serrata* is the deepest living species, being found at a depth of 650 m by day and with some indications of a slight upward migration by night. However, in this case the differences in the mean depths of the hauls in this depth range, by day and by night, may account for this apparent migration. The information for *V. pentacantha* is too scant to include although it appears mainly to occur at a depth of 600–625 m, between *V. glabra* and *V. serrata*.

Family Diphyidae

In general, the polygastric diphyid individual consists of two similar but distinct definitive nectophores. These are usually referred to as the anterior (an) and posterior (pn) nectophore. Sometimes the posterior one is not developed, e.g. *Muggiaea* spp., and sometimes there can be more than one present, e.g. *Sulculeolaria* spp. The larval nectophore in the diphyid family appears to be caducous after budding off the anterior nectophore, and only one of these latter nectophores is usually produced, although certain species retain the potential to develop another if the first is lost. There is often some delay in the budding of the posterior nectophore which results, in *Chelophyes appendiculata* for example, in a preponderance of the anterior ones. However, it should be possible with most of the species of this family to make quantitative estimates of populations by considering the numbers of anterior nectophores present.

Sub-family Sulculeolariinae

Only the depth distributions of the anterior nectophores are given in Tables 1 and 3, and the occurrences of the posterior nectophores are noted in the text.

Sulculeolaria quadrivalvis Blainville, 1834

Fourteen anterior and seven posterior nectophores were isolated from eleven hauls of which five were horizontal ones; at 40 m (5827 (5); 4 an, 2 pn), 50 m (5801 (3); 1 an), 85 m (5828 (1); 3 an), 200 m (5806 (3); 1 an) and 415 m (5796 (3); 1 an). The majority of specimens were thus found in the top 85 m but the data are insufficient to indicate any possible diurnal variations in numbers.

Sulculeolaria quadrivalvis is widely known from the three Great Oceans and the Mediterranean, despite the confusing synonomy, and Leloup (1932, 1933) has found it in the vicinity of the Canary Islands. Bigelow & Sears (1937) found 70 % of their specimens of the species in nets towed at 43 m or shallower, and Totton (1954) reports it from the

surface waters in the Gulf of Aden. Alvarino (1971) also reports its presence in several hauls from various localities at depths down to 156 m. It would appear that *S. quadri-valvis* is generally a near-surface form and is probably commoner at Fuerteventura than is indicated by the SOND collections, due to the insufficiency of sampling in the shallow depths.

Sulculeolaria biloba (Sars, 1846)

Eleven hauls were found to contain a total of twelve anterior and ten posterior necto-phores of this species. Seven of the hauls were horizontal ones, at depths of 100 m (5819 (3); 1 an), 150 m (5814 (2); 1 an, 1 pn), 160 m (5816 (7); 1 an), 205 m (5816 (6); 1 an, 1 pn), 415 m (5806 (1); 1 an), 580 m (5817 (1); 1 an) and 615 m (5810 (2); 1 an). Two of the shallower obliques, 50–0 m (5817 (2); 1 an) and 90–0 m (5814 (2); 2 an, 3 pn), contribute to an indication that, in general, the species is a shallow-living form, confined in the main to the top 200 m. The isolated occurrences of the species below this depth may be due to contamination or to dead, sinking specimens.

Sulculeolaria biloba is probably the most widely known and most confused species of this genus. Leloup (1955) described it as a mesopelagic form but the previous depth distribution data are very limited. Leloup & Hentschel (1935) found it in the upper 50 m of water, while Alvarino (1971) quotes several depths from the surface to 200 m. The present data from the SOND collections are too sparse to add much to our present know-ledge of the species.

Sulculeolaria monoica (Chun, 1888)

This is another well-known species of *Sulculeolaria*, although only five anterior and five posterior nectophores were found in five hauls from the SOND collections. The single horizontal haul which contained specimens was at 200 m (5806 (3); 2 an, 2 pn) and all of the four oblique hauls (5795 (2); 1 an, 1 pn; 5811 (2), 1 pn; 5811 (1), 1 pn; 5809 (3), 2 an) passed through this depth. Bigelow (1931) described *Sulculeolaria monoica* as epipelagic and Alvarino (1971) quotes figures for its depth distribution of between 200 m and the surface with which the present records are approximately in agreement.

Sulculeolaria turgida (Gegenbauer, 1843)

This species was found only in two hauls, one a N113 horizontal haul at 85 m, which contained three anterior and three posterior nectophores, and the other an oblique IKMT haul (5801 (1); 800–0 m) which yielded a single anterior nectophore.

There has been a great deal of confusion in the past over the identification of this species but Totton (1954) has reviewed this adequately. He also quotes numerous records for this species from both the Atlantic and Indian Oceans. However, almost all of these hauls were made with open nets to the surface from depths ranging from 5 to 1400 m. There was one closing net sample at a depth range of 500–250 m. Bigelow & Sears (1937) estimated that 83 % of their catches of *Galetta australis* (= *S. turgida*) were from depths of 43 m or less and the present record at 85 m would seem to agree with this. It is concluded that *S. turgida* is an epipelagic species.

Sulculeolaria chuni (Lens & van Riemsdijk, 1908)

Three anterior and one posterior nectophores were found in two horizontal N113 hauls at 40 and 50 m. Although there have been only a few previous records for the species, they indicate that it is cosmopolitan. Alvarino (1971) found specimens at various depths from the surface to 200 m, while Totton (1954) found it at the surface in the Gulf of Aden. The species thus appears to be a near-surface form.

Although the numbers of specimens of each of the five species of *Sulculeolaria* found at Fuerteventura are all very low, it appears in general that the species are all epipelagic forms. Because the sampling procedure used during the SOND cruise did not adequately sample the near-surface layers it is very difficult to obtain a true picture of their depth distribution patterns.

Sub-family Diphyinae

The polygastric stages of this sub-family are generally characterized by the presence of only two nectophores, an anterior and a posterior one, although the latter one is frequently reduced or suppressed altogether.

Diphyes dispar Chamisso & Eysenhardt, 1821

Although a total of 193 anterior and 55 posterior nectophores of *Diphyes dispar* were found in 47 samples, only fourteen of the hauls were horizontal ones and these contained 36 anterior and 8 posterior nectophores. The posterior nectophores were found in two hauls at 50 m (5801 (3); 6 pn) and 200 m (5806 (3); 2 pn). Over half of the total specimens were found in hauls at 40 or 50 m and a further quarter were in hauls down to 200 m. The remainder were found at various depths down to 780 m. The data are inadequate to show any diurnal depth variations.

Diphyes dispar is a well-documented species and has a widespread distribution in the warmer waters of the three Great Oceans and in the Mediterranean. Moore (1949) considered it to be one of the less common diphyids in the Bermuda region restricted to the top 50 m of water, and with a mean day level at 10 m. In the Florida Current (Moore, 1953) he found it to have a mean day level of 40–59 m and a spread of 76–104 m. Leloup & Hentschel (1935), however, found specimens in the Central Atlantic Ocean to have a depth range of 0–500 m. Stepanyants (1967) concluded that *D. dispar* could be found at virtually any depth between 40 and 3000 m, but Totton (1954) has found it at the surface and it is frequently caught in 'Discovery' surface nets. In general it appears that the species is epipelagic with occasional occurrences at greater depths. The presence of the eudoxid phase was noted in several hauls but the numbers were insignificant.

Diphyes bojani (Eschscholtz, 1829)

Only a single anterior nectophore of this species was found in a N113 haul at 800 m (5823 (2)). The scarcity of the species at Fuerteventura is surprising as it is a cosmopolitan and common species. Moore (1949) found it to be common off Bermuda with a mean day level of 40 m, spread 25 m. In the Florida Current (Moore, 1953) its day level was between 29 and 72 m. Leloup & Hentschel (1935) found it at various depths

down to 1000 m, but the majority of specimens were epipelagic, living close to the surface. It is probable that the lack of hauls in the surface layers during the SOND cruise would explain the absence of this species from the collections. However, it did not appear in any of the neuston net samples.

Lensia multicristata (Moser, 1925)

A total of 421 anterior nectophores of the species were found in 35 of the 38 N113 horizontal hauls, and their day/night depth distribution is shown in Fig. 5. Eight of the IKMT horizontal hauls also contained nectophores. The results of the N113H series show there to be a considerable difference between the numbers of nectophores found during the day and during the night. Although the species was present in the shallowest hauls, the major part of the population was at greater depths and so it is unlikely that the difference in numbers is due to a migration at night into the unsampled surface layers. It is possible that the timing of the hauls was such that the main population was missed in the night hauls. However, the species appears to have a wide depth distribution occurring from 40 to 960 m but with the possibility of a peak during the day at about 300 m and with 63·6% of the population being found between 250 and 450 m. At night the population appeared to be much more widespread with no particular population peak.

Lensia multicristata is a well-documented species, especially from the Atlantic Ocean, and Margulis (1971), who has recently reviewed the distribution in the Atlantic of almost all of the *Lensia* species, records that it has been found at localities from 54° N to 42° S. Bigelow & Sears (1937) found only a few specimens from the Mediterranean at depths shallower than 43 m, but from 200 to 400 m the population increased to a maximum. Below this depth, down to 800 m, specimens were occasionally found. Similarly Totton (1954) only rarely found specimens shallower than 200 m, but Margulis (1971) reviews all the previous records and suggests a depth distribution over a wide range from 40 to 1645 m. The present results clearly fit in with these previous ones as the population was mainly found between 250 and 450 m, during the day at least, but had a very wide overall depth distribution.

Lensia achilles Totton, 1941

Three hundred and sixty-five anterior nectophores of *Lensia achilles* were isolated from the SOND collections and 346 of these were found in the N113 horizontal hauls. The day/night depth distribution of the nectophores from these latter hauls is shown in Fig. 5, after correction of the data for the short daytime haul at 600 m (see Roe (1972a) for discussion on this point). Like *L. multicristata*, there was a large discrepancy between the total numbers of nectophores found in the two series of hauls. During the day the peak level of distribution was at 570 m (39·9%) with 68·6% of the population being found in the 570–625 m range. At night the population appeared to be much more diffuse, but with some indication of a small vertical migration to 500 m (35·8%). The fact that there were no hauls at night between 580 and 660 m may help in accounting for the discrepancy in numbers of nectophores found, but it is interesting to note that the species was completely absent from the 550 m night haul. There appeared to be a fairly sharp upper limit in the depth distribution of the species at the level of the population peak, with

small numbers of nectophores being found in most of the deeper hauls down to the deepest depth sampled. Some of these latter occurrences may have been due to sample contamination or to dead specimens. Three damaged specimens of *L. ?achilles* were, however, found in one of the shallowest hauls at 50 m.
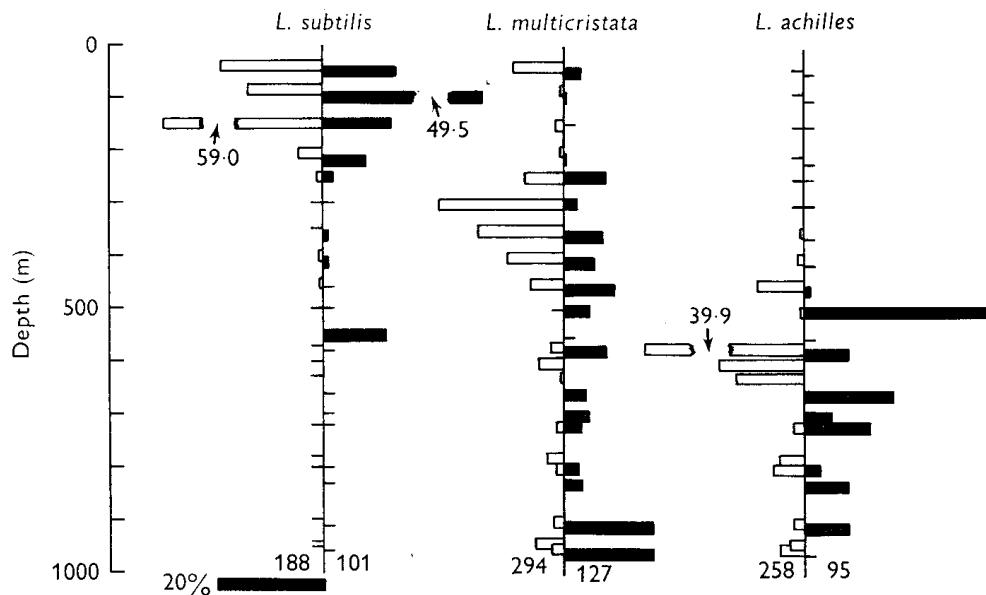
Fig. 5. The depth distributions of the anterior nectophores of *Lensia subtilis*, *L. multicristata* and *L. achilles* as shown by the N113 net captures, plotted as in Fig. 1 A.

There is not a great deal of information available on this species, although it has been found from 54° N (Fraser, 1961) to 34° S (Totton, 1941) in the Atlantic Ocean. Totton (1941) found it at depths from 900–1000 to 2000–2500 m, but Margulis (1971) quotes depth ranges of 0–62 m at night and 548–624 m during the day in equatorial Atlantic regions, and of 653–743 and 1643–1976 m at 41° N, 13° W. It would appear that the results for the depth distribution of the specimens of *Lensia achilles* caught during the SOND cruise, indicate a much narrower band of distribution than the previous results, with the majority of the population being found between 500 and 660 m and with occasional specimens below these depths.

Lensia subtilis (Chun, 1886)

Anterior nectophores of this species were found in 20 samples from the SOND collections, of which fifteen were derived from N113 horizontal hauls. The day and night depth distribution patterns of the nectophores from these latter samples is shown in Fig. 5. The peak day level is at 150 m (59·0 % of the population) and very few specimens were found below this depth. At night 49·5 % of the population was found at 100 m, but there was quite a large difference in the number of nectophores found in the day and night series, which might indicate that *Lensia subtilis* migrates into the surface layers at night. One of the night neuston net samples (St. 5802 (12)) was found to contain a necto-phore of this species. The haul at 50 m was carried out at a time very late in the night

(05.07–06.07 h) and one might have expected the population to have migrated down through this level by then.

Margulis (1971) reviews the distribution of *Lensia subtilis* in the Atlantic as widespread from 50° N to 37° S. Chun (1888) found the species in the Canary Islands region but Leloup & Hentschel (1935) only found it further south. These latter authors suggested that 0–50 m was the main depth range for the species, although it could be found down to 800 m. Moore (1949, 1953) found mean day levels at 140 and 35 m for Bermuda and the Florida Current respectively, with 30 and 150 m spreads. He found no evidence for any diurnal migrations however. Patriti (1964) found large numbers of the species in the top 25 m of the Gulf of Marseille, and it is common in the surface waters at Villefranche-sur-Mer. Thus the disparity in the numbers of nectophores of *L. subtilis* found in the day and night series of SOND collections is probably explicable by a vertical migration into the unsampled surface layers at night. The true magnitude of this migration cannot be gauged but it is certainly more pronounced at Fuerteventura than on the other side of the Atlantic (Moore, 1949, 1953).

Lensia meteori (Leloup, 1934)

Seventy-nine anterior nectophores of *Lensia meteori* were isolated from fifteen N113 horizontal hauls, and their depth distribution is shown in Fig. 7. Because of the small numbers of nectophores of this and the succeeding *Lensia* species which were found in the SOND collections, the day and night numbers have been combined and the depth distributions of the totals are shown. A distinction has been made in the histograms to show whether the percentages at each depth were derived from specimens taken by day or by night. *Lensia meteori* is found over a wide range depth from 100 to 830 m, but the results seem to indicate that there are two or three populations in existence. There is a shallow population with a peak at 150 m, from which may be subdivided a slightly deeper group found between 250 and 400 m. Finally there is a deep population existing between 580 and 830 m. None of these populations appear to show any indication of diurnal migration.

Lensia meteori is well known from the Atlantic Ocean and Mediterranean, and has occasionally been found elsewhere. Leloup & Hentschel (1935) found it at several depths down to 1000 m and Totton (1954) quotes open and closing net depths over a wide range. Margulis (1971) gives a depth distribution from the surface to 700 m. The present results similarly indicate a wide depth range for the species but give no indication of any diurnal migrations.

Lensia cossack Totton, 1941

Seventy-three nectophores of *Lensia cossack* were found, of which 65 were in the N113 horizontal hauls. The depth distribution of the latter is shown in Fig. 6. 73·8 % of the population occurred in the 40–50 m range and, since these were the shallowest day and night hauls, one can only infer a diurnal migration by the fact that fewer nectophores were found by night than by day. It should be remembered that the two shallow hauls were carried out with the fine mesh net, and so it is possible that the population between 85 and 100 m has been underestimated. However, the ten specimens from below these

depths are probably due to some form of contamination of the samples, or at least can be considered to be unusual. *Lensia cossack* appears to be a species which lives very close to the surface although none of the neuston net samples contained any specimens.

The records in the literature for this species are sparse, although Totton (1941) quotes several localities from the Atlantic, Pacific and Indian Oceans. Moore (1949, 1953) found it to occur sporadically in small numbers, and found a mean day level at 35 m, spread 43 m, in the Florida Current. Margulis (1971) reviews the Atlantic distribution as from 60° N to 42° S and records the species from the Canaries–Azores region. He concludes that it is associated with the surface layers of water, but occurs down to 450 m (Fraser, 1961) in the North-eastern Atlantic and to 700 m (Totton, 1941) in tropical regions. At Fuerteventura a single nectophore was found at 950 m but the major part of the population was found close to the surface.

Lensia grimaldi Leloup, 1933

Sixty-four anterior nectophores were found in the SOND collections, all but two of which were in the N113 horizontal series of hauls. Their depth distribution is shown in Fig. 7. 90·3% (56 an) of the population was found between 400 and 410 m, so that there was no indication of a diurnal migration but a considerable disparity in the day and night numbers. The remaining six specimens were all found at greater depths and could well be due to contamination or dead specimens. Thus a very narrow band of distribution is indicated for this species.

Most of the previous records for *Lensia grimaldi* have been from the Atlantic Ocean, from 41° N to 34° S, at depths ranging from 0–600 m to 2000–1500 m (Margulis, 1971). Alvarino (1967) caught the species in the Pacific at a depth of 690–840 m. Thus, although some of the previous closing net records seem to indicate a slightly deeper depth distribution for *Lensia grimaldi* than that found at Fuerteventura, the greater specificity of the latter results adds considerably to our knowledge of this rare *Lensia* species.

Lensia hotspur Totton, 1941

The depth distribution of the 43 anterior nectophores of *Lensia hotspur* found in eight N113 horizontal hauls is shown in Fig. 6. An additional nectophore was found in an IKMT oblique haul (5817 (2); 50–0 m). Apart from one nectophore, the population was found entirely in the top 250 m of water, with 62·8% occurring in the 85–100 m band. The fact that it was found in neither of the shallowest hauls is of interest, especially as they had finer mesh netting, but the discrepancy between the day and night total figures (37:6) most likely indicates a diurnal migration into the surface layers at night. As mentioned earlier the shallow (50 m) N113 night haul was carried out at a time (05.07–06.07 h) very late in the night when it might be expected that a slowly undulating population would have passed below that level. A nectophore was also found in one of the neuston net samples (5802 (11), 21.52–21.57 h), indicating that at least some of the population moves close to the surface at night.

Lensia hotspur is known from various localities in the Atlantic Ocean from 59° N (Fraser, 1967) to 43° S (Totton, 1941) but has not previously been recorded from the Canary Islands. The previous specimens have usually been found in open nets brought

to the surface from various depths ranging from 5 to 2000 m (Totton, 1941). Alvarino (1971) found specimens in closing net hauls from 141–120 and 141–100 m which agree with the present findings.

Lensia fowleri (Bigelow, 1911)

Seventeen out of a total of 28 anterior nectophores of *Lensia fowleri* were found in four horizontal hauls at 85, 100, 150 and 205 m (see Fig. 6), and nine others were in two IKMT horizontal hauls at 70 and 110 m. Thus all but three of the specimens were found in the top 110 m of water, but it is impossible to assess any diurnal depth variations because of the small numbers of specimens. No nectophores were found at the surface in the neuston net samples.

Lensia fowleri is known from 61° N to 34° S in the Atlantic Ocean (Margulis, 1971), and Leloup (1955) records it from the Canary Island region. In equatorial regions Margulis (1971) found the species in almost all the hauls from the surface to 550 m, but with a maximum at about 200 m. Moore (1949, 1953) found mean day levels of 165 and 100 m for the Bermuda and Florida Current areas, while Bigelow & Sears (1937) found, in the Mediterranean, very few specimens at the surface and a population peak at 200 m with a rapid decline in numbers down to 400 m. They state, however, that 'it is unfortunate that no systematic towing was done between 43 and 200 m, for this gap in the data leaves open the possibility that the center of abundance for this species may have lain somewhere between these hauls, or (more likely) that it may have been as abundant at 100 m as at 200 m'. Leloup & Hentschel (1935) found specimens over a wide range of depths from the surface to 800 m. The general implication of the present and previous results is that *L. fowleri* is commonest in the surface to 200–250 m of water, but the SOND collections indicate a maximum at about 100 m at Fuerteventura.

Lensia campanella (Moser, 1925)

Eighteen nectophores of *Lensia campanella* were found in three N113 hauls at 40, 50 and 100 m (see Fig. 6) and one IKMT horizontal haul at 110 m. The species is thus closely associated with the surface although no specimens were found in the neuston net samples. Most of the previous records for *L. campanella* have been from the South Atlantic although it is well known in the Mediterranean. Margulis (1971) quotes its occurrence in the region south of the Azores, and Moore (1949, 1953) found specimens in the Bermuda and Florida Current areas. The latter author found mean day levels of 60 and 17 m in the two localities, while Leloup & Hentschel (1935) give an overall range of 0–400 m. Margulis (1971) concluded that *L. campanella* is mainly found close to the surface, which is borne out by the present results.

Lensia lelouveteau Totton, 1941

The depth distribution of the 13 anterior nectophores isolated from eight N113 horizontal hauls is shown in Fig. 7. No specimens were found shallower than 700 m and the majority were in the deepest hauls between 900 and 960 m (8 an), indicating that the species is bathypelagic. *Lensia lelouveteau* has been found almost exclusively in the Atlantic Ocean from 54° N (Fraser, 1961) to 33° S (Totton, 1941). Alvarino (1967) gives
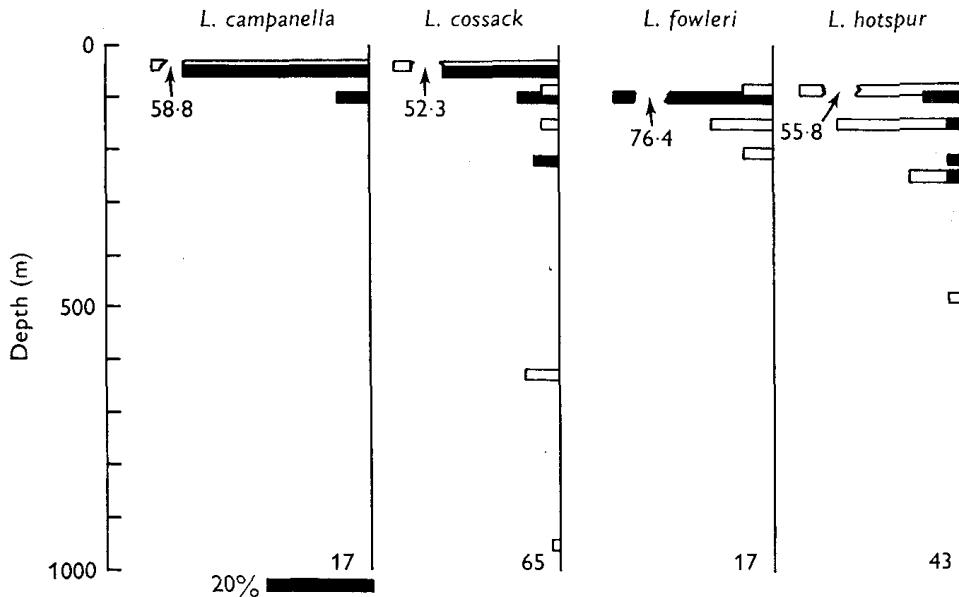
Fig. 6. The depth distributions of the anterior nectophores of *Lensia campanella*, *L. cossack*, *L. fowleri* and *L. hotspur* as shown by the N113 net captures. As the numbers of specimens were small the day and night totals have been combined and the values plotted are a percentage of this total, as in Fig. 1B.

the only records for another ocean, the Pacific. Totton (1941) concluded that it was a midwater species as he found it in four hauls shallower than 600 m, although a fifth haul was from 1000 to 220 m. Alvarino (1967), however, found it in eleven hauls between 685 and 2630 m, with a majority below 1710 m, and thus concluded that it was a bathy-pelagic species. Similarly Patriti (1965) found the species in the Gulf of Gascogne between 1200 and 500 m. Finally, Margulis (1971) records finding *L. lelouveteau* to the north of the Canary Islands and considers its depth distribution to range from 50–100 to 800–1000 m in the Atlantic Ocean.

Lensia exeter Totton, 1941

Only six anterior nectophores of *Lensia exeter* were found in four N113 hauls at 350, 410, 450 and 780 m (Fig. 7). The species is very rare and has only been recorded by Totton (1941) from specimens found in the south Atlantic and by Margulis (1971) at about 41° N off Portugal. The latter author notes that there are no records for the species between 41° N and 33° S and so the SOND collections represent a step toward uniting the two regions. The species has in fact also been identified at 18° N, 25° W ('Discovery' St. 7089). Margulis (1971) quotes the depth distribution of the species as in the 500–750 m and 1423–1645 m (in daytime) layers and in total catches from 0 to 450 and 0 to 1500 m. The present data do little to improve our knowledge of this species, except in the fact that five out of six of the nectophores were found between 350 and 450 m.
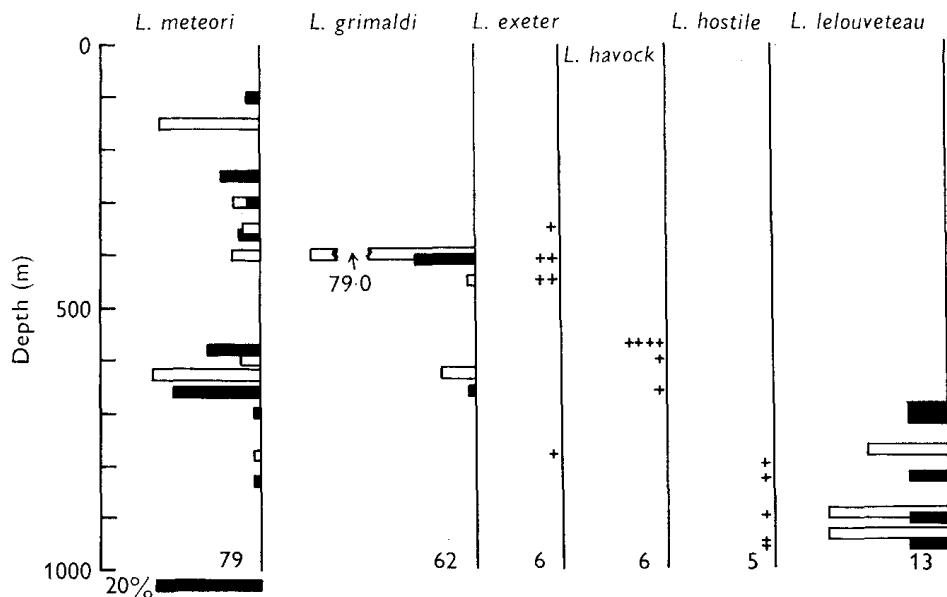
Fig. 7. The depth distributions of the anterior nectophores of *Lensia meteori*, *L. grimaldi*, *L. exeter*, *L. havock*, *L. hostile* and *L. lelouveteau* as shown by the N113 net captures. The percentage values are plotted as in Fig. 6, except for *L. exeter*, *L. havock*, and *L. hostile* where, because of the very small numbers of specimens isolated, the individual data have been plotted.

Lensia havock Totton, 1941

Stepanyants (1967) has reclassified *Lensia havock* as *Muggiaea havock* on the basis that (*a*) no posterior nectophore has so far been separated and identified (*Muggiaea* species do not develop a posterior nectophore while *Lensia* species do, although they have not been identified in all the species), and (*b*) the relative profundity of the hydroecium, in comparison with some of the other species, is closer to the state found in *Muggiaea* species. Margulis (1971) apparently follows this reclassification as he does not mention the species in his discussion of the genus *Lensia*. However, I consider that until it can be definitely established that the species does or does not develop a posterior nectophore, it should remain within the genus *Lensia* with which it has greater affinities. The 'anterior' nectophore of *L. havock* has seven very distinct ridges which contrasts with the five usually found in *Muggiaea* species, except possibly for *M. bargmannae* which has very distinct ridges. Also the shape of the hydroecium, better illustrated by Totton (1941) than by Stepanyants (1967), especially in the presence of the ventral slit, is quite unlike that found in the *Muggiaea* species but closely resembles *L. hostile*, a multistriate form. This latter species is not actually described by Stepanyants (1967), but Margulis (1971) retains it within the genus *Lensia* although its hydroecium is relatively profound and its posterior nectophore unknown.

Only six anterior nectophores of *Lensia havock* were found in three N113 horizontal hauls from the SOND collections. The depth distribution of these nectophores, shown in Fig. 7, ranged from 570 to 660 m. An additional nectophore was found in an IKMT oblique haul (5803 (2); 310–0 m), which did not cover the depth range for the other nectophores. This rare species is mainly known from the south Atlantic Ocean between 33 and 57° S (Totton, 1941) and the SOND results represent the first indications of its

presence in the North Atlantic. Other records from the Indian and Pacific Oceans show that it has a wide geographical distribution. The depths from which the previous specimens were captured vary, but most of the data come from open nets fished over wide depth ranges. Most of these results cover the fairly narrow range of distribution for *L. havock* found at Fuerteventura (570–660 m).

Lensia hostile Totton, 1941

Individual anterior nectophores of *Lensia hostile* were found in five N113 horizontal hauls at 800, 830, 900, 950 and 960 m (see Fig. 7), indicating a bathypelagic habitat for this rare species. *Lensia hostile* has only previously been recorded by three authors. Totton (1941) found specimens at four 'Discovery' stations, one west of Cape Town (1000–0 m) and the others in the Indian Ocean (at depths of 2100–1500, 1450–1000 and 3000–2000–(0) m). Alvarino (1967) identified specimens from four depths, namely 840–690, 1030–860, 1040–890 and 1242–1090 m, in the Pacific Ocean (30° 30' N, 120° 00' W), and Margulis (1971) found anterior nectophores in five catches from the equatorial Atlantic and in the region between the Azores and Canary Islands. The latter author quotes catches in the 540–565 m layer and in total catches from 0–630 and 8–2730 m. Thus, apart from the two shallow records of Margulis (1971), all the others indicate a bathypelagic nature for this species, and the results of Alvarino (1967) are in very close agreement with the present ones.

Lensia species – General Discussion

A survey of the literature to date shows that at least 28 species of *Lensia* have been described, although some of the more recently described species may be open to some doubt in that they represent specimens of other species which have been damaged or have been badly preserved resulting in shrinkage and distortion. Since there is some variability in, for instance, the somatocyst length, volume, angle, etc., within a given species, any distortion of these characteristic parts could be misleading and so the identification of *Lensia* species must be carried out with some care.

At Fuerteventura, thirteen species of *Lensia* were identified, and this compares with the fifteen found by Margulis (1971) in the Atlantic hauls of the 'Petr Lebedev'. However, the main feature of interest which arises from the SOND results lies in a comparison of the depth ranges of each individual species. Apart from *Lensia multicristata* whose population appears to be fairly evenly spread throughout the whole water column studied, a large proportion of the populations of the other species is found within fairly narrow depth limits. Thus in the two shallowest N113 hauls at 40 and 50 m (day:night) *L. cossack* and *L. campanella* were represented by 73·8 and 94·1 % of their total populations respectively. In the 85–100 m band 82·3 % of the *L. fowleri* specimens were found while *L. subtilis* and *L. hotspur* had slightly wider depth ranges with 87·3 % of the former population occurring between 40 and 150 m, and 86·0 % of the latter between 85 and 150 m. These five species are quite distinctly demarcated, on a depth basis, from the remaining *Lensia* species, excepting *L. multicristata*, but the situation in the surface layers is undoubtedly more complex than the present results indicate. The issue is complicated by the facts that (*a*) no hauls were made shallower than 40 m, (*b*) the shallowest N113

night haul at 50 m was fished at a time relatively late in the night, and (c) the mesh size of the shallowest nets was finer than for the others, due to the absence of the catch-dividing bucket (see Roe, 1972a), which would possibly lead to an overestimation of the populations in these hauls, e.g. *L. cossack* and *L. campanella*. Their exact effects on the results are impossible to gauge but it is most likely that any diurnal vertical migration of these species would be masked. Thus, although *L. fowleri* appeared to be present within a fairly narrow band of water (85–100 m) with no obvious diurnal variation, it was also found right at the surface in the neuston net samples, as also were *L. subtilis* and *L. hotspur*. The two shallowest species, *L. cossack* and *L. campanella*, did not, however, appear in these samples.

Apart from *Lensia multicristata*, only one species, *L. meteori*, appeared to be present in any numbers in the 150–400 m range. This species appeared to have two populations, one between 100 and 400 m with 45·5 % of the total number of specimens, and the other, after a gap of 180 m, between 580 and 660 m, where 50·7% of the total population occurred. Between these two populations were two species with narrow depth distribution ranges. *Lensia grimaldi* was found between 400 and 410 m (90·3 % of the population) and *L. exeter* between 410 and 450 m (66·7%). After a further gap of 50 m, *L. achilles* appeared (500–625 m, 61·5 % of the total numbers) and this population slightly overlapped at its deeper limit with *L. havock* (580–660 m, 100%) and with the deeper population of *L. meteori*. Finally all of the *L. lelouveteau* population was found below 700 m, with 61·6% lying between 900 and 950 m, and all of the *L. hostile* population was found between 800 and 960 m. There is thus an indication of a stratification among the various *Lensia* species although the present data are not sufficient for a firm conclusion along these lines.

Of the three species found by Margulis (1971) but not found at Fuerteventura (Margulis does not include *Lensia* ? = *Muggiaea havock*) two are rare and their northerly limits are between 10° and 18° N in the Atlantic Ocean. The third, *L. conoidea*, is, however, one of the commonest and best documented of the *Lensia* species and its absence is somewhat surprising. However, a survey of the literature on this species shows that, although the vicinity of the Canary Islands has frequently been investigated, catches of the species have only been made on four occasions (Leloup, 1933, 1934) in the area. The absence of *L. conoidea* in the SOND collections is thus possibly a significant, although negative, piece of evidence towards an understanding of the geographical distribution of the species in the different water masses of the seas. When further detailed information is available on the depth distribution of the various species in different localities then perhaps one will begin to understand the reasons behind the variations in the geographical distributions of these siphonophore species.

Muggiaea atlantica Cunningham, 1892

As was mentioned in the discussion of *Lensia havock*, the species of *Muggiaea* only develop a single (anterior) nectophore in their polygastric phase. The species are generally thought to be neritic and not common in deep water. In the case of *Muggiaea atlantica* only a single nectophore was found, in a N113 horizontal haul at 700 m. Bigelow & Sears (1937) found the species to be common in the Mediterranean, occurring in the

top 100–200 m of water. Haeckel (1888) records *M. pyramidalis* (= *M. atlantica*) from the Canary Islands but most of the records are for continental coastal regions. Leloup & Hentschel (1935) have noted its presence in hauls down to 450 m in the Atlantic, and so it is quite unusual to find a specimen as deep as 700 m.

Muggiaea kochi (Will, 1844)

Two nectophores of *Muggiaea kochi* were found in a N113 haul at 780 m. Like *M. atlantica*, this species is generally considered to be neritic but Chun (1888) has recorded it from the Canary Islands. In coastal regions it is generally found close to the surface but in the open ocean Leloup & Hentschel (1935) have found it at depths down to 800 m.

Chelophyes appendiculata (Eschscholtz, 1829)

Specimens of *Chelophyes appendiculata* were found in all but eleven of the horizontal hauls, and the day/night distributions of the anterior nectophores for both the N113 and IKMT nets is shown in Fig. 8. A total of 9375 anterior and 2108 posterior nectophores were found in the SOND collections, although the majority occurred in the oblique hauls. The depth distributions for both types of nectophores in the horizontal series of nets are given in Tables 1 and 3. Initially it appears that the depth distribution patterns of the nectophores found in each net are entirely different, but I consider that most of these differences can be accounted for by differences in the timings of the hauls. It is possible also that a lot of the small catches from depths greater than 400 m may be due to either contamination of the nets whilst being hauled to the surface, or to the presence at those depths of dead nectophores. However the result for the IKMT haul (St. 5794 (2)) at 650 m, where 221 anterior and 139 posterior nectophores were found, would seem to contradict this.

Taking the results for the IKMT hauls first, it would appear that there is a diurnal migration of the species into the surface layers at night. Thus 76·3 % of the total number of anterior nectophores in the IKMT night hauls was found in the shallowest haul at 70 m. The main population probably approaches the surface for nearly all the neuston net samples (St. 5802) from 20.51 h to 01.35 h contain specimens of this species. The IKMT results further indicate that the population migrates down during the day to about 250 m, where 40·7 % of the daytime population was found. It is interesting to note that the 205, 250 and 300 m IKMT day hauls were carried out at virtually the same times (15.10–17.10 h for the 205 and 300 m hauls, and 15.20–17.20 h for the 250 m one). The virtual absence of the species in the 205 and 300 m hauls indicates that the main population of *Chelophyes appendiculata* is confined over a fairly narrow depth range. There is some evidence for hold-up in the net as the horizontal part of the haul at 250 m contained 260 anterior nectophores while its oblique portion contained 3260. It is possible that the oblique part of the haul passed through the main population of *C. appendiculata* but there is no evidence for this from the 205 m haul, including its oblique part. Similarly the oblique portion of the 300 m haul only contained 433 anterior nectophores which does not compare with the 250 m haul. It is possible also that a large part of the actual population was not sampled as there was a considerable difference between the total numbers of nectophores found in the day and night hauls. The absence of specimens

in the shallower IKMT day hauls would be expected if the species was undergoing a diurnal migration of 200+ m.

The situation with the N113 samples is, however, much more complicated. 37·6% of the night population was found in the shallowest haul at 50 m but it must be remembered that this may be an overestimate due to the change in the mesh size of the net (Roe, 1972a). However, 22·8% of this population remained at 220–250 m and even the timing of the hauls allows no obvious explanation for this. In the case of the daytime N113 hauls, the large percentage of the population found in the shallowest haul, at 40 m, may again be an overestimate due to the mesh size of the net, although there is an indication from
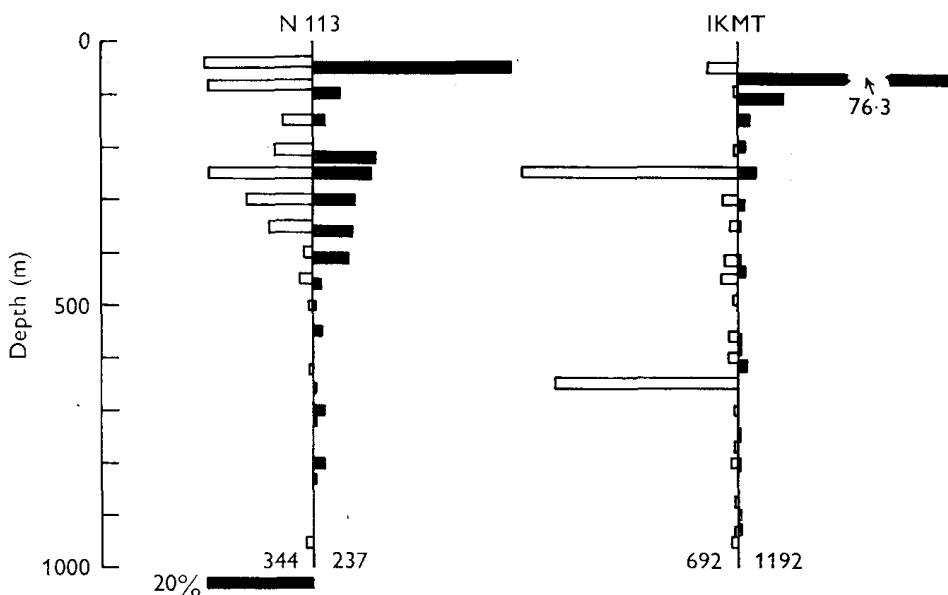
Fig. 8. The depth distribution of the anterior nectophores of *Chelophyes appendiculata* as shown by the N113 and IKMT net captures, plotted as in Fig. 1 A.

the IKMT series of a small near-surface population. The 85 m haul was fished between 08.00 and 09.00 h, a time at which it is possible that the animals are still moving down from their near-surface night-time level, and so the presence of 19·8 % of the population at this level need not be unexpected. The 150 and 205 m hauls were fished at times relatively late in the day when the top of the population was possibly already moving upwards, resulting in specimens being present in small numbers. In contrast, the deeper hauls at 250 and 300 m were fished relatively early in the day when the population would be still migrating downwards, if the diurnal migration of these species is indeed a slow, continuous cycle without any prolonged sojourn at the extremities.

Because of the variations in the timings of these N113 hauls it is difficult to assess either the 'mean day level' of the species or, in fact, whether the population has been under- or overestimated. In this case the total day numbers are higher than the night ones, which, as discussed earlier, may be due to the relatively late hour at which the shallowest night haul was fished. The two sets of results clearly indicate the advantages of fishing the various depths at approximately the same time of day, as in the IKMT

series. By this method one at least knows where the main part of the population is for that particular time, even though it may not necessarily indicate the greatest depth to which this population migrates by day. The time at which this latter depth is reached may vary from species to species. However, it is concluded that, at Fuerteventura, the main population of *Chelophyes appendiculata* moves into the 250 m depth region by day and undergoes a 200+ m diurnal migration, so that at least the top of the population enters the surface layers at night.

Chelophyes appendiculata is probably the commonest and most widely distributed species of siphonophore, and because of this quite a lot of information has accumulated on its depth distribution. Leloup & Hentschel (1935) found the major abundance of the species between the surface and 100 m, with a secondary peak at 400–600 m, and an occasional specimen down to 1000 m. Similarly, Bigelow & Sears (1937) concluded that the species was commonest in the top 200 m in the Mediterranean, and at 200 m in the Atlantic Ocean, although their sampling was inadequate in the shallower depths (cf. *Lensia fowleri*). Moore (1949, 1953) found the mean day level of nectophores to be at 75 m (spread 130 m) in the Bermuda region, and 48–74 m (spread 81–100 m) in the Florida Current. He also found marked migrations at night with ranges of 87 and 5–48 m respectively. Moore & Corwin (1956) have discussed the theoretical depth distribution of four species of siphonophore, including *C. appendiculata*. They calculated, from a consideration of the temperature and light regimes, and by relating these to the vertical distribution of the siphonophores, that a population at a station 40 miles east of Miami should exist at a depth at least twice that of a population at 10 miles from Miami. In fact they found that the mean day levels at these two stations for *C. appendiculata* were 74 and 221 m respectively.

Moore (1953) found that there was a significant correlation between the variations in the day level of the Florida Current siphonophores and the depth of the 15 °C isotherm. Although this will obviously not apply to all siphonophore species the population of *Chelophyes appendiculata*, whose mean day level was somewhat above this isotherm, appeared to vary with it. It is interesting to note that at St. 5796 and 5808 (see Currie *et al.* 1969) during the SOND cruise, the 15 °C isotherm lay at about 220 m, while the main daytime population of *C. appendiculata* was found below this at 250 m, where the temperature was 14·4–14·5 °C.

Eudoxoides mitra (Huxley, 1859)

A total of 201 anterior and only two posterior nectophores of *Eudoxoides mitra* were found in the hauls examined, and the day/night depth distribution for the anterior nectophores from the N113H series is shown in Fig. 9. Most of the population is present in the top 150 m of water, and since a large proportion of the hauls from 200 to 960 m contain one or two specimens it is possible that these are the result of net contamination or the presence of dead sinking specimens. The results indicate that the species is a near-surface form with the majority of specimens found in the shallowest day and night hauls. Thus there is no indication of any diurnal vertical migration except that the disparity in the total numbers found in each series might indicate some slight upward movement at night. No specimens of this species were, however, found in the neuston net

samples. Because of the difference in the mesh size of the net it is difficult to be certain where the actual population peak lies, but it might be deeper than the results seem to to indicate. The timings of the 85 m (08.00–09.00 h) and 150 m (17.01–18.01 h) day hauls and the 50 m (05.07–06.07 h) night one are such that they may also confuse the results.

The posterior nectophore of *Eudoxoides mitra* appears either to be easily lost in the net because of its small size or is only rarely developed, for only a few of them are ever found. Of the two found in the SOND collections one was in an N113 haul at 950 m (5827 (4)) and the other in an IKMT haul from 150 m to the surface (5806 (3)).

Eudoxoides mitra is widely recorded from all three Great Oceans and in the Mediterranean. Leloup (1933) has found it in the Canary Island region, at depths between 500 and 1000 m, but Leloup (1934) found the majority of the 'Meteor' collection specimens of this species in hauls at 100–50 m and 50–0 m, which agrees closely with the present results. Patriti (1970) found most of his specimens in 200–0 m hauls, and Alvarino (1971) reports several finds in hauls shallower than 164 m.

By far the most detailed analysis of the depth distribution of *Eudoxoides mitra* is given in the papers by Moore. Moore (1949) found the species to be one of the commonest of the Bermuda siphonophores, with a mean day level of 125 m and a spread of 105 m. He also found a marked but not extensive diurnal migration, similar to that which appears to occur at Fuerteventura. In the Florida Current (Moore, 1953) the species maximum was at 63–124 m (spread 45–69 m), and there was a diurnal migration there of the order of 44–50 m. *Eudoxoides mitra* was also included in the analysis of depth distribution made by Moore & Corwin (1956) and the basic conclusions are the same as those reached in the case of *Chelophyes appendiculata*. However, the calculation of the mean day level at the 40 Mile Station, which was similar to the SOND result for *C. appendiculata*, produced a figure of 270 m for *E. mitra*, although there was a very high vertical spread of 209 m. Even though the SOND results are difficult to interpret fully, there is no indication that the daytime depth distribution of *E. mitra* extends much below 150 m.

Eudoxoides spiralis (Bigelow, 1911)

Seven hundred and twenty-two anterior nectophores of *Eudoxoides spiralis* were found in the SOND collections and the depth distribution of the 640 of these which were found in the N113 series of hauls is shown in Fig. 9. 96·6 % of the day population was found in two hauls at 50 and 84 m, and it is probable that most of the individual deeper records are due to contamination of the net as they were brought up through the shallower waters. Since the population at 40 m is probably overestimated because of the change in mesh size of the net, it would appear that the mean day level or population peak of this species lies closer to 85 m than 40 m. 71·8 % of the night population was found in the shallowest haul at 50 m, although again this may be an overestimate. However, there is a considerable difference in the total number of nectophores found by day and by night, which is interpreted as indicating that the main population of *E. spiralis* rises into the top 50 m at night. This is borne out by the observation of several specimens in the night-time neuston net samples (St. 5802).

Eudoxoides spiralis is a well-known cosmopolitan species and there are many records

for it from the Atlantic Ocean. The depth distribution records obtained by Bigelow & Sears (1937) are rather confused but indicate a chief zone of distribution for the species in the 40–50 m and surface regions, with a rapid decline in numbers from 100 to 400 m, and only isolated occurrences below this. This is quite similar to the SOND results but since the nets they used were non-closing ones their deeper records could easily be due to contamination. Leloup (1934) similarly found specimens down to 1000 m, but with the vast majority in the top 100 m. Moore (1949, 1953) records the species as being common with mean day levels of 65 m (spread 65 m) and 45–69 m (spread 50–75 m) for the Bermuda and Florida Current areas respectively. In the latter locality he found a diurnal migration with a range of 30–33 m, while at Bermuda there was a marked migration with a range of 47 m, and a distinct indication of increment from below 250 m. The depth distribution of the species was also found to be correlated with light and temperature.
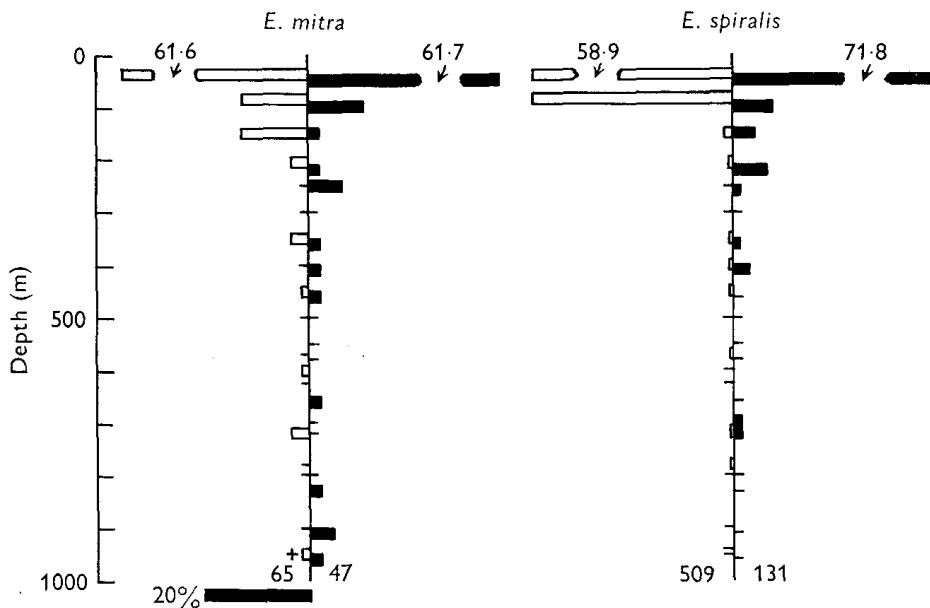
Fig. 9. The depth distributions of the anterior nectophores of *Eudoxoides mitra* and *E. spiralis* as shown by the N113 net captures, plotted as in Fig. 1 A. The haul in which the posterior nectophore of *E. mitra* was found is indicated (+).

Dimophyes arctica (Chun, 1897)

Two forms of *Dimophyes arctica* were found in the SOND collections. Chun (1897) originally noted that his specimens of *Diphyes* (= *Dimophyes*) *arctica* were of two kinds basically distinguishable on size, although the shape of the hydroecium was also different, but he did not consider separating them specifically or sub-specifically. Stepanyants (1967) discusses in some detail the differences between the two forms which she found. One of her forms has a nectosac with powerfully developed musculature absent from the other. She does not, however, note any size difference between the forms and only illustrates a slight difference in the shape of the hydroecium. The forms which have been found in the North-east Atlantic, not only in the region of Fuerteventura, are distinguishable by several features. There is a clear size difference, the larger form is deficient in nectosac musculature, while its presence in the smaller form gives it a distinct opacity.

In the larger form the roof of the hydroecium is recurved as it approaches the ventral side, as illustrated by Chun (1897, Taf. 1, Figs. 1 and 3) and by Stepanyants (1967, Fig. 134, A, B), while in the smaller form the roof of the hydroecium approaches the ventral surface of the animal at a right angle or is only very slightly recurved, as shown by Totton (1965, Fig. 122) and Chun (1897, Taf. 1, Fig. 2). The situation regarding these forms is thus rather complicated for although the two SOND collection forms are quite distinct the 'muscular' form of Stepanyants (1967) appears to be an intermediate one, of similar size to the non-muscular one and also having a distinctly recurved roof to the hydroecium. It may be that these different forms represent different growth stages.
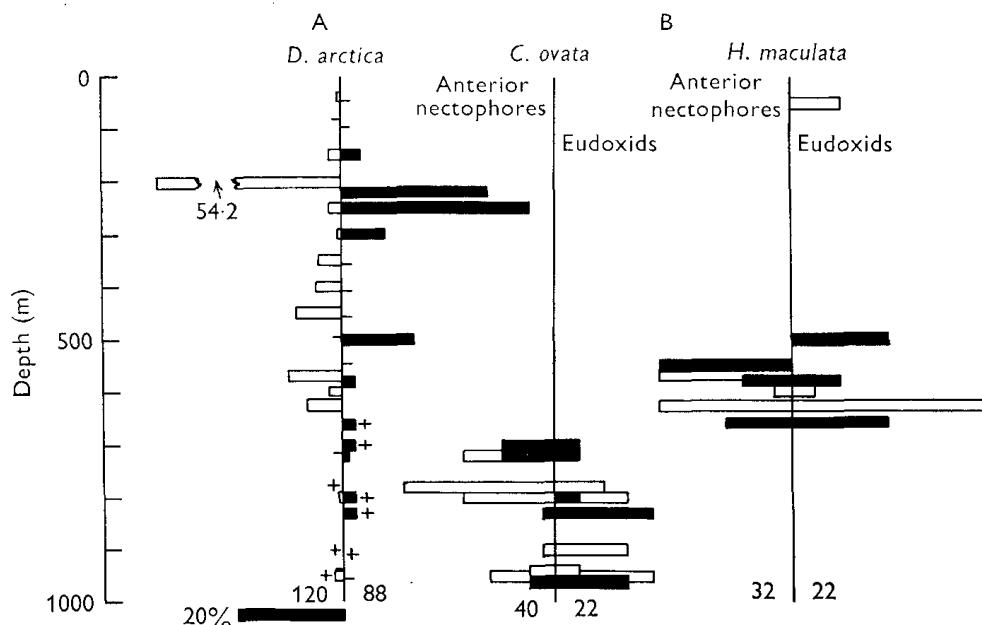
Fig. 10A. The depth distribution of the anterior nectophores of *Dimophyes arctica* as shown by the N113 captures, plotted as in Fig. 1A. The depths at which the eudoxid phase were found are indicated (+). B. The depth distributions of the anterior nectophores and eudoxids of *Clausophyes ovata* and *Heteropyramis maculata* as shown by the N113 net captures, plotted as in Fig. 1B.

In the SOND collections only two anterior nectophores of the larger form of *Dimophyes arctica* were found. They occurred in two N113H hauls at 720 m (5825 (7)) and at 780 m (5827 (2)), and these are not included in Table 1. Of the smaller form, 219 anterior nectophores, 23 eudoxid bracts and several gonophores were found in 34 hauls. The depth distribution of the 208 anterior nectophores which were found in the N113H series of hauls, by day and night, is shown in Fig. 10A. Only one nectophore was found in an IKMT horizontal haul (St. 5814 (1), 250 m). The depths at which the eudoxids were found are also indicated. This form is seen to occur over a wide depth range varying from 40 to 950 m, but with 56·7% of the population by day and 62·5% by night lying within the 205–250 m range. The apparent existence of a reverse migration as indicated by the histograms is probably anomalous due to the fact that there were no night hauls between 150 and 220 m, so that the main night population may have been missed. This might help to explain the slight disparity in the total numbers of nectophores found by day and

by night. There appears, however, to be very little diurnal variation in the depth of the population.

Eudoxids were only found in hauls deeper than 660 m. Stepanyants (1967) had proposed that the optimal temperature for the reproduction of *Dimophyes arctica* was about 2·5 °C for the Kara Sea, but that eudoxids had been observed in waters with temperatures over a range of 1·5–10 °C. The species is known to exist, as the polygastric asexual stage, over a much wider temperature range. Thus the presence of the eudoxids only in the deeper hauls at Fuerteventura, where the temperature ranged from 7·5 to 9·6 °C, would seem to fall within the maximum range for reproduction which Stepanyants proposed. Totton (1954), however, found eudoxids to be present at temperatures between 11·7 and 17·21 °C, and recently hauls from 250 m at 30° N, 23° W ('Discovery' St. 7856), where the temperature was approximately 16 °C, have yielded large numbers of eudoxids.

The most complete discussion of the depth and geographical distribution of *Dimophyes arctica* is given by Totton (1954). He also reviews the distribution of the species on the basis of temperature and concludes that although it has been recorded at temperatures ranging from −1 to 22 °C it is usually found between +1 and 3 °C. At Fuerteventura, specimens were found at temperatures ranging from 7·5 to 20 °C, with the population maximum being found in the 14·5–15 °C range (200–250 m). The species has not previously been found from the Canary Islands region, but Leloup (1933, 1934, 1955) records it for the Azores and Cape Verde Islands. The previous depth distribution records are quite varied, ranging from shallow depths in the colder waters to bathypelagic ones in subequatorial zones. Temperature is probably an important factor in controlling the depth distribution of the species and it is surprising to find the main population at such a shallow depth at Fuerteventura. Mackintosh (1934) found moderate numbers of *D. arctica* in the Antarctic 'Discovery' collections and concluded that there was no real diurnal variation in numbers. This conclusion is borne out by the present results but a great deal more information is required before we can understand the depth and temperature ranges of both the asexual, polygastric and sexual, eudoxid stages properly. The suggestion was made by Totton (1954) that the differences in the geographical distributions of *D. arctica* and *Diphyes antarctica*, which has a very limited distribution, might be brought about by the possibility of the former species resorting to different depths, and thus different temperatures of water, at different stages of its life-cycle. The present results where the main polygastric population was found at 200–250 m, while the eudoxids occurred at depths below 660 m, are consistent with this idea.

Family Clausophyidae

This family is represented by a small number of species of mid- and deep-water calycophoran siphonophores. The polygastric phase consists of two different definitive nectophores, the anterior and posterior, but it differs from the Diphyidae in that the posterior nectophore possesses a somatocyst. The eudoxid phases are also quite distinct.

Clausophyes ovata (Kefferstein & Ehlers, 1860)

A total of 40 anterior and 14 posterior nectophores, plus 22 eudoxid bracts were found in 11 N113 horizontal hauls, and an additional anterior nectophore occurred in an IKMT

oblique haul from 495 m to the surface (5798 (2)). The depth distributions of the total numbers of anterior nectophores and eudoxid bracts from the N113 series are directly compared in Fig. 10B and an indication is given as to whether the specimens were caught during the day or at night. It can be seen that both the polygastric and the eudoxid stages are bathypelagic and that there is no apparent difference in their depth distributions either diurnally or in relation to one another. The entire population is found between 700 and 960 m.

There is not a great deal of information available on this species and the results for the SOND cruise add considerably to it. Most of the previous records have come from the Atlantic Ocean, with a few on the Mediterranean and Indian Ocean. Leloup & Hentschel (1935) found *Clausophyes ovata* at depths between 400 and 600 m, and Patriti (1965 b) found it in hauls from 1200 to 320 m. However, the majority of the previous depth distribution data comes from Totton (1954) who records specimens from depths varying from the surface to 3000 m. Most of these records, however, cover the range of distribution which was found at Fuerteventura.

Chuniphyes multidentata Lens & van Riemsdijk, 1908

Only nine anterior and four posterior nectophores of *Chuniphyes multidentata* were found in six horizontal and two oblique hauls. The depths for the horizontal hauls were 600, 625, 660, 700 and 720 m for the N113 series, and an IKMT haul at 925 m. The last haul only contained one specimen so that the majority was found in the 600–720 m depth region.

Most of the previous records for the species are from the Atlantic Ocean, with several from the Canary Island region. Leloup & Hentschel (1935) found specimens in hauls between 300 and 1000 m, with a maximum in the 600–800 m range. Similarly Bigelow & Sears (1937) found most specimens below 400 m, but with occasional appearances at the surface. Alvarino (1967) only found the species below 400 m, and Stepanyants (1967) considered it to be bathypelagic, mainly at depths from 300 to 400 m. Although the SOND collection of *Chuniphyes multidentata* is small, the narrowness of the depth distribution range is useful in advancing our knowledge of the species.

Heteropyramis maculata Moser, 1925

The depth distributions of the 32 anterior nectophores and 22 eudoxid bracts of *Heteropyramis maculata* found in the N113 series of hauls are directly compared in Fig. 10B (cf. *Clausophyes ovata*). Apart from the record of two complete eudoxids from the shallowest night haul at 50 m, all the specimens were located in the 500–660 m range, with no obvious difference between the depth distributions of the two stages either by day or by night. The indication that the main population by day of both stages is squeezed between two night populations is misleading as there was no night haul between 580 and 660 m, and no day haul between 625 and 720 m.

The majority of the limited number of records for *Heteropyramis maculata* are from the Atlantic Ocean although it does not appear to have been reported previously from the Canary Islands region. Leloup (1934) found eudoxids at depths ranging from 200 to 800 m, and Patriti (1970) found a single bract between 400 and 200 m. Alvarino (1967)

appears to have recorded the species in virtually all of her day hauls from 0 to 3040 m, but only in the 1030–860 m and 1240–1090 m night ones. The majority of the depth records, however, are given by Totton (1954) and almost all fall into the 450–1500 m range. The records from Fuerteventura not only considerably increase the numbers of known specimens but also offer some detailed information on the depth distribution of this rare siphonophore.

Family Abylidae

The abylid polygastric stages, like the diphyids, are comprised of two nectophores, except in the case of *Enneagonum hyalinum* which only has one. Unlike the diphyids, however, the two nectophores are usually very different in shape and in size. This is probably a reflexion of the fact that the anterior nectophore is the larval nectophore which is retained and which buds off the definitive, posterior, nectophore. The development of one abylid, *Abylopsis tetragona*, has been followed closely by C. Carré (1967). Since the definitive nectophore is always budded off, except in *E. hyalinum*, it is more usual to find almost equal numbers of both anterior and posterior nectophores in a haul, in contrast to the diphyids. There is, however, a delay of a few weeks between the completion of the development of the larval (anterior) nectophore and the budding of the definitive one, so that in certain seasons the former could preponderate. It should be possible to distinguish these as they only have a single large gastrozooid and tentacle, and cormidia are not formed until after the appearance of the nectophore bud. However, no such analysis has been made in the present study.

The family Abylidae is split into two sub-families which are distinguished mainly on differences in the mode of articulation of the posterior and anterior nectophores.

Sub-family Abylinae

Abyla trigona Quoy & Gaimard, 1827

Only one anterior and one posterior nectophore of *A. trigona* were found, in an IKMT oblique haul from 575 m to the surface (5798 (1)). Four eudoxid bracts of the 'trigona-group' of *Abyla* species were also found in one horizontal haul (5817 (2), 1 eb) and two oblique ones (5798 (3), 1 eb; 5814 (2), 2 eb) from a maximum depth of 160 m. The speciation of these bracts has not been fully worked out as yet. *Abyla trigona* has been recorded from several localities in the three Great Oceans, and Bedot (1904) and Leloup (1955) have found it to the north-west of the Canary Islands. There is, however, very little information on the depth distribution of this or, in fact, any of the *Abyla* species. Sears (1953) found specimens in the DANA collections at depths from 2000 to 50 m, but most were concentrated in the 100–50 m region. Patriti (1970) found some anterior nectophores in a haul from 200 m to the surface, and Totton (1954) found specimens at the surface in the Gulf of Aden.

Ceratocymba sagittata (Quoy & Gaimard, 1827)

Although 237 anterior and 165 posterior nectophores, plus 27 bracts and 24 gonophores of the eudoxid were found in the SOND collections, almost all of them were in the IKMT oblique hauls. Only 29 anterior and 24 posterior nectophores, plus 7 bracts

and 5 gonophores of the eudoxid, were found in horizontal hauls. Two IKMT night hauls from 70 and 110 m contained 15 anterior and 9 posterior nectophores, plus 3 bracts and gonophores, while the rest of the specimens were scattered throughout the water column down to 925 m. The majority of specimens appear to exist in the top 100–200 m of water. The depth distributions of the anterior and posterior nectophores from the horizontal hauls are given in Tables 2 and 4, and those for the eudoxids are listed in Appendix II.

Ceratocymba sagittata is common in warmer waters and Chun (1888, 1897), Moser (1925) and Leloup (1955) have recorded it from the Canary Islands region. Leloup (1934) took it in one haul from 50 to 100 m, while Bigelow & Sears (1937) found it only in their 16 and 43 m hauls in the Mediterranean, although they review that it had previously been found at depths down to 100 m. Alvarino (1971) mentions occurrences of the species down to 640 m, but with the majority in shallower waters. However, the present data are too confusing to add much to our knowledge of the depth distribution patterns of *C. sagittata*.

Sub-family Abylopsinae

Abylopsis tetragona (Otto, 1823)

Sixty-seven anterior and 21 posterior nectophores, plus 16 bracts and 12 gonophores of the eudoxid phase, were found in the SOND collections and almost all occurred in the horizontal series of nets. The shallowest N113H night haul at 50 m contained 47 anterior and one posterior nectophore, and, in the hauls from 40 to 110 m, 62 anterior and 14 posterior nectophores, plus 9 bracts and 7 gonophores were found. This indicates that the species is an epipelagic form living close to the surface. The deepest occurrence of the species was one specimen in a horizontal haul at 615 m (5810 (2)). The depth distributions of the anterior and posterior nectophores in the horizontal series of hauls are given in Tables 2 and 4, and those for the eudoxids are listed in Appendix II.

Abylopsis tetragona is a well-documented species, especially from the Atlantic Ocean and Mediterranean. The apparent vertical distribution of the species has also been discussed by many authors, although it is still not fully understood. The general conclusion is that the species occurs mainly quite close to the surface although it can be found at greater depths, and this agrees with the situation at Fuerteventura. Leloup & Hentschel (1935) thus found it in hauls down to 100 m but with the majority between the surface and 100 m. Similarly Bigelow & Sears (1937) found most of their 'Thor' specimens of the species in their 16 and 43 m hauls, but with isolated occurrences in considerable numbers at greater depths. The analyses by Moore (1949, 1953) are the most detailed so far published. He found mean day levels at 55 m (spread 25 m) and 85–104 m (spread 63–122 m) at Bermuda and in the Florida Current, and found marked diurnal migrations with ranges of 89 and 70–80 m respectively. Apart from being amongst the species where a positive correlation was found between the variations in its peak day level and the 15 °C isotherm (Moore, 1953) it was also included in a further analysis by Moore *et al.* (1953), though not as an individual species. Moore & Corwin (1956) compared the 10- and 40-mile Florida Current stations and found mean day levels of 104 and 188 m respectively,

but with large spreads of 63 and 234 m. Although the present records are too confused and inadequate for one to come to any definite conclusions on the depth distribution of *A. tetragona*, it does appear that the species is generally distributed in water shallower than that suggested by these latter authors.

Abylopsis eschscholtzii (Huxley, 1859)

Only fourteen anterior (an) and eighteen posterior (pn) nectophores, plus 31 bracts (eb) and 3 gonophores (eg) of the eudoxid were found in four horizontal and four oblique hauls. The four horizontal hauls were all N113 night ones at depths of 50 (12 an, 14 pn, 26 eb), 100 (2 eb), 150 (1 eb) and 410 m (1 an, 1 pn, 1 eb, 1 eg). The absence of the species in the day hauls is somewhat surprising but it is clear that it mainly exists close to the surface and so the lack of specimens is probably a reflexion of the absence of hauls in this zone.

Abylopsis eschscholtzii, like *A. tetragona*, is well documented from warmer waters, especially in the Atlantic Ocean. Data on its depth distribution are, however, infrequent and are based mainly on the work of Moore. Leloup & Hentschel (1935) found the species to be commonest in the top 100 m, but with specimens in closing nets down to 400 m, while Totton (1954) records it from the surface in the Gulf of Aden. Moore (1949, 1953) calculated a mean day level of *ca.* 40 m (spread 80 m) for the species at Bermuda and 12–58 m (spread 51–78 m) in the Florida Current. Moore found little or no sign of diurnal migration in the former locality but in the Florida Current a migration over a range of 6–48 m was noted. The species was also used in the analyses of Moore *et al.* (1953) and Moore & Corwin (1956), and in the latter case the mean day levels at the 10- and 40-mile Florida Current stations were 58 m (spread 51 m) and 171 m (spread 219 m) respectively. He was able to correlate the daytime depth distribution with the 15 °C isotherm but not with light variations.

Bassia bassensis (Quoy & Gaimard, (1833) 1834)

The depth distribution patterns, by day and by night, for the anterior nectophores and for the eudoxid bracts found in the N113 series of hauls are shown in Fig. 11. This series contained the majority of the specimens from a total of 358 anterior and 621 posterior nectophores, with 263 eudoxid bracts. The numbers of anterior nectophores found both in the day and the night hauls closely agrees with the numbers of posterior nectophores in the corresponding hauls, but there is a wide disparity between the total numbers of each type of nectophore found in the day and night series (Table 2). This is also true for the eudoxid bracts. Almost the entire population of both stages of *Bassia bassensis* found in the night series of hauls occurred in the shallowest haul at 50 m, and there were only isolated records below this depth. However, two factors should be taken into account. First, there is the probability that the majority of the population was above this level and was not sampled, and secondly there is the fact that the population at 50 m is probably being overestimated due to the change in the mesh size of the net.

These facts will also apply to the polygastric stages in the day series of hauls for again the population maximum occurred in the shallowest haul at 40 m, although fairly large proportions were also found in the 85 m haul. This would tend to indicate that the mean

day level for the polygastric stage of *Bassia bassensis* lies below 40 m, a fact which is borne out by the absence of the eudoxid stage in the shallowest haul. It should also be noted that the timings of the day hauls at 85 m (08.00–09.00 h) and 150 m (17.01–18.01 h) are such that they may mask the true picture for the depth distribution of the species.

The results are thus difficult to interpret. It is considered that the night-time population of *Bassia bassensis* is mainly at or above 50 m in depth and there are several records for the species in the neuston net samples which indicate its presence in the surface layers at night. During the day it is possible that the population either moves more completely
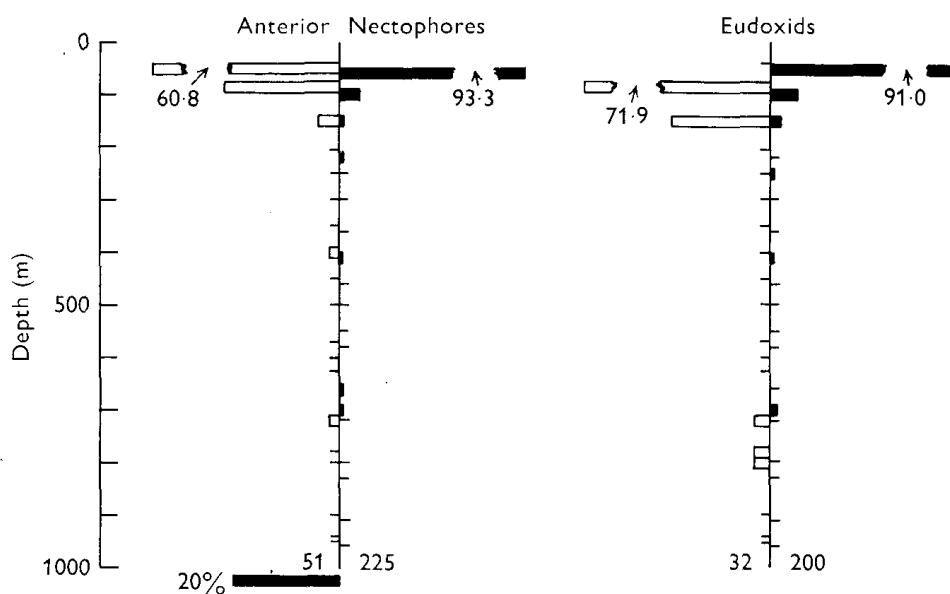
Fig. 11. The depth distributions of the anterior nectophores and eudoxids of
Bassia bassensis as shown by the N113 net captures, plotted as in Fig. 1A.

into the surface layers, which could explain the small numbers of specimens caught in this series of hauls, or conversely it is possible that the timing of the 85 and 150 m hauls is such that the majority of the population was never sampled although it might have undergone a vertical migration down through these depths. In this second case if one assumes that the missing specimens during the day are below 40 m, then, in the case of the anterior nectophores, the number found at 40 m would reduce to only 14 % of the total population. Their presence in this proportion at that depth would thus not be unexpected, especially as it is probably an overestimate for reasons explained earlier.

Bassia bassensis has a world-wide distribution and is especially well known from the Atlantic Ocean and the Mediterranean. Most previous depth records show that it generally occurs in the top 200 m of water and most often close to the surface. Thus Leloup & Hentschel (1935) found most of their specimens in the top 50 m of water, with some down to 100 m, and then only an occasional specimen at individual depths down to 1000 m. Bigelow & Sears (1937) found a seasonal difference in their Atlantic population such that *B. bassensis* was spread fairly evenly down to 200 m in winter, but, with the stabilization of the water column in summer, the species was confined to the surface 50 m.

Moore (1949, 1953) gives figures for the mean day level of *Bassia bassensis* of 50 m

(spread 40 m) for Bermuda, and 13–59 m (spread 29–275 m) in the Florida Current. At Bermuda he found no evidence for a diurnal migration of the species and no correlation between day level and cloud. However, in the Florida Current a migration of the order of 28–41 m was noted, together with a correlation of the day level with the 15 °C isotherm. The SOND results can add little to this information, as the shallow depths, where it is presumed that most of the population is to be found, were not sampled.

Enneagonum hyalinum Quoy & Gaimard, 1827

The day and night depth distributions of the nectophores and eudoxid bracts of *Enneagonum hyalinum* from the IKMT series of horizontal hauls are shown in Fig. 12. The totals for the two stages which were found in the SOND collections were 535 nectophores, 990 bracts and 278 gonophores of the eudoxid. The day and night peak levels for both stages are similar, but the daytime populations appear to be a little more diffuse. In the case of the nectophores 94·0% of the population was found between 415 and 435 m at night, while only 63·0% of the day population occurred between 415 and 450 m. A small secondary population then occurs between 560 and 700 m but whether this represents a diurnal migration by a small part of the population into deeper water during the day is difficult to assess.
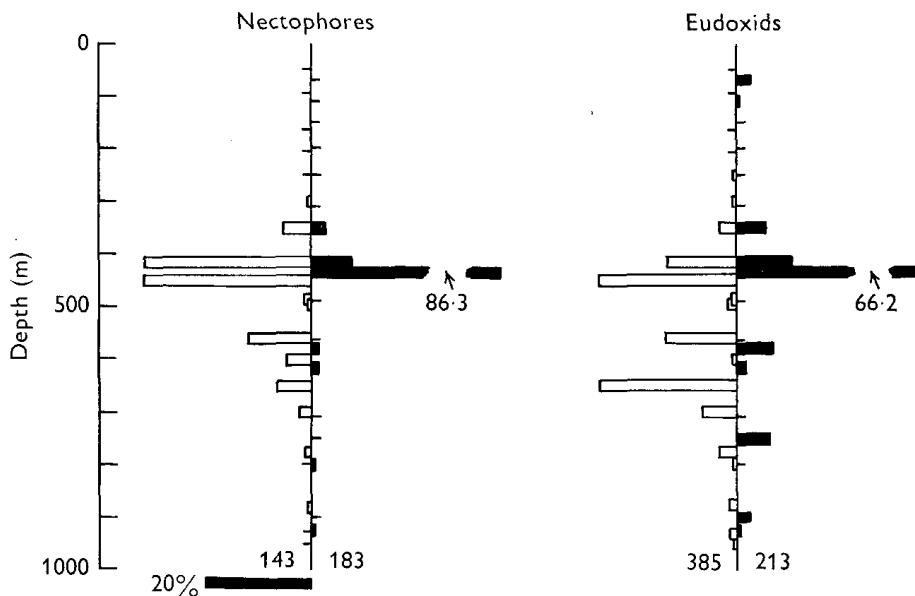
Fig. 12. The depth distributions of the anterior nectophores and eudoxids of *Enneagonum hyalinum* as shown by the IKMT net captures, plotted as in Fig. 1A.

A similar feature can be observed in the depth distribution pattern of the eudoxid stage. 76·5% of the population at night occurs between 415 and 435 m, while during the day only 39·0% is found between 415 and 450 m. There again is a secondary peak between 560 and 700 m, where 46·2% of the population is found. There is quite a considerable disparity between the total numbers of eudoxids found by day and by night and since there were no night IKMT hauls between 615 and 710 m it is possible that some of the

population has not been sampled. This would not, however, apply to the polygastric stage where larger numbers of nectophores were found at night than by day.

Enneagonum hyalinum is quite well known from the Pacific and Atlantic Oceans, and the Mediterranean. Chun (1888, 1892) and Leloup (1936) have reported the species from the region around the Canary Islands. Leloup & Hentschel (1935) found a few specimens at various depths from the surface to 400 m. Bigelow & Sears (1937), however, found that nectophores of *E. hyalinum* were less abundant in the upper 16 m than at greater depths. This also applied to the eudoxid phase, except that in winter they tended to aggregate in the 16–60 m zone. In both the Mediterranean and Atlantic the nectophores were abundant in the 100–533 m range with a maximum from 333 to 533 m. Below 533 m they noted an abrupt decline in numbers for the Atlantic population, but a more gradual one in the Mediterranean, where specimens were found down to 800 + m. The SOND results are somewhat in accord with this in that the main population peaks lie in the 415–450 m range, but there were only isolated occurrences of specimens above 350 m, while others were found in most of the hauls down to 960 m.
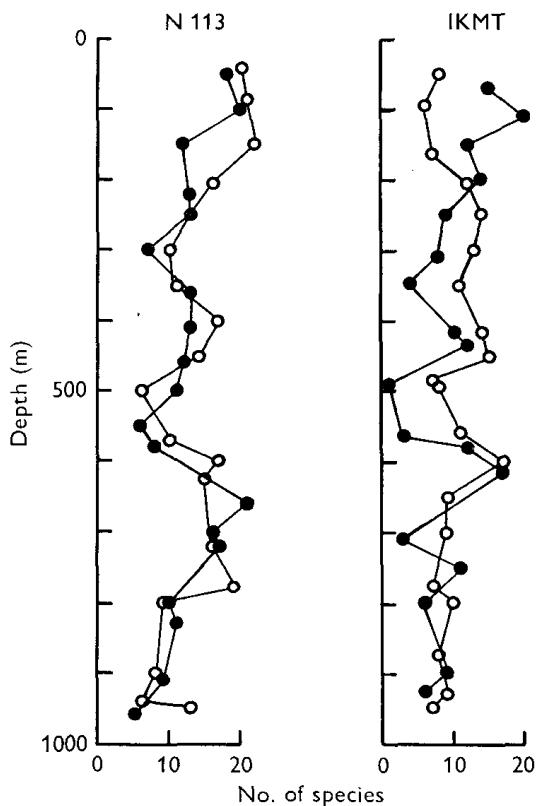
Fig. 13. The number of siphonophore species found at each mean depth for the N113 and IKMT series of hauls. Open circles–day, filled circles–night.

Vertical changes in the species composition

The total number of siphonophore species present at each mean depth sampled in the day and night series of both the IKMT and N113 nets is shown graphically in Fig. 13. As would be expected, and unlike the decapods (Foxton, 1970*b*), there is no marked variation in the overall depth distribution of the species by day and by night. The results

for the two nets in fact appear to contradict each other. In the shallower IKMT hauls, down to 200–205 m, there are always more species present in the night hauls than in the day ones. This trend is then reversed and in the deeper hauls down to 600–615 m there were more species present in the day hauls. In the deepest hauls approximately equal numbers of species were found. These results are probably what one might expect if there was some degree of diurnal vertical migration in the shallow-living species, migrating upwards at night and back down into deeper water during the day. However, the results for the N113 series, although rather erratic, show an opposite trend, with a greater number of species being present in the shallower day hauls than the night ones. In the hauls deeper than 250 m the numbers in the two series were comparable. It appears, therefore, that little can be gained from any detailed analysis of these depth variations for the total numbers of species of siphonophores present.

REVIEW AND CONCLUSIONS

The previous authors in this series of papers on the zooplankton taken during the 'Discovery' SOND cruise have discussed several difficulties which arise when any attempt is made to compare their results with those of other workers. Similar difficulties arise with the siphonophores, but the drawbacks in the sampling methods which have been discussed in this paper still do not detract from the fact that the SOND collections probably represent the most comprehensive study of the vertical distribution of siphonophores in a single area available so far. In any study of vertical distribution the geographical location will obviously be of great importance. The physical features of the water mass, e.g. its temperature/salinity/depth interrelationships, and also the origins of the separate water layers which constitute the water column, will be important factors in determining not only its total species composition but also the numbers of individuals present and their depth distribution. The TSD profiles undertaken at Fuerteventura are described by Currie *et al.* (1969), and these indicate the presence of deep, saline Mediterranean water below about 650 m, while the rest of the water column, apart from the surface layers, has characteristics corresponding to those for North Atlantic Central Water.

In this context, the presence at Fuerteventura of certain siphonophores whose geographical distributions are generally thought to be fairly limited may enable them to be used as biological indicators of water masses. For instance, *Marrus orthocanna* is generally considered to be a high Arctic form and so its presence at 720 m in the SOND samples may be indicative of the presence of some waters of polar origin. Similarly the diphyid, *Dimophyes arctica*, which occurs mainly in the colder polar waters, was found to have a widespread vertical distribution at Fuerteventura. The presence of water which originated in the Mediterranean is also indicated by the occurrence of the prayid, *Rosacea cymbiformis*. This species is thought to be uncommon in the Atlantic Ocean. Another diphyid species, *Lensia conoidea*, is, however, also common in the Mediterranean but was not found in the SOND collections. This anomaly is probably explicable by the fact that the water had a deep origin in the Mediterranean and *L. conoidea* is a near-surface-living form, as shown by Bigelow & Sears (1937). The absence of *R. plicata*, the common Atlantic prayid, is also of interest.

The species composition of any water mass may also be affected by the season. The virtual absence of the eudoxid stage of the commonest siphonophore, *Chelophyes appendiculata*, may indicate a distinct breeding season for this species. Bigelow & Sears (1937) found indications in the Mediterranean for a breeding season in spring and early summer for this species, and its total population was depleted in the winter. However, Moore (1949) found no signs of a seasonal maximum at Bermuda, although the proportions of the two generations were variable throughout the year. These data indicate that the possibility of a seasonal variability in the population should always be borne in mind in any study of this kind.

Roe (1972a) has pointed out that the results which are obtained from any study will depend to a greater or lesser extent on the type of net used, both in its mesh size and in the sampling procedure. In the case of the nets used during the SOND cruise, a further complication arises in the inadvertent change in the mesh size of the N113 net when the catch-dividing bucket was removed for the two shallowest hauls. This, in conjunction with the absence of some very shallow hauls, does complicate the interpretation of the data for the few species whose distribution is within this range. The series of hauls from the two nets must also be treated as separate, since comparison of the two is made difficult by such factors as differences in the mesh sizes, filtering areas and efficiencies, the speed of towing, and differences in the time of day or night at which the individual hauls were made.

The differences in the timings of the individual hauls has been discussed in detail for certain species. The observed differences in the gross distribution of some species as shown by the two nets may be due to the slight variation in the depths at which the corresponding hauls were fished, for it appears that many of the non-migrant siphonophores have fairly narrow depth ranges. This has been illustrated by comparing the vertical distributions of the species of the genus *Lensia*. The species of this genus also showed an interesting stratification in their distribution, there being very little overlap in the water column. A similar stratification is also illustrated by the species of the family Hippopodiidae, which are probably congeneric. This situation has also been commented upon by several previous authors in this series of SOND papers. Thus Baker (1970) found, particularly for the non-migrant species in the 'longicorne' group of the euphausiid genus *Stylocheiron*, that there was very little overlap in the population maxima of certain congeneric species. Foxton (1970b) not only found indications of stratification of the species of the two subgenera of the decapod genus *Sergestes*, during the day, but also that the subgenera themselves were clearly separable into the shallower *Sergestes* and the deeper *Sergia* species.

There are two major studies with which the present data can be compared in detail, despite the difficulties which are involved in any such comparison. However, these papers themselves have certain drawbacks. First the work of Bigelow & Sears (1937), although of fundamental interest in that it represents the first major study of the seasonal and vertical distribution of siphonophores from the Mediterranean, has the drawback that all the samples were obtained using open nets. This meant that the depth distribution of any species could then only be estimated. Secondly, the work of Moore, although extremely detailed, is difficult to compare with the present results as he only studied the

limited populations of siphonophores which were present in the top 300 m of water. This constituted only 24 species in the Bermuda region (Moore, 1949) and 20 in the Florida Current (Moore, 1953). However, the results which he obtained were of great importance especially as he was able to demonstrate some correlation between the daytime depth distribution of many zooplankton species and the light intensity or temperature. In this way he was able to predict the 'mean day level' of certain species at various localities (Moore *et al.* 1953; Moore & Corwin, 1956). For instance, he demonstrated that the 'mean day level' of *Chelophyes appendiculata* could be correlated with the level of the 15 °C isotherm, and the applicability of this observation to the present results is discussed here for that particular species.

The present results also indicate the considerable depth range covered by some of the weakly swimming siphonophores in the course of diurnal migration. *Amphicaryon acaule*, which has very limited swimming powers, was found by day to reach a depth of about 250 m, rising at night to a level of 70 m or less. A similar range was also noted for *Hippopodius hippopus*. It is inferred from the present results that some siphonophore species which undergo diurnal migrations do so in a continuous cycle, never remaining at any one depth for any length of time. This makes such terms as Moore's 'mean day level' rather confusing and so perhaps they should be avoided in the context of siphonophores. However, the ranges of vertical migration which Moore (1949, 1953) found for the two aforementioned species are much smaller than at Fuerteventura and this may be related to the differences in the temperature/depth profiles in the different localities.

TABLE 1. SPECIES OF THE FAMILY DIPHYIDAE FOUND IN THE N113 DAY AND NIGHT SERIES

DAY

Species		5827(5)	5828(1)	5816(7)	5816(6)	5816(4)	5816(3)	5816(2)	5816(1)	5814(1)	5814(2)	5825(1)	5825(5)	5825(2)	5827(1)	5827(2)	5825(4)	5827(3)	5825(3)	5827(4)	Total
E. spiralis	n	300	192	7	1	—	—	2	1	1	—	—	1	—	2	2	—	—	—	—	509
E. mitra	an	40	8	8	2	—	—	2	—	1	—	1	—	2	—	—	—	—	—	1	65
C. appendiculata	pn	20	20	13	19	47	21	9	4	—	—	—	1	—	3	—	—	—	—	—	157
C. appendiculata	an	71	68	19	25	68	43	28	6	8	1	—	—	—	2	1	—	—	—	4	344
D. arctica	an	1	—	3	65	3	1	5	6	10	—	12	3	8	—	—	1	—	—	1	120
M. kochi	n	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1
L. hostile	an	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	2
L. havock	an	—	—	—	—	—	—	—	—	—	—	4	1	—	—	—	—	—	—	—	5
L. exeter	an	—	—	—	—	—	—	1	—	2	—	—	1	—	—	—	—	—	—	—	4
L. lelouveteau	an	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	3	3	—	—	8
L. campanella	an	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10
L. fowleri	an	—	1	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
L. hotspur	an	—	24	9	—	3	—	—	—	1	—	—	—	—	—	—	—	—	—	—	37
L. grimaldi	an	—	—	—	—	—	—	—	—	49	1	—	4	—	—	—	—	—	—	—	54
L. cossack	an	34	2	2	—	—	—	—	—	—	—	—	4	—	—	—	—	—	1	—	43
L. meteori	an	—	—	15	—	—	—	2	2	4	—	—	3	16	1	—	—	—	—	—	43
L. subtilis	an	36	28	111	9	2	—	—	1	1	—	—	—	—	—	—	—	—	—	—	188
L. achilles	an	—	—	—	—	—	—	1	3	23	—	103	41	33	5	11	15	4	6	12	258
L. multicristata	an	28	1	4	1	21	69	47	31	19	—	8	14	2	4	10	5	6	16	8	294
D. dispar	an	4	3	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	8
S. chuni	an	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
S. turgida	an	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
S. biloba	an	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
S. quadrivalvis	an	4	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7
Mean depth (m)		40	85	150	205	250	300	350	400	450	500	570	600	625	720	780	800	900	940	950	Total

TABLE 1 (cont.)

NIGHT

Species	Type	50	100	150	220	250	300	360	410	460	500	550	580	660	700	720	800	830	910	960	Total
E. spiralis	n	94	10	6	9	2		2	4						2	2		1	2	1	131
E. mitra	an	29	5	1	1	3		1	1	1				1				2			47
C. appendiculata	pn	21	8	5	10	14	3	9	4	2	1				2	2	5	2			83
C. appendiculata	an	89	12	6	28	26	19	17	16	4	2	4		1	5	1	2	2			237
D. arctica	an			3	24	31	7				12		2	2	2	1	2	2			88
M. atlantica	an														1						1
L. hostile	an																1	1		1	3
L. havock	an													1							1
L. exeter	an							2													2
L. lelouveteau	an												1	1		1	1	1			5
L. campanella	an	6	1																		7
L. fowleri	an		13																		13
L. hotspur	an		3	1	1	1															6
L. grimaldi	an							7					1								8
L. cossack	an	14	5		3																22
L. meteori	an		2		6	2	3				8	13	1			1					36
L. subtilis	an	14	50	13	8	2		1	1			12									101
L. achilles	an									1	34		8	16	5	12	3	8	8		95
L. multicristata	an	4	1		1	10	3	9	7	12	6		10	5	6	4	3	4	21	21	127
D. bojani	an														1						1
D. dispar	an	1																			1
S. chuni	an		1																		1
S. biloba	an		1																		1
Mean depth (m)		50	100	150	220	250	300	360	410	460	500	550	580	660	700	720	800	830	910	960	
Station		5819(5)	5819(3)	5819(2)	5819(1)	5818(6)	5818(5)	5818(4)	5818(3)	5818(2)	5818(1)	5819(4)	5823(5)	5825(6)	5823(1)	5825(7)	5823(2)	5823(3)	5825(8)	5823(4)	Total

TABLE 2. SPECIES OF THE FAMILIES PRAYIDAE, HIPPOPODIIDAE, CLAUSOPHYIDAE AND ABYLIDAE FOUND IN THE N113 DAY AND NIGHT SERIES

N113 Day

Sample	Mean depth (m)	A. acaule (pg)	P. dubia (eb)	R. reticulata (eb)	Rosacea sp. (n)	R. cymbiformis (eb)	N. natans e	N. natans n	N. spinosa e	N. spinosa n	N. thetis e	N. thetis n	H. hippopus (n)	V. glabra (n)	V. spinosa (n)	V. serrata (n)	V. pentacantha (n)	C. ovata an	C. ovata e	C. multidentata (an)	H. maculata an	H. maculata e	C. sagittata (an)	A. tetragona (an)	B. bassensis an	B. bassensis pn	B. bassensis e	E. hyalinum n	E. hyalinum e
5827 (5)	40	8											12	4										4	31	24	23	1	1‡
5828 (1)	85	3	1		2	38							19	12			2							1‡	16	16	6		1‡
5816 (7)	150	4			5								7	33									3	1‡	2	5			
5816 (6)	205	1		28		8							6	6	1											1			
5816 (4)	250	3			2								8	17										1‡					
5816 (3)	300				2											5	5						3‡					3	
5816 (2)	350	2			3									1	12										1				1
5816 (1)	400												1	2															1‡
5814 (1)	450								4	1*				11			12									2			1‡
5814 (2)	500									3																			
5825 (1)	570										2	1		45							8								2‡
5825 (5)	600										1	1		20		8				1‡	1	1				1		2	2‡
5825 (2)	625										4	1		27		15				1	8	8						1	2
5827 (1)	720	1												2				3‡		2‡		1							2
5827 (2)	780				3		1								9			11‡	2								1		2‡
5825 (4)	800										1							7	2							1	1		2‡
5825 (3)	900							1			2			1				1	3						1	1	1		
5825 (3)	940																	2	1										
5827 (4)	950						1											5‡	4										
Total		22	1	28	17	46	2	1	4	4	10	3	53	181	22	28	19	29	12	4	17	10	6	7	51	51	32	7	15

* Definitive nectophore. † Posterior nectophore present. ‡ Eudoxid gonophores present.

TABLE 2 (cont.)

N113 Night

Station	Mean depth (m)	E. hyalinum e	E. hyalinum n	B. bassensis e	B. bassensis pn	B. bassensis an	A. eschscholtzii pn	A. eschscholtzii an	A. tetragona an	H. maculata e	H. maculata an	C. multidentata an	C. ovata e	C. ovata an	V. pentacantha n	V. serrata n	V. spinosa n	V. glabra n	H. hippopus n	N. thetis e	N. thetis n	N. spinosa e	N. spinosa n	N. diomedeae n	R. cymbiformis eb	Rosacea sp. n	P. dubia eb	P. dubia n	A. acaule pg
5819 (5)	50			182	204	210	14	12	47‡	2									47							4			12
5819 (3)	100			10	19	8												3	1						5				2
5819 (2)	150			4	2	2												26								3			
5819 (1)	220				1	1												13								1			1
5818 (6)	250	3§		1														43											
5818 (5)	300	4§													3			1								2			
5818 (4)	360	4§	1	1	1	2											7	5											
5818 (3)	410	5§	1		2		1	1									19	15					1						
5818 (2)	460	3§			1													6					3						
5818 (1)	500									4	8				54			30					1*						
5819 (4)	550				4					2	3						1	4											
5823 (5)	580			2						4	4		1	4		35		2											
5825 (6)	660	1§				1						1‡	1	4‡	1	8				2		1		1		1			1
5823 (1)	700											1						1											
5825 (7)	720					1							1	1		7		2			1	1		(1)†			35	2	
5823 (2)	800																												
5823 (3)	830	1§			1								4																
5825 (8)	910	1§											3																
5823 (4)	960													2‡															
Total		22	2	200	235	225	15	13	47	12	15	2	10	11	58	50	27	151	48	2	1	2	5	1	5	11	35	2	16

* Definitive nectophore.   † Eudoxid.   ‡ Posterior nectophore.   ‡ Posterior nectophore(s) present.   § Eudoxid gonophores present.

TABLE 3. SPECIES OF THE FAMILY DIPHYIDAE FOUND IN THE IKMT DAY AND NIGHT HORIZONTAL SERIES

Night series

Night station	Mean depth (m)	E. spiralis (n)	E. mitra (an)	C. appendiculata (pn)	C. appendiculata (an)	L. campanella (an)	L. fowleri (an)	L. grimaldi (an)	L. cossack (an)	L. subtilis (an)	L. multicristata (an)	D. dispar (an)	S. monoica (an)	S. biloba (an)
5817 (3)	70	25	30	146	910	—	2	—	5	—	1	—	—	—
5817 (2)	110	15	7	16	106	1	7	—	1	—	3	3	—	—
5814 (2)	150	2	1	11	27	—	—	—	—	2	—	1	—	1
5806 (3)	200	2	—	7	17	—	—	—	—	—	—	1	2	—
5814 (1)	250	—	1	16	42	—	—	—	—	—	2	—	—	1
5806 (2)	310	1	—	6	15	—	—	—	—	—	—	—	—	—
5803 (2)	350	—	—	2	5	—	—	—	—	—	—	—	—	—
5806 (1)	415	1	—	1	2	—	—	—	—	—	1	2	—	1
5793 (3)	435	—	—	8	16	—	—	—	—	—	—	—	—	—
5905 (1)	490	—	—	—	—	—	—	—	—	—	—	—	—	—
5811 (2)	565	—	—	—	1	—	—	—	—	—	—	—	—	1
5817 (1)	580	—	1	2	7	—	—	—	—	—	—	1	—	1
5810 (2)	615	2	1	10	21	—	—	—	—	—	—	1	—	—
5811 (1)	710	1	—	—	—	—	—	—	—	—	1	—	—	—
5809 (3)	750	—	—	—	3	—	—	—	—	—	—	—	—	—
5807 (2)	800	—	—	3	9	—	—	1	—	—	—	—	—	—
5809 (2)	900	—	—	—	2	—	—	1	—	—	—	—	—	—
5810 (1)	925	—	—	2	9	—	—	—	—	—	—	—	—	—
Total		49	41	230	1192	1	9	2	6	2	8	9	2	4

Day series

Day station	Mean depth (m)	E. spiralis (n)	E. mitra (an)	C. appendiculata (pn)	C. appendiculata (an)	L. subtilis (an)	L. multicristata (an)	D. dispar (an)
5801 (3)	50	2	—	2	34	—	—	13
5801 (2)	95	—	—	—	1	—	—	—
5800 (2)	165	—	—	—	—	—	—	—
5798 (3)	205	—	—	1	6	—	—	3
5795 (3)	250	—	2	133	260	1	—	—
5796 (4)	300	—	1	8	19	—	4	—
5795 (2)	350	—	—	1	9	—	—	—
5796 (3)	415	—	—	2	15	—	—	—
5793 (2)	450	—	—	11	20	—	1	1
5803 (1)	485	1	—	1	2	—	—	—
5800 (1)	495	—	—	—	2	—	—	—
5794 (1)	560	—	—	5	12	—	—	—
5798 (2)	600	—	—	4	13	—	—	1
5794 (2)	650	—	—	32	129	—	—	—
5798 (1)	700	—	—	—	1	—	—	—
5797 (2)	775	1	1	6	1	—	—	—
5799 (2)	800	—	1	2	9	—	1	—
5796 (2)	875	—	—	1	4	—	—	—
5801 (1)	930	1	—	1	2	—	—	—
5813 (1)	950	—	—	—	8	—	—	—
Total		5	5	317	639	1	6	18

TABLE 4. SPECIES OF THE FAMILIES PRAYIDAE, HIPPOPODIIDAE, CLAUSOPHYIDAE AND ABYLIDAE FOUND IN THE IKMT DAY AND NIGHT HORIZONTAL SERIES

IKMT Day

Station	Mean depth (m)	A. acaule (pg)	A. ernesti (pg)	M. praeclara (ln)	P. dubia n	P. dubia eb	P. reticulata n	P. reticulata eb	Rosacea sp. n	N. spinosa n	N. spinosa e	N. thetis n	N. thetis e	H. hippopus n	V. glabra n	V. spinosa n	V. serrata n	V. pentacantha n	C. sagittata an	C. sagittata pn	A. tetragona an	B. bassensis an	B. bassensis pn	B. bassensis e	E. hyalinum n	E. hyalinum e
5801 (3)	50	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	1	—	—	—	—	—	4	—	—	—
5801 (2)	95	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	3	—	—
5800 (2)	165	17	1	—	—	—	—	—	—	—	—	—	—	3	5	6	5	—	—	7	—	—	—	—	—	—
5798 (3)	205	53	—	—	—	—	—	—	—	—	—	—	—	18	29	11	—	—	—	—	—	1	1	1	—	—
5795 (3)	250	4	—	—	—	—	—	—	4	—	—	—	—	423	62	5	—	—	—	—	—	—	1	1	1	2
5796 (4)	300	3	—	—	—	—	—	—	—	—	—	—	—	69	75	7	1	—	—	—	—	—	1	1	8	3
5795 (2)	350	1	—	1	3	—	—	—	29	1	—	—	—	8	6	68	1	—	—	—	1	1	5	—	45	12†
5796 (3)	415	2	—	—	—	1	—	—	28	2	—	—	—	9	22	75	—	—	—	—	—	—	—	—	45	50†
5793 (2)	450	1	—	—	—	—	—	—	14	—	—	—	—	2	60	185	—	—	—	—	—	—	—	—	2	100†
5803 (1)	485	—	—	—	—	—	—	—	3	—	—	—	—	—	85	—	—	—	—	—	—	—	—	—	1	4†
5800 (1)	495	3	—	—	—	—	—	—	2	—	—	—	—	—	119	13	7	—	—	—	—	—	5	—	17	7†
5794 (1)	560	2	—	—	—	31	—	—	17	1	5	11	9	5	805	6	—	—	—	—	—	—	3	—	7	51†
5798 (2)	600	2	—	—	—	4	9	11	7	—	4	17	15	—	444	2	38	8	2	—	—	—	1	—	10	3†
5794 (2)	650	1	—	—	2	18	—	—	2	1*	1	10	15	—	157	—	—	—	—	—	—	—	1	—	4	99†
5798 (1)	700	2	—	—	—	—	—	—	—	—	—	2	3	—	7	—	—	—	—	—	—	—	—	—	2	25†
5797 (2)	775	—	—	—	—	—	—	—	—	1	—	—	—	—	29	2	9	—	—	—	—	—	1	—	—	14†
5799 (2)	800	—	—	—	—	—	—	—	—	—	—	1	1	—	16	—	—	—	—	—	—	—	1	—	1	1
5796 (2)	875	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—	—	—	—	—	—	—	—	—	—	7†
5801 (1)	930	—	—	—	—	—	—	—	—	—	—	—	—	—	11	14	13	—	—	—	—	—	—	—	—	6
5813 (1)	950	—	—	—	—	—	—	—	—	—	—	—	—	—	23	13	3	—	—	—	—	—	—	1	—	1
Total		93	1	1	5	54	9	11	106	6	10	41	43	537	1981	408	77	8	2	7	1	2	24	7	143	385

Prayidae — A. acaule, A. ernesti, M. praeclara, P. dubia, P. reticulata, Rosacea sp., N. spinosa, N. thetis
Hippopodiidae — H. hippopus, V. glabra, V. spinosa, V. serrata, V. pentacantha
Abylidae — C. sagittata, A. tetragona, B. bassensis, E. hyalinum

* Definitive nectophore.   † Eudoxid gonophores present.

TABLE 4 (*cont.*)

IKMT Night

		Prayidae										Hippopodiidae							Abylidae							
	Mean depth (m)	*A. acaule*	*P. dubia*		*P. reticulata*	*Rosacea* sp.	*D. annectens*	*N. spinosa*		*N. thetis*		*H. hippopus*	*V. glabra*	*V. spinosa*	*V. serrata*	*V. pentacantha*	*C. multidentata*	*C. sagittata*		*A. tetragona*		*B. bassensis*			*E. hyalinum*	
		pg	n	eb	n	n	n	n	e	n	e	n	n	n	n	n	an	an	pn	an	pn	an	pn	e	n	e
5817 (3)	70	15	—	—	—	—	—	—	—	—	—	47	—	—	—	1	—	9	8	5	6	6	48	7	—	6†
5817 (2)	110	5	—	—	—	—	—	—	—	—	—	25	1	8	—	—	—	6	1	5	6	8	14	6	—	2
5814 (2)	150	1	—	—	—	—	—	—	—	—	—	—	26	—	—	—	—	—	1	—	—	—	5	—	—	—
5806 (3)	200	1	—	—	—	—	7	—	—	—	—	—	57	4	—	—	—	—	—	—	—	—	5	—	—	—
5814 (1)	250	—	—	—	—	—	—	—	—	—	—	1	25	23	—	—	—	—	—	—	—	—	—	1	—	—
5806 (2)	310	—	—	—	—	2	—	—	—	—	—	—	51	11	—	—	—	1	1	—	1	—	—	—	—	—
5803 (2)	350	—	—	—	—	—	—	—	—	—	—	—	32	19	—	—	—	—	—	—	—	—	—	—	5	12†
5806 (1)	415	—	—	1	—	—	—	—	—	—	—	—	68	50	—	—	—	—	—	—	—	—	1	—	14	22†
5793 (3)	435	2	—	3	—	2	—	4	—	—	—	2	171	71	—	—	—	—	—	—	—	—	2	—	158	141†
5805 (1)	490	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
5811 (2)	565	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
5817 (1)	580	—	1	1	—	1	—	1	1	2	6	—	64	—	5	—	—	1	1	—	—	—	—	—	2	6†
5810 (2)	615	2	—	—	—	3	—	1	—	1	—	2	51	1	8	—	—	2	1	1	1	1	1	—	2	4†
5811 (1)	710	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
5809 (3)	750	1	1	—	—	7	—	—	—	2	—	—	6	1	—	—	—	2	—	—	—	—	—	—	—	13†
5807 (2)	800	—	—	—	—	—	—	—	—	—	1	—	2	—	—	—	—	—	—	—	—	—	—	—	1	—
5809 (2)	900	—	—	—	2	2	—	—	—	—	—	—	22	2	—	—	—	—	—	—	—	—	—	—	—	5†
5810 (1)	925	—	—	—	—	—	—	—	—	—	—	—	18	—	—	—	1*	—	1	—	—	—	—	—	1	2
Total		27	2	5	2	17	7	6	1	5	7	77	597	191	13	1	1	21	14	11	14	15	76	14	183	213

* Posterior nectophore present. † Eudoxid gonophores present.

I am deeply indebted to the late Mr A. K. Totton for the help, inspiration and guidance which he so generously afforded to me during the last year and a half of his life when I was honoured to know him. His preliminary identifications of some of the SOND material aided me greatly in my introduction to the siphonophores. I also wish to thank Mr P. M. David for his advice on the preparation and critical reading of the manuscript.

APPENDIX I

Species of the sub-order Physonectae found in the N113 and IKMT horizontal hauls.*

Apolemia uvaria: 5825 (8), 19 n, st; **5795 (2)**, 2 n, st.

Agalma sp.: **5795 (2)**, 9 n.

Agalma okeni: **5816 (6)**, 1 jn; **5825 (1)**, 12 n, 31 b, st.

Halistemma rubrum: **5827 (5)**, 4 n; **5828 (1)**, 2 n; **5816 (7)**, 27 n, st; **5816 (6)**, 19 n, 1 b, st; **5816 (4)**, 48 n, 2 b, st; **5816 (3)**, 2 n; **5816 (1)**, 2 n; **5814 (1)**, 6 n, st; **5814 (2)**, 18 n, 19 b, st; **5825 (5)**, 49 n, st; **5825 (2)**, 44 n, 8 b, st; **5827 (1)**, 9 n, 1 b; **5825 (3)**, 11 n, 4 b; 5819 (3), 19 n, st; 5819 (2), 2 ex; 5819 (1), 12 n, b; 5818 (4), 1 n; 5823 (1), 1 n; 5825 (8), 1 n.

    5798 (3), 2 n; **5795 (3)**, 17 n, st; **5796 (4)**, 5 n, st; **5795 (2)**, 3 n, st; **5793 (2)**, 17 n; **5803 (1)**, 4 n, 1 b, st; **5800 (1)**, 15 n; **5798 (2)**, 48 n, 19 b, st; **5797 (2)**, 4 n, 2 b; **5796 (2)**, 18 n; **5801 (1)**, 1 n; 5817 (3), 16 n, st; 5817 (2), 69 n, 12 b; 5814 (2), 15 n, 1 b; 5806 (3), 46 n, 8 b, st; 5814 (1), 24 n, 5 b; 5806 (2), 19 n, 5 b, st; 5793 (3), 3 n, 1 b; 5817 (1), 32 n, 8 b, st; 5809 (3), 2 b; 5809 (2), 7 n, 12 b, st.

Nectalia loligo: **5797 (2)**, 1 n.

Marrus orthocanna: 5825 (7), 22 n, 71 b, st.

Nanomia bijuga: **5827 (5)**, 12 n; 5819 (3), 2 n, 1 b.

Physonect C: **5827 (2)**, 5 n, 9 b, st; **5825 (4)**, 4 n, 5 b; **5827 (3)**, 1 n, 1 b; **5827 (4)**, 20 n, 42 b, st; **5825 (6)**, 3 n; **5823 (1)**, 2 n, 3 b; **5825 (7)**, 4 n; **5823 (2)**, 3 n, 2 b; **5798 (1)**, 1 n; **5799 (2)**, 7 n.

Bargmannia elongata: **5825 (1)**, 24 n; **5825 (5)**, 7 n, **5825 (2)**, 69 n; **5827 (1)**, 21 n; **5827 (2)**, 9 n; **5827 (4)**, 1 n; 5818 (4), 7 n; 5818 (1), 43 n; 5825 (6), 9 n; **5793 (2)**, 1 n; **5801 (1)**, 20 n; 5806 (1), 1 n.

Physophora hydrostatica: **5816 (4)**, 1 n; **5827 (4)**, 20 n; **5800 (2)**, 8 n, 12 p, st; **5798 (3)**, 1 p; **5795 (3)**, 5 n, 3 p; 5810 (2), 1 n; 5809 (2), 1 n.

Melophysa melo: **5801 (3)**, ?1 n, 6 b.

Forskalia edwardsii: 5825 (6), 2 n; **5798 (3)**, 1 n.

* In this Appendix and Appendix II the station and series numbers are given first (day in bold), followed by the numbers of the individual pieces of the siphonophore found in the hauls. The details for the N113 hauls are listed before those for the IKMT ones.

  b, bract(s); ex, example (pneumatophore + stem, etc.); jn, juvenile nectophore(s); n, nectophore(s); p, palpon(s); st, stem fragment(s).

APPENDIX II

1. The distribution of *Amphicaryon acaule* in the N113 and IKMT horizontal hauls.

5827 (**5**), 4 w, 4 vn; **5828** (**1**), 2 w, 1 vn; **5816** (**7**), 3 w, 1 ln; **5816** (**6**), 1 ln; **5816** (**4**), 2 w, 1 ln; **5816** (**1**), 1 w, 1 vn, 1 ln; **5827** (**1**), 1 w; 5819 (5), 6 w, 6 ln, 2 vn; 5819 (3), 2 w; 5819 (1), 1 w; 5825 (6), 1 w.

5798 (**3**), 15 w, 2 vn; **5795** (**3**), 35 w, 18 vn, 13 ln; **5796** (**4**), 3 w, 1 ln; **5795** (**2**), 2 w, 1 vn; **5796** (**3**), 1 vn; **5793** (**2**), 1 w, 1 vn; **5803** (**1**), 1 ln; **5794** (**1**), 3 w; **5798** (**2**), 2 w; **5794** (**2**), 1 w, 1 vn, 1 ln; **5798** (**1**), 1 w; **5797** (**2**), 1 w, 1 ln; **5801** (**1**), 1 vn, 1 ln; **5813** (**1**), 1 w; 5817 (2), 4 w, 1 vn, 1 ln; 5814 (2), 1 vn, 1 ln; 5806 (3), 1 w; 5793 (3), 1 w, 1 vn; 5810 (2), 2 w; 5809 (3), 1 ln.

ln, larval nectophore; vn, vestigial nectophore; w, whole polygastric phase.

2. The distribution of the eudoxid bracts (eb) of *Rosacea cymbiformis* in the horizontal hauls.

5816 (**7**), 38 eb; **5816** (**4**), 8 eb; 5819 (2), 5 eb.

3. The distributions of the species of *Nectopyramis* in the IKMT oblique hauls.

Nectopyramis diomedeae: **5797** (**2**), 2 n, 2 e; 5807 (2), 1 n; 5810 (1), 1 e.

N. natans: **5794** (**2**), 1 n; **5797** (**2**), 1 eb; **5799** (**2**), 1 eb, 1 ec; **5813** (**1**), 1 ec; 5809 (2), 1 n.

N. spinosa: **5798** (**3**), 1 dn; **5798** (**2**), 1 dn, 4 eb; **5797** (**2**), 1 eb.

N. thetis: **5798** (**3**), 1 e; **5803** (**1**), 1 n; **5794** (**1**), 2 n, 3 e; **5798** (**2**), 6 n, 13 e; **5794** (**2**), 7 n, 10 e; **5798** (**1**), 2 n, 3 e; **5797** (**2**), 4 n, 7 e; **5799** (**2**), 1 n, 3 e; **5796** (**2**), 1 n, 7 e; 5811 (2), 2 e; 5817 (1), 2 e; 5810 (2), 1 n; 5811 (1), 1 e; 5809 (3), 1 n, 3 e; 5807 (2), 1 n, 1 e.

dn, definitive nectophore; e, eudoxid; eb, eudoxid bract; ec, complete eudoxid (bract + asexual swimming bell); n, nectophore.

4. The distribution of the eudoxid phase of *Ceratocymba sagittata* and *Abylopsis tetragona* in the horizontal hauls.

Ceratocymba sagittata: **5816** (**7**), 1 eg; **5796** (**4**), 3 eb, 1 eg; 5817 (3), 1 eb, 1 eg; 5817 (2), 2 eb, 1 eg; 5806 (2), 1 eb.

Abylopsis tetragona: **5828** (**1**), 6 eb, 5 eg; **5816** (**7**), 2 eg; **5816** (**6**), 2 eb, 2 eg; **5816** (**4**), 1 eb, 1 eg; 5819 (1), 1 eb.

5795 (3), 1 eb; 5817 (3), 1 eb, 1 eg; 5817 (2), 2 eb, 1 eg.

eb, eudoxid bract; eg, eudoxid gonophore.

APPENDIX III

Station data for the two series of horizontal IKMT hauls.

Station	Date	Time	Average speed (knots)	Mean depth (m)	Closing depth (m)
		Day			
5801 (3)	21. x. 65	16.09–18.09	2·73	50	o
5801 (2)	21. x. 65	13.42–15.42	2·90	95	60
5800 (2)	20. x. 65	11.10–13.10	2·82	165	110
5798 (3)	18. x. 65	15.20–17.20	2·81	205	160
5795 (3)	15. x. 65	15.11–17.11	2·66	250	210
5796 (4)	16. x. 65	15.15–17.15	2·79	300	260
5795 (2)	15. x. 65	12.11–14.11	2·85	350	290
5796 (3)	16. x. 65	12.15–14.15	2·85	415	360
5793 (2)	13. x. 65	14.08–16.08	2·88	450	350
5803 (1)	23. x. 65	08.15–10.15	2·95	485	435
5800 (1)	20. x. 65	08.11–10.12	2·79	495	460
5794 (1)	14. x. 65	08.20–10.20	2·95	560	450
5798 (2)	18. x. 65	12.06–14.06	2·86	600	475
5794 (2)	14. x. 65	14.20–16.20	2·84	650	550
5798 (1)	18. x. 65	08.21–10.23	2·89	700	575
5797 (2)	17. x. 65	14.26–16.26	2·87	775*	650
5799 (2)	19. x. 65	15.13–17.13	2·88	800	675
5796 (2)	16. x. 65	08.35–10.35	2·86	875	700
5801 (1)	21. x. 65	08.37–10.37	2·78	930	800
5813 (1)	10. xi. 65	08.27–10.27	2.84	950	800
		Night			
5817 (3)	15. xi. 65	01.44–03.44	2·88	70	o
5817 (2)	14/15. xi. 65	23.16–01.16	2·73	110	50
5814 (2)	11/12. xi. 65	22.45–00.45	2·75	150	110
5806 (3)	4. xi. 65	02.10–04.10	2·92	200	150
5814 (1)	11. xi. 65	19.58–21.58	2·89	250	210
5806 (2)	3/4. xi. 65	23.18–01.18	2·83	310	250
5803 (2)	23. x. 65	20.15–22.15	2·93	350	310
5806 (1)	3. xi. 65	20.05–22.05	2·98	415	350
5793 (1)	13. x. 65	20.34–22.34	2·95	435	350
5805 (1)	2. xi. 65	20.08–22.08	2·86	490	460
5811 (2)	8/9. xi. 65	23.48–01.48	2·83	565	510
5817 (1)	14. xi. 65	20.15–22.15	2·81	580	480
5810 (2)	8. xi. 65	00.52–02.52	2·75	615	500
5811 (1)	8. xi. 65	20.15–22.15	2·89	710	600
5809 (3)	7. xi. 65	01.20–03.20	2·78	750*	600
5807 (2)	5. xi. 65	00.23–02.23	2·87	800	700
5809 (2)	6. xi. 65	20.40–22.40	2·75	900	800
5810 (1)	7. xi. 65	20.37–22.37	2·81	925	800

* Depth estimated.

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