THE DISTRIBUTION OF SIPHONOPHORES IN A TRANSECT ACROSS THE NORTH ATLANTIC OCEAN AT 32 °N

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Abstract: A study has been made of the distribution of siphonophores in a series of twelve oblique (0–1000 m) hauls made in a transect across the North Atlantic at 32 °N, from 16 °W to 60 °W. A total of 66 species was identified, of which twelve were physonect siphonophores and the remainder calycophorans. In order to assess the changes in the population of the nineteen most abundant species, the species correlation coefficient matrix was calculated and six factors were extracted and rotated to simple structure. The first two factors indicated a clear east–west trend in the distributional pattern for thirteen of these siphonophore species. The coefficient of proportional similarity between stations was also calculated using the data for all of the species present.

From this it was possible to divide the stations into two clear zones, namely the first three and the last eight, while the fourth station was intermediate. A comparison of these results with the TSD data for these stations showed that the fourth station was in the transitional zone between the eastern North Atlantic water and that characteristic of the Sargasso Sea, and that these two major water masses were distinguishable at all the depths where siphonophores would be expected to be found. It is concluded that there was some interrelationship between the physical features of the separate water masses and the composition of the siphonophore populations found in each. The problems involved in deciding on a sampling programme for such a study as this are also discussed.

INTRODUCTION

In recent years much work has been carried out to try to understand some of the factors which may affect or determine the observed patterns of geographical distribution of pelagic and planktonic animals in the world's oceans. The factors involved are clearly diverse, but the principal features which have been studied are the physical and chemical characteristics of water masses. The principal of subdividing the oceans into various water masses was firmly established by Sverdrup, Johnson & Fleming (1942) and is based principally on their temperature/salinity relationships, although many other factors have subsequently been included (*cf.*, McGowan & Williams, 1973). The earliest attempts to establish species distribution patterns for some plankton groups, as reviewed by McGowan (1971), merely subdivided the oceans into major regions and subregions of warm and cold water. It was not until the work of Sverdrup *et al.* (1942) that attempts could be made properly to correlate these distributional patterns with physically defined water masses, rather than with temperature alone. The principal studies which have been carried out along these latter lines include Pickford (1946) for the cephalopod, *Vampyroteuthis infernalis*; Haffner (1952) for the fish genus, *Chauliodus*; David (1958) on Antarctic and Bieri (1949) on Pacific chaetognaths; McGowan (1960) on the aberrant polychaete, *Poeobius meseres*; and Brinton (1962) on Pacific euphausiids. A review of this earlier literature is given by Banse (1964).

The geographical distribution of mesopelagic fishes within various waters has been particularly well studied. Ebeling (1962) and Ebeling & Weed (1963) have studied the worldwide distribution of melamphaid fishes from the Dana collections, and Backus et al. (1965, 1969, 1970) have considered the mesopelagic fishes particularly in the western North Atlantic Ocean. These latter authors have analysed their data statistically and have been able to show some clear trends for the distribution of certain fish species within the various identifiable water masses. The possible disadvantages of their sampling method will be discussed later. Fager & McGowan (1963) studied the multispecies group selection of four zooplankton taxa, namely euphausiids, chaetognaths, pteropods, and heteropods in the North Pacific Ocean. They were able to show that certain species from the various taxa tended to have a strong group selection for individual water masses. These, and other data, have shown, as McGowan (1971) states, that there is a remarkable amount of agreement between the position and shape of the distributional boundaries of species from various zooplankton taxa and that these distributions are almost identical with the boundaries of the water masses.

More recently, Foxton (1971/72) has considered the vertical distributions of species of the decapod genus *Acanthephyra* from a line of Discovery stations in the eastern North Atlantic. He was able to show a strong association between the geographical distribution of the various species and the principal water masses of the North and South Atlantic Ocean and also that in the mesopelagic zone the observed variations in the depth ranges of each species were associated with the geographical gradients of temperature. Angel & Fasham (1975) and Fasham & Angel (1975) have carried out an analysis of the ostracod data derived from the same line of Discovery stations. They have analysed the vertical and geographical distributions of the abundant species. Using principal components analysis, they have been able to delineate species communities and to associate some of the species groupings or assemblages with certain water masses. These assemblages may not always be distinguishable on the basis of their temperature–salinity relationships but are clearly differentiated on a geographical basis.

The information on the geographical and vertical distribution of siphonophores is rather scattered. Bigelow & Sears (1937) were the first to make any concerted effort at an understanding of the vertical distribution of siphonophores, and more recent work, e.g., Moore (1949, 1953) and Pugh (1974), has increased our knowledge on this subject considerably. Alvariño (1971) has collected together much of the earlier information on the geographical and vertical distribution of siphonophores, particularly for the Pacific Ocean. From these data one is able to conclude that, with a few exceptions where certain species appear to be restricted to polar regions or to the Mediterranean, most siphonophore species are cosmopolitan. Alvariño considered that the distributional patterns of siphonophores do not correspond with water masses but that they may be related to the depths of certain isotherms; however, some preliminary work has recently been published in which an attempt

has been made to relate the distribution of siphonophores to water masses. Musayeva (1971) concluded that in the eastern Indian Ocean siphonophores lived mainly in regions where there was a rapid change of temperature with depth, *i.e.*, in the thermocline, and to some extent in the mixed layer. Margulis (1972) has attempted to draw composite maps for the distribution of siphonophore species in the Atlantic Ocean but has only made subdivisions into boreal, tropical, and equatorial forms.

This present paper describes the distribution of siphonophores at latitude 32 °N across the North Atlantic Ocean. The animals were derived from a series of twelve oblique (0–1000 m) hauls. Since most of the species found were cosmopolitan, the data were subjected to factor analysis to determine whether there was any change in the siphonophore population as a whole across this transect.

METHODS

A series of twelve successful oblique hauls, from 0 to 1000 m, were made from *R.R.S. Discovery* using a RMT 1+8 combination net (Baker, Clarke & Harris, 1973) across the Atlantic Ocean on approximately 32 °N. Details of these hauls are given in Table I and their positions are given in Fig. 1. The hauls were all carried out at

TABLE I

Station data: *some difficulty in closing net: + TSD only.

Haul No.	Station	Start Position		Date 1973	Time GMT	Duration of haul (min)
		Lat. °N	Long. °W			
1	8262	32°05.2′	16°13.7′	24.ii	21.11–23.25	134*
2	8263	32°05.9′	20°26.1′	25.ii	22.36–00.39	123
3	8264	32°11.2′	23°49.2′	26.ii	22.16–00.19	123
4	8265	32°01.0′	27°12.1′	27.ii	21.36–23.29	113
4A	8267+	32°04.0′	30°39.7′	28.ii	–	
5	8270	32°00.5′	34°22.7′	1.iii	22.35–00.45	130
6	8271	31°58.0′	39°02.4′	2.iii	22.56–00.57	121
7	8272	31°57.7′	43°37.4′	3.iii	23.13–01.27	134
8	8274	31°58.2′	47°18.5′	4.iii	23.43–01.50	127
9	8275	32°01.4′	50°33.5′	5.iii	23.39–01.50	131
10	8276	31°55.8′	54°05.0′	6.iii	23.45–01.48	123
11	8277	32°05.4′	57°40.0′	8.iii	00.04–02.25	141
12	8279	32°21.7′	60°23.6′	8.iii	23.36–01.35	119

night at approximately the same local time and the same procedure was adopted for all. The combination net was lowered over the side of the ship and opened at the surface using the acoustic release system. The warp was then payed out at ≈ 0.5 m/sec *i.e.*, 1 knot, and the depth of the net monitored *via* the signals received by the echo-sounding Mufax on board ship (see Baker, Clarke & Harris, 1973, for a detailed explanation). By timing the interval between the flow counts originating from an

impeller device mounted beside the net monitor, it was possible to regulate the speed of the ship so that the nets themselves were towed at 2 kt, the standardized speed for all our combination nets; a ship's speed of 2.5–3 kt was usually required to overcome the effects of paying out.
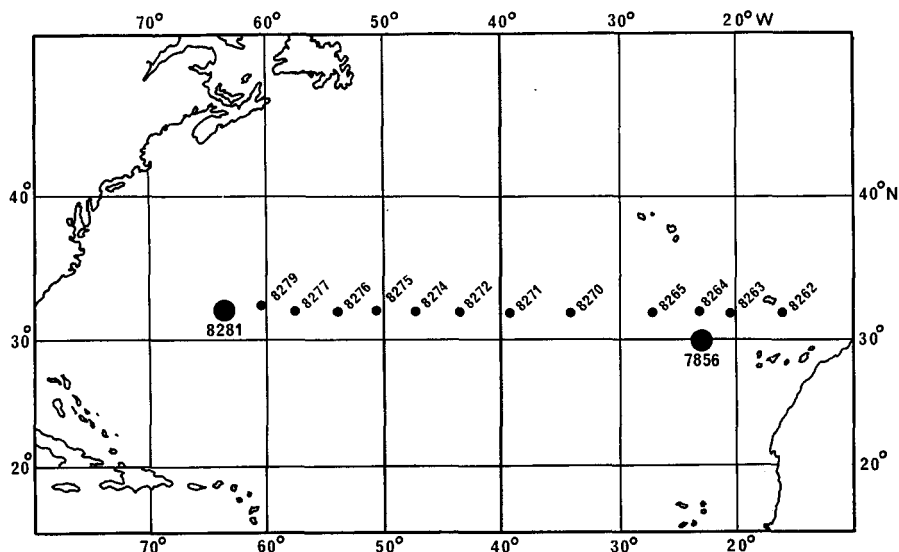

Fig. 1. Station positions.

When the nets reached a depth of 1000 m paying out was stopped and the second acoustic release operated, thereby closing the nets. These were then recovered and the catches preserved in 5 % formalin in sea water. The hauls were carried out on consecutive nights (the acoustic release gear mechanism failed to operate correctly at Station 8267-8 and so the catches were discarded) and each haul was preceded by a TSD (temperature/salinity/depth) profile from 0 to 1000 m.

RESULTS

The siphonophores from the RMT 8 catches only were separated and identified, and the data are presented in the Appendix. Factor analyses of the results were very kindly carried out by Dr M. J. R. Fasham, using his programmes and following the procedures outlined in Angel & Fasham (1975).

A total of 66 species of siphonophores were identified from the twelve hauls. Of these species, twelve were physonects and the remainder calycophorans. (For an explanation of the terminology and system of classification of siphonophores see Totton, 1965). Among these species there are three which have hitherto been undescribed, and several records of rare species including *Desmophyes annectens* [1]

[1] For all taxonomic authorities, see Appendix pp. 94–97.

and a single specimen of the eudoxid bract of *Thalassophyes crystallina*. The presence of several eudoxid and polygastric stages of *Clausophyes massiliana* is of great interest since they have hitherto only been described from the Planier canyon near Marseilles in the Mediterranean. Indeed, this species appears to be not uncommon in the eastern North Atlantic Ocean and is the new species mentioned by Totton (1954) from Discovery Station 2084 (28°53′S : 13°20′E).

Many of the commoner siphonophores were found in all of the hauls, although they usually showed some distinct change in abundance during the course of the transect. Thus, the commonest species, *Eudoxoides mitra*, of which 1815 anterior nectophores were isolated, clearly had its maximum distribution to the west since 335 nectophores were found in the last haul compared with one in the first. In contrast, the next most common species, *Chelophyes appendiculata*, had its maximum distribution (453 anterior nectophores) in the first haul with considerably reduced numbers in the last.

In order to assess these changes in species population more fully, the data were subjected to statistical analysis. In a series of papers Angel & Fasham (1973, 1974, 1975) have shown that multivariate methods and especially factor analysis are useful for the interpretation of large amounts of plankton distributional data. The data used in those particular cases were derived from horizontal tows but the methods are equally applicable to oblique hauls. A species correlation coefficient matrix for the nineteen most abundant species has, therefore, been calculated. These species are indicated by asterisks before their names in the appendix and are referred to in Tables II and IV. With the exception of *Ceratocymba sagittata*, the abundance of the asexual, polygastric phase is referred to, but for *C. sagittata* it is the sexual, eudoxid phase which is considered.

From the analysis, six factors were extracted and rotated to simple structure (see Angel & Fasham, 1975, for a detailed description of the statistical methods). This analysis produces two matrices – the factor loading and the factor score (see *e.g.*, Harman, 1967). In ecological terms species with similar patterns of distribution will have high factor loadings on the same factor. Thus, the factor loading matrix may be used to group species by assigning them to the factor on which they have their highest loading. The rotation to simple structure ensures that most species have a high loading on only one factor. If, however, a species distribution is intermediate between two factor types it will have loadings of the same magnitude on both factors. Having thus assigned a species to one particular factor, the factor scores will represent an 'average' distribution pattern for the species which have a high loading on that factor.

The six species groups which were extracted from the factor analysis are given in Table II, and the factor scores for each group are plotted in Fig. 2. The units of the figure are standardized scores, *i.e.*, in units of the standard deviations of the log transform of the original data. The first factor or group has three species with a high positive loading and two with high negative loadings. Such factors with positive and

negative loadings are called bipolar and indicate that the species tend to be mutually exclusive; hauls with large numbers of species with high positive loadings will tend to contain small numbers of those with high negative loadings. In this particular case, the factor scores (Factor 1, Fig. 2) show that the species with positive loadings were found mainly in Hauls 1, 2, 3, and 5, while those with negative loadings occurred in Hauls 8, 9, and 10. This factor shows, therefore, an east–west trend.

TABLE II

The species groupings and maximum factor loadings for the factor analysis of the species inter-relationships.

Group	Species	Max. loading
1⁺	*Chelophyes appendiculata*	0.86
	Amphicaryon acaule	0.75
	Ceratocymba sagittata	0.73
1⁻	*Abylopsis eschscholtzii*	−0.80
	Hippopodius hippopus	−0.58
2⁺	*Rosacea* sp.	0.93
	Vogtia spinosa	0.87
	Clausophyes ovata	0.68
	Lensia multicristata	0.65
2⁻	*Abylopsis tetragona*	−0.80
	Vogtia glabra	−0.78
	Lensia fowleri	−0.69
	Eudoxoides mitra	−0.62
3	*Bassia bassensis*	0.92
	Vogtia serrata	0.58
4	*Chuniphyes multidentata*	0.94
5	*Eudoxoides spiralis*	0.84
	Diphyes bojani	0.68
	Eudoxoides mitra	0.60
6	*Lensia conoidea*	0.95

Factor 2 is also a bipolar factor having four species with high positive and four species with high negative loadings. As the factor scores show (Fig. 2) this factor has an even more pronounced east–west trend, with a transition point between Hauls 4 and 5 (Stations 8265 and 8270). This is precisely the distributional pattern noted from the raw data for the commonest siphonophore in this series, *Eudoxoides mitra*. It is somewhat surprising, therefore, that this species does not have a very high factor loading (0.62) for Factor 2 and that it appears again with only a slightly lower loading (0.60) in Factor 5 which indicates a peak of distribution in Hauls 2–5 and 10–12. The numbers for this species were at their lowest in Hauls 1 to 5 and Haul 6 had more than twice the number of anterior nectophores present as did Haul 5. The fact that this species does appear in Factor 5, although not with a very high loading, is possibly because of the very low numbers of nectophores found in Haul 1; of the two other species assigned to Factor 5 one, *Eudoxoides spiralis*,

was absent from the first haul and the other, *Diphyes bojani*, was represented by only two anterior nectophores. In these two latter cases the factor scores in Group 5 fit the raw distributional data very well and so it appears that the near absence of all three species in the first haul has led to their being grouped together.
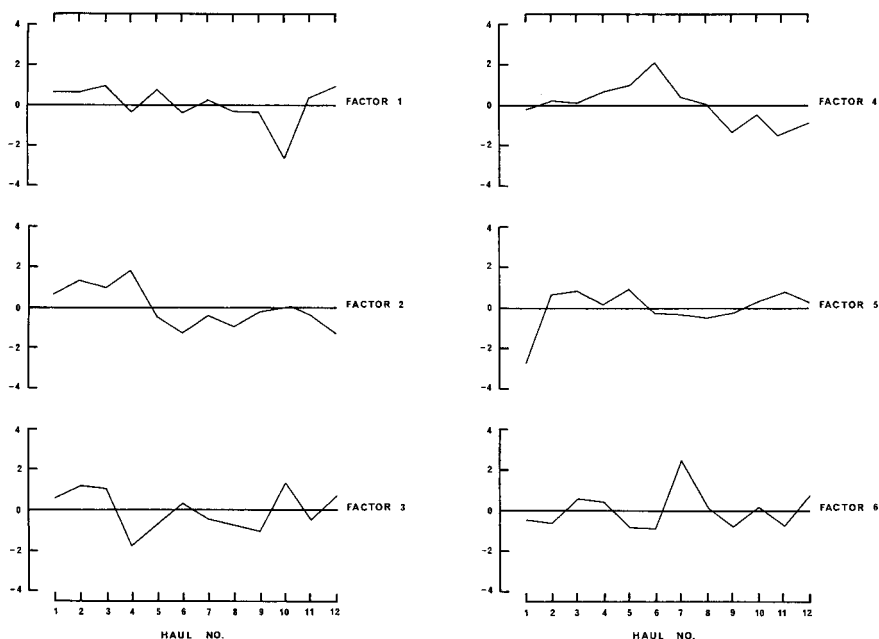

Fig. 2. Factor scores for the six factors extracted from the correlation coefficient matrix for the nineteen most abundant siphonophore species: individual species are given in Table II: standardized units.

None of the remaining factors show any systematic east-west trend. Two species, *Vogtia serrata* and *Bassia bassensis*, have high loadings on Factor 3 and are caught mainly at the two ends of the transect. Factors 4 and 6 contain only one species, each of which has a high loading, although in Factor 4 *Chuniphyes multidentata* does appear to show some east-west trend being commoner in the former but with a maximum of abundance in the mid-Atlantic. Thus, although the results for Factors 3 to 6 are somewhat confused it is clear that this method of species correlation, which has assembled more abundant species into groups with similar patterns of distribution, demonstrates that at least two of the groups (1 and 2) have an east–west trend. These two factors in fact encompass thirteen (including *Eudoxoides mitra*) of the nineteen species subjected to this analysis.

Another way of studying the changes in a population of animals along a given transect is to analyse the matrix of correlations between the stations based on the observed abundances of all the species present. In this case the similarity between stations was calculated using the coefficient of proportional similarity (Imbrie & van Andel, 1964) rather than the straightforward correlation coefficient. Ninety-four

entities were used in the analysis, the eudoxid, sexual stages from 28 of the 66 species present being treated separately from the asexual, polygastric phase, which was found for all the species. The calculated factor loadings on the first three rotated factors are shown in Table III. On the basis of these loadings it is possible to divide the series of stations into two major zones, Hauls 1 to 3 being in the first zone and Hauls 5 to 12 in the second, while Haul 4 is intermediate. Thus, there is also a clear indication of an east-west trend in the siphonophore population from these station interrelationships as well as from the first two factors in the species correlation analysis. From Fig. 2 it may be seen that it is the eight species in Factor 2, showing a change over between Hauls 4 and 5, which contribute most to the zonation detected by the analysis of the station correlations.

TABLE III

The factor loadings for the first three rotated factors derived from the analysis of the station interrelationships.

Haul	Station	Factor		
no.	no.	1	2	3
1	8262	0.30	0.91	0.20
2	8263	0.43	0.78	0.25
3	8264	0.46	0.59	0.44
4	8265	0.46	0.38	0.77
5	8270	0.77	0.39	0.38
6	8271	0.78	0.35	0.29
7	8272	0.75	0.36	0.38
8	8274	0.82	0.29	0.35
9	8275	0.81	0.36	0.31
10	8276	0.68	0.27	0.25
11	8277	0.85	0.40	0.19
12	8279	0.82	0.37	0.22

Finally, and to a minor extent, some possible indication of an east-west change in the population of siphonophores comes from a comparison of the volumes of these animals isolated from each haul (Fig. 3). The volume of siphonophores in the first two hauls (Stations 8262 and 8263) was considerably larger than in any of the other hauls. Hauls 3 to 6 were intermediate while the volumes in the remaining six hauls were comparatively low. Unfortunately no data for the total volume of each catch are available, but there is some indication that the later hauls were larger in volume than the more easterly ones. This would indicate a considerable change in the percentage contribution of siphonophores to the catch volume, being high in the easterly stations and very low in the westerly ones. Since these volumes were estimated on preserved samples it is difficult to relate them back to their true 'live' volume because of shrinkage during preservation (Ahlstrom & Thrailkill, 1963). This shrinkage is generally large for siphonophores and so it is probable that the volume percentage

of siphonophores in the more easterly catches was considerably larger than in the more westerly ones. Although the first haul (Station 8262) had the lowest number of siphonophore species, there is no general indication of a change in the total species number for any of the hauls (Fig. 3).
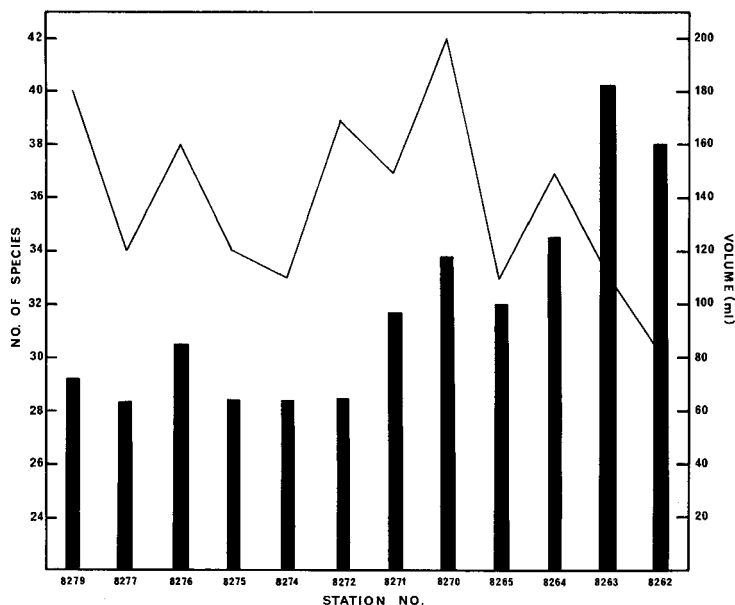

Fig. 3. The volume (histograms) and number of species of siphonophores found in each haul.

DISCUSSION

It is difficult to decide on the type of sampling programme which should be adopted when one is considering a short term study of the geographical distribution of zooplankton. Backus *et al.* (1965, 1969) have criticized the 'classical' programme of midwater trawling whereby a rigid scheme of arbitrarily chosen depths is followed, considering it to be unsatisfactory and without any rational basis. They point out that with this procedure only one environmental property is likely to be held approximately constant, namely, pressure. This factor is considered to be of little significance to midwater animals in comparison with others such as temperature, ambient light level, dissolved oxygen content, etc., many of which may vary considerably during such a transect as reported here. They carried out their sampling programme on the basis of the depth of the deep-scattering layer and, in shallower depths, its associa-tion with critical points on a temperature–depth curve, as derived from bathythermo-graphs. This type of sampling is useful to ichthyologists since there is clear evidence for an association between the distributions of certain fishes and these layers; to obtain a large number of fish it would be best, therefore, to trawl these depths. Even so, unless all the hauls are carried out either by day or by night, there will be

a tendency to mix together the deeper living non-migrant species, which will be caught only during the day, with the migrant species, which will be caught both by day and by night. This could cause some confusion when the data are subjected to statistical analysis, particularly of the 'first and last capture' type which was used by these authors.

Banse (1964) has also recommended that fishing nets between standard depths should be abandoned and that hauls should be made in relation to the thermal structure of the water. It is unlikely, however, that any single factor will be solely affecting the depth distributions of the zooplankton. Furthermore, Moore & Corwin (1956) have shown that the vertical distribution patterns of several zooplankton species can be modelled on the interaction of three factors, namely light, pressure and temperature. Even this, however, may prove to be simplistic. Temperature may control the limits of the vertical distribution of both migrant and non-migrant species, while some other factor such as light intensity may regulate the distributional patterns within these limits. The response of some species to sharp discontinuities are, perhaps, examples of this behaviour (Banse, 1964), but the discontinuities may be haloclines, or even biological ones as in toxic blooms. Moreover, Moore (1949) has demonstrated that the depth to which certain siphonophore species migrate at night is affected by moonlight. Since siphonophores have no well-developed light-sensing organs, it would seem probable that this effect may be caused by a complicated biological interaction between the siphonophores and their prey.

One of the disadvantages of fishing on isotherms is that it is liable to give a false impression that the animals are responding solely to temperature. This may not be the only factor which affects the occurrence of a species on an isotherm which, for instance, is at different depths in two localities. Light intensity or biotic factors may be playing more significant rôles. Alternatively, the species may have a broad vertical distribution which embraces both the depths sampled. Fishing isotherms also requires careful controls if one is to avoid including the answer into the sampling design. For instance, the hauls should all be carried out at the same time of day so as to overcome the fact that the specific composition and structure of the zooplankton population at a single depth constantly varies throughout a 24-h period (Roe, 1974). Even so, the light intensity at a given depth may vary from day to day and this could affect the population. Sophisticated fishing techniques are also required, involving opening/closing net systems and continuous *in situ* temperature monitoring (*e.g.*, Baker *et al.*, 1973). It is preferable to sample the whole water column, at least to 1000 m, with a series of discrete depth horizontal hauls and thereby build up a complete picture of the depth distributions of the populations present. This procedure is time consuming and if time limits the sampling programme then oblique hauls over the complete potential depth horizon should be employed, which implies that the chances of catching a species are as consistent as possible between hauls and that variations in the species composition and relative abundances are more likely to be representative of the total water column.

The present series of hauls was designed to sample the more abundant species from a wide variety of zooplankton taxa. Since the relationships between the horizontal or vertical distributions of many of these groups and the various physical factors are not understood, it was decided to maintain the 'classical' style of sampling over a constant depth range since time did not allow a more detailed sampling programme. It is interesting to note that the majority of the siphonophore species which show the most significant changes across the present east–west transect (Groups 2, Table II & Fig. 2) are deeper living forms (Pugh, 1974 and unpubl.) and include *Clausophyes ovata* which is generally found between 600 and 1000 m. These species would not have been taken at all if, on the assumption that most siphonophores live in the top 250 m and that they are often associated with the thermocline (Musayeva, 1971), a shallow isotherm had been fished.

Factor analysis was applied to the present data because as McGowan (1971) points out, this form of principal component analysis is particularly useful for studying sets of samples where all the entities are almost always present. This is certainly the case where most of the common siphonophore species are cosmopolitan. If this were not the case then other statistical methods should be employed. Backus *et al.* (1965) introduced the method of "first and last captures" since for them it was a much better way of considering the distribution of fishes in the North Atlantic, and showing the differences which occur between the various water masses.

It is interesting to compare the distributions of the siphonophore populations which result from this principal component factor analysis with the temperature and salinity structure of the water at the various stations sampled. The distribution of the isotherms, together with the smoothed bottom profile, along the 32 °N transect is shown in Fig. 4. It is seen from this that there is a marked change in the temperature structure of the water between Stations 8267 and 8270, *i.e.*, between 30 and 35 °W. The isotherms down to 750 m become much deeper to the west of this region and there is a thick band of water with a temperature between 17 and 18 °C. Below 750 m the isotherms to the west become more densely spaced while those in the east are widely spread. This results in the water at 1000 m being 2 °C colder to the west.

The temperature and salinity structure of the water column at Stations 8270 to 8279 shows features typical of the Sargasso Sea. There is an abundance of the characteristic 18 °C-water, as described by Worthington (1959). Worthington places the eastern limit of the Sargasso Sea at about 40 °W, but the present data seem to indicate that it extends slightly further east to about 35 °W. The transition between the two clearly distinguishable water masses is seen slightly to the west of the 'Azores branch' of the Mid-Atlantic Ridge and the typical structure of the Sargasso Sea water, at least in the top 1000 m appears to be well established by 35 °W.

To investigate further the possible relationships between the observed populations of siphonophores and the physical structure of the Sargasso Sea and eastern North Atlantic water masses, the T/S relationships have been plotted in Figs 5 and 6 for specific depths from all the TSD stations of the present transect. It is generally found
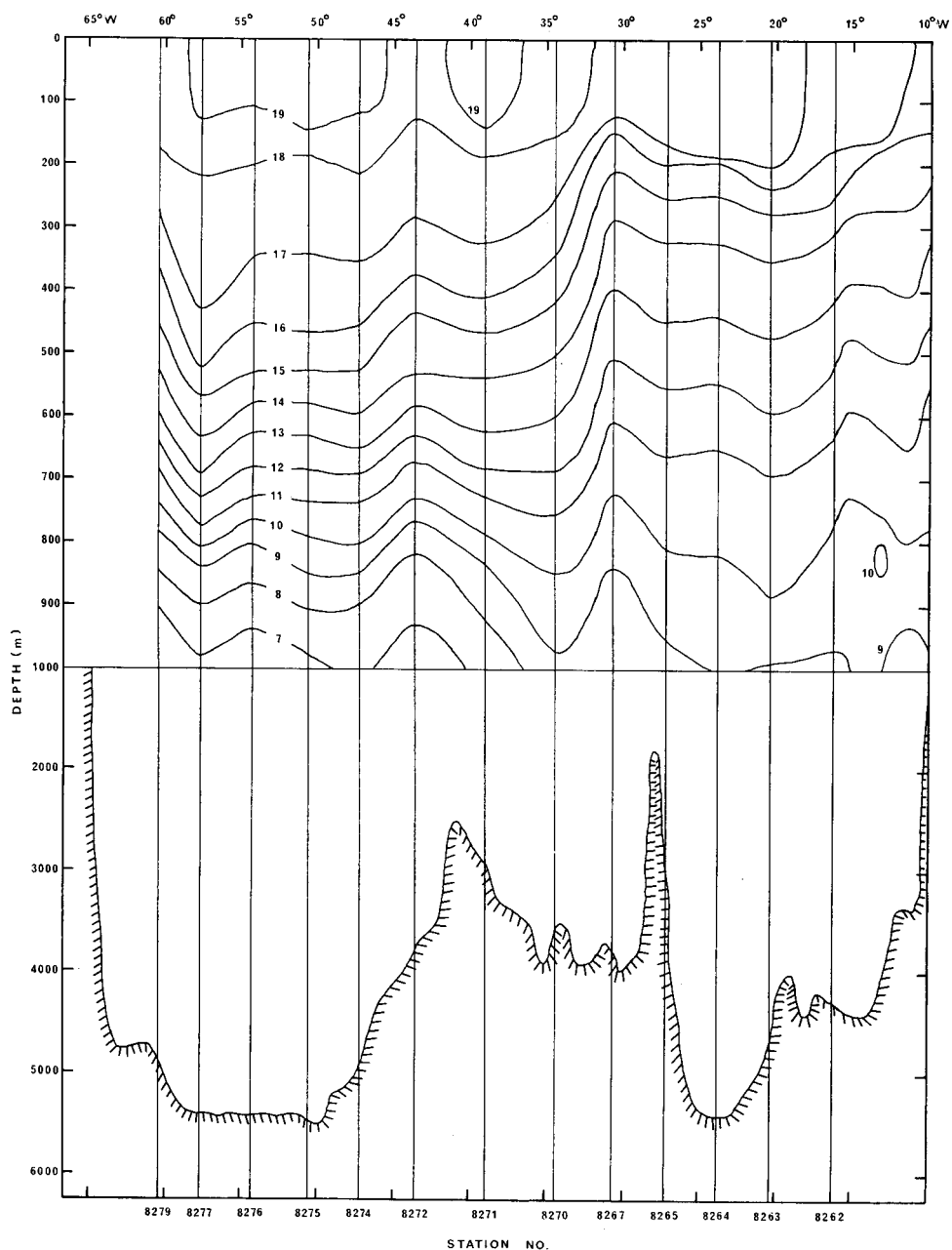
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Fig. 4. The distribution of isotherms and the smoothed bottom profile along the 32 °N transect: positions of the stations indicated.

that the majority of siphonophores live in the upper 250–300 m of water and so the temperatures and salinities at 100 and 250 m have been plotted in Fig. 5. At 250 m the Sargasso Sea water is clearly distinguishable from the eastern North Atlantic Water by its higher salinity and temperature. There is an indication at 100 m that Stations 8265 (Haul 4) and 8267 could be separated as intermediate between the two water masses. It would appear, therefore, that if there were any relationship between the species and numerical composition of the siphonophore population and the various water masses, the distinction of the intermediate zone at Station 8265, based on the factor analysis of the station interrelationships (see Table III), would mainly be due to the shallow living forms. The factor analysis of the individual species distributions of the commoner siphonophores does not indicate any one species which can be related absolutely with this zone, and the situation obviously reflects a much more complex interrelationship between all the species.
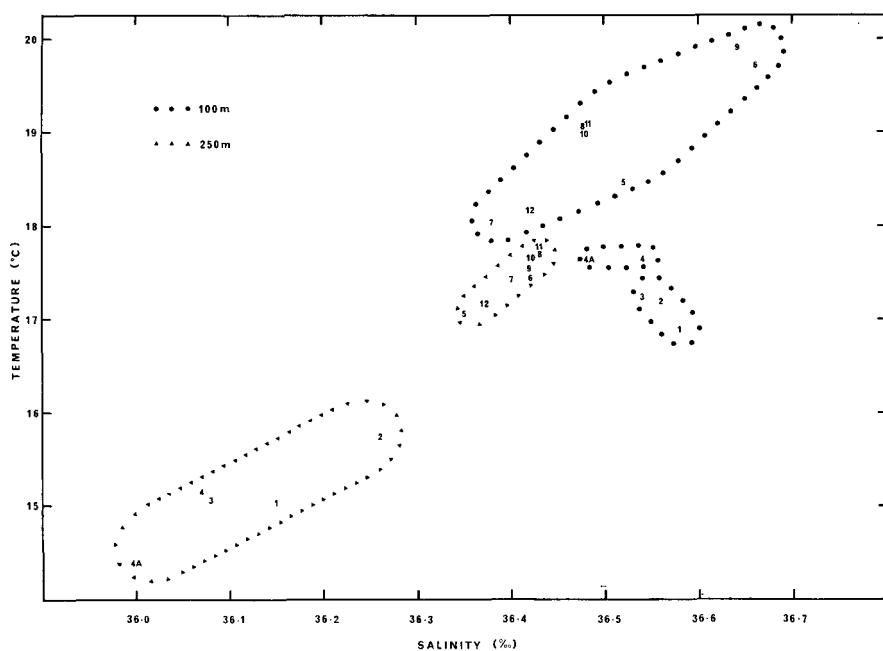

Fig. 5. The temperature/salinity relationships at 100 m and 250 m for all the stations in the 32 °N transect: numbers represent the haul numbers (see Table I).

It was noted earlier that the majority of species, five out of eight, in Group 2 of the factor analysis (see Table II) which show a clear east–west trend in their distributions, are deeper living forms. Consequently the T/S relationships for the waters at 500 and 800 m from all the stations have been plotted in Fig. 6. These depths roughly represent the limits of the vertical distributions of these deeper living species. Four of these, *Rosacea, Vogtia spinosa, V. glabra* and *Lensia multicristata*, live mainly

in the 500–600 m range. The T/S diagram for 500 m shows a clear distinction between the two major water masses with the intermediate zone associated with the easterly stations. This is in accordance with the factor analysis for Group 2 species where the transition in the populations is between Stations 8265 and 8270 (Fig. 2).

Clausophyes ovata lives at depths of about 800 m or deeper, and at 800 m it may be seen that the Sargasso Sea and eastern North Atlantic waters are becoming less distinct; however they are still distinguishable, especially if Stations 8267 and 8270 are treated as transitional. Thus it does appear that there is some relationship between the physical features of the two water masses and the composition of the population found within them. It would also appear that if an arbitrary isotherm had been sampled this relationship would not be so evident since not only would the number of species caught have been considerably less but it may have confused the interrelationships which clearly exist between the species, especially congeneric ones, throughout the water column (see Pugh, 1974).
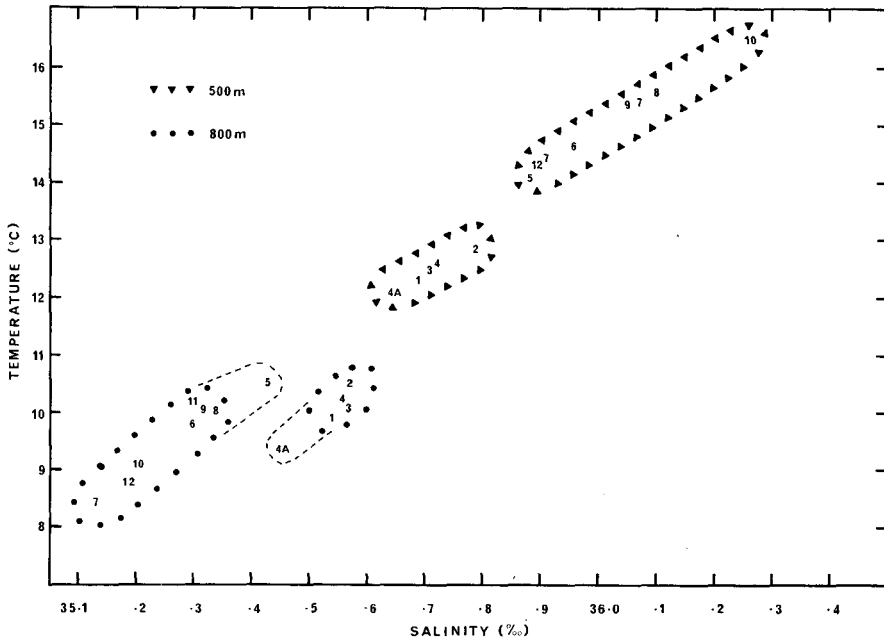

Fig. 6. The temperature/salinity relationships at 500 m and 800 m for all the stations in the 32 °N transect: numbers represent the haul numbers (see Table I).

The evidence that there is a transition in the composition of the siphonophore population from east to west is further borne out by an analysis of the vertical distributions of these animals at two comparable stations on either side of the North Atlantic Ocean. A complete analysis of the vertical distribution of siphonophores by day and by night, has been carried out at Discovery Stations 7856 (30 °N: 23 °W)

and 8281 (32 °N: 64 °W). For an outline description of the sampling programme reference should be made to Baker *et al.* (1974). The total number of individuals of the nineteen species considered here, caught at night in all the hauls in the top 1000 m from these two vertical series has been calculated. The ratios of these numbers (east : west) are given in Table IV, together with the factor group to which each of

TABLE IV

A comparison of the ratios of the species distributions in the eastern and western North Atlantic with the species groupings derived from the factor analysis: + the total numbers of individuals found for each species at Stations 7856 (30 °N: 23 °W) and 8281 (32 °N: 64 °W) in the night time series of hauls down to 1000 m have been used in the calculation of these ratios: * see Table II.

Species	Ratio E:W[+]	Factor grouping*	
Lensia multicristata	11.19	2+	
Clausophyes ovata	11.17	2+	Eastern
Vogtia spinosa	5.57	2+	spp.
Rosacea sp.	5.03	2+	
Chuniphyes multidentata	4.07	4	
Amphicaryon acaule	1.99	1+	
Ceratocymba sagittata	1.91	1+	
Vogtia serrata	1.85	3	
Chelophyes appendiculata	1.59	1+	
Hippopodius hippopus	1.23	1−	
Vogtia glabra	0.60	2−	
Abylopsis eschscholtzii	0.58	1−	
Bassia bassensis	0.45	3	
Diphyes bojani	0.35	5	
Eudoxoides spiralis	0.31	5	
E. mitra	0.26	2−/5	
Lensia conoidea	0.21	6	
Lensia fowleri	0.08	2−	Western
Abylopsis tetragona	0	2−	spp.

these species was assigned in the present analysis. It may be seen that those species which were placed in Group 2 and so show the most distinct east–west trend have, with the exception of *Vogtia glabra*, the most extreme ratios of total numbers from the two vertical series. The species with a positive loading have the highest ratios indicating that they are eastern forms and, conversely, those with negative loadings have the lowest ratios and are western forms. The species in Groups 1 and 3 are intermediate, the factor analysis indicating that the species have a similar distribution on either side of the Atlantic. The ratios from the two detailed stations indicate that alhough there are some differences, the species in Groups 1 and 3 are less than twice as common on one side of the Atlantic as the other. The single species in Group 4, *Chuniphyes multidentata*, appears from the data of the vertical series to be pre-

dominantly an eastern form, and this is in accord with its factor scores (Fig. 2) although these data indicate that it has a maximum abundance in the mid-Atlantic. The Group 5 and 6 species are mainly western Atlantic species. These two sets of data, the two vertical series and the transect of oblique hauls, show good agreement and the close connection between the east/west ratios and the various species groupings is of particular significance.

Sverdrup, Johnson & Fleming (1942) divided the North Atlantic Ocean into two principal water masses, namely, the North Atlantic Central Water with a nearly straight line T/S curve between $T = 8$ °C, $S = 35.10^0/_{00}$ and $T = 19$ °C, $S = 36.70$ $^0/_{00}$, and a deep bottom water mass. The T/S relationships shown in Figs 5 and 6 indicate that the waters at the particular depths chosen would fit into this pattern. It appears, however, from the present results that the temperature/salinity/depth relationships of the waters studied in this 32 °N transect may have some relationship to the composition of the siphonophore population. On this transect it is possible to subdivide the Central Water into two major divisions, namely, the Sargasso Sea, characterized by the 18 °C water, and the eastern North Atlantic Water. This latter water mass is undoubtedly of a composite nature since in the deeper regions, around and below 1000 m, the influence of Mediterranean water can clearly be seen. Backus *et al.* (1970) commented on the boundary circumscribing the Sargasso Sea both as a physical feature and as a faunal boundary for fish populations.

Alvariño (1971) concluded that the distributional pattern of siphonophores did not correspond to the water masses, but might be better correlated with the depths of certain isotherms. The present study, however, whilst not precluding the possibility that the depths of certain isotherms may be limiting to a certain siphonophore species, seems to indicate that it is the more complex interrelationships of the physical features of the separate water masses which may be more important. Clearly the conclusions which may be reached from such a study as this are very tentative. To understand more fully the factors which may influence the vertical and geographical distributions of the zooplankton a much more thorough sampling programme is required. It is thus hoped that a detailed analysis of the siphonophore data from a series of Discovery stations in the eastern North Atlantic, similar to that of Angel & Fasham (1975) will shed more light on this subject.

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APPENDIX

THE DISTRIBUTION OF THE INDIVIDUAL SPECIES OF SIPHONOPHORES IN THE HAULS

an, anterior nectophore; b, bract; dn, definitive nectophore; eb, eudoxid bract; ec, complete eudoxid; eg, eudoxid gonophore; gz, gastrozooid; lb, larval bract; ln, larval nectophore; n, nectophore; pn, posterior nectophore; st+pn, stem+ pneumatophore; vn, vestigial nectophore; w, whole polygastric stage.

Physonect sp.: *8262*: 18n, 2St+pn; *8263*: St+pn; *8271*: St+pn.

Physonect C: *8262*: 1n; *8270*: 6n; *8271*: 13n; *8272*: 9n; *8274*: 8n, 1 1b; *8275*: 21n; *8276*: 26n, 2 1b; *8277*: 3n; *8279*: 18n.

Apolemia sp.: *8262*: 5n St+pn; *8264*: 7n; *8271*: 10n; *8276*: 12n; *8279*: 1n.

Agalma okeni Eschscholtz: *8263*: 21n, 9b, St+pn; *8264*: 62n, 35b; *8265*: 16n; *8270*: 31n, 52b, 2 St+pn; *8271*: 18n, 48b, St+pn; *8274*: 135n, 106b, St+pn; *8275*: 53n, 175b, St+pn; *8276*: 36n, 88b, St+pn; *8277*: 4n, 3b.

Agalma ? elegans Sans (Fewkes): *8272*: 4n, 2b; *8279*: 34n, 63b, St+pn.

Halistemma rubrum (Vogt): *8262*: 89n, 75b, St+pn; *8263*: 145n, 44b, St+pn; *8264*: 67n, 35b; *8265*: 37n, 4b; *8270*: 23n, 8b; *8271*: 82n, 41b, St+pn; *8272*: 15n, St+pn; *8274*: 181n, 144b, 3 St+pn; *8275*: 41n, 39b, St+pn; *8276*: 73n, 64b, 2 St+pn; *8277*: 65n, 50b, St+pn; *8279*: 29n, 16b.

H. sp. nov.: *8277*: 2n, 3b.

Nanomia bijuga (Chiaje): *8265*: ?2n; *8276*: 7n.

Erenna richardi Bedot: *8270*: 2n, 1 gz.

Bargmannia elongata Totton: *8272*: 1n.

Physophora hydrostatica Forskål: *8271*: 1n, St+pn.

Melophysa melo (Quoy & Gaimard): *8265*: 6n, 13b.

Forskalia sp.: *8270*: 1n.

**Amphicaryon acaule* Chun: *8262*: 15w; *8263*: 6w; *8264*: 6w; *8265*: 5w, 1 1n, 1 vn; *8270*: 3w; *8271*: 3w; *8272*: 7w; *8274*: 1 1n; *8275*: 2w; *8277*: 2w; *8279*: 6w.

A. ernesti Totton: *8270*: 4w, 1 1n, 1 vn; *8271*: 3w, 1 1n, 1 vn; *8272*: 2w, 3 1n, 1 vn; *8274*: 1 1n; *8275*: 1w, 2 1n, 2 vn; *8277*: 3w; *8279*: 4w, 3 1n, 2 vn.

A. peltifera (Haeckel): *8262*: 2w; *8263*: 2 1n; *8276*: 1w; *8279*: 1w.

Maresearsia praeclara Totton: *8262*: 1 eb; *8263*: 1 1n, 3 eb; *8264*: 4 dn, 1 1n, 1 eb; *8271*: 1 w, 1 dn, 2 ln, 2 eb; *8279*: 1w, 1 eb.

*Rosacea sp.: *8263*: 269n; *8264*: 56n; *8270*: 1n, 1 eb; *8271*: 1n, *8272*: 2n, 1 eb; *8274*: 1n; *8275*: 3n; *8276*: 6n; *8279*: 1n.

R. plicata sensu Bigelow: *8265*: 100n; *8277*: 4n.

R. cymbiformis (Chiaje): *8262*: 32n, 58 1n, 1 eb; *8263*: 5 eb.

Praya dubia (Quoy & Gaimard): *8279*: 4n, 16 eb.

Desmophyes annectens Haekel: *8262*: 2n; *8263*: 14n; *8264*: 4n; *8271*: 1n.

Nectopyramis diomedeae Bigelow: *8270*: 1n, 1 eb; *8272*: 2 ec; *8274*: 1 ec; *8275*: 1 ec; *8276*: 1 ec; *8279*: 1n, 1 ec.

N. thetis Bigelow: *8263*: 3 ec; *8264*: 1n, 4 ec; *8265*: 1 ec; *8270*: 1n, 2 ec; *8271*: 1n, 4 ec; *8279*: 1 ec.

N. spinosa Sears: *8262*: 4 1n; *8263*: 1 1n; *8272*: 1 1n.

**Hippopodius hippopus* (Forskål): *8262*: 88n; *8263*: 86n; *8264*: 137n; *8265*: 89n; *8270*: 177n; *8271*: 131n; *8272*: 266n; *8274*: 150n; *8275*: 119n; *8276*: 339n; *8277*: 18n; *8279*: 94n.

*Vogtia spinosa Kefferstein & Ehlers: *8262*: 8n; *8263*: 7n; *8264*: 19n; *8265*: 57n; *8270*: 6n; *8272*: 4n; *8276*: 1n.

V. pentacantha Köllicker: *8264*: 1n; *8265*: 11n; *8270*: 9n; *8271*: 13n; *8272*: 4n; *8274*: 19n.

**V. serrata* (Moser): *8262*: 41n; *8263*: 54n; *8264*: 36n; *8270*: 4n; *8275*: 13n; *8276*: 4n; *8277*: 12n; *8279*: 25n.

**V. glabra* Bigelow: *8262*: 67n; *8263*: 99n; *8264*: 96n; *8265*: 60n; *8270*: 153n; *8271*: 174n; *8272*: 123n; *8274*: 125n; *8275*: 87n; *8276*: 130n; *8277*: 125n; *8279*: 158n.

Sulculeolaria quadrivalvis Blainville: *8262*: 1 an, 4 pn; *8263*: 1 an, 2 pn; *8264*: 2 pn; *8272*: 3 an, 2 pn; *8277*: 1 an.

S. biloba (Sars): *8270*: 2 an; *8276*: 1 an.

S. turgida (Gegenbauer): *8270*: 3 an, 5 pn; *8271*: 4 an, 2pn; *8272*: 5 an, 3 pn, *8274*; 2 an, 3 pn; *8275*: 1 an; *8276*: 6 an, 4 pn; *8277*: 12 an, 17 pn; *8279*: 3 an, 5 pn.

S. angusta Totton: *8275*: 1 an, 3 pn.

S. chuni (Lens & Van Riemsdijk): *8263*: 5 an, 9 pn; *8265*: 1 an, 1 pn; *8270*: 2 pn; *8272*: 1 pn.

S. monoica (Chun): *8265*: 1 an; *8270*: 13 an, 17 pn; *8271*: 1 an, 1 pn; *8272*: 3 an, 4 pn; *8274*: 2 an, 3 pn; *8275*: 2 an, 7 pn; *8276*: 1 an, 1 pn; *8277*: 23 an, 23 pn; *8279*: 3 an, 2 pn.

Diphyes dispar Chamisso & Eysenhardt: *8262*: 5 an, 3 pn, 4 eb, 3 eg; *8263*: 2 an; *8264*: 3 an, 1 pn; *8265*: 4 an, 2 pn, 2 eb; *8270*: 34, an, 22 pn, 47 eb, 8 eg; *8271*:

1 an, 1 pn, 5 eb, 3 eg; *8272*: 5 an, 3 pn, 5 eb, 2 eg; *8274*: 2 an, 1 pn; *8275*: 2 an;
    8276: 6 an, 2 pn, 2 eb, 1 eg; *8277*: 4 an, 2 pn; *8279*: 2 an, 1 pn, 2 ec.

*D. bojani (Eschscholtz): *8262*: 2 an; *8263*: 37 an, 6 pn, 5 eb, 1 eg; *8264*: 31 an, 4 pn,
    4 eb, 6 eg; *8265*: 41 an, 4 pn; *8270*: 110 an, 10 pn, 7 ec; *8271*: 39 an, 4 pn, 14 ec,
    2 eg; *8272*: 23 an, 1 pn, 6 ec, 2 eg; *8274*: 46 an, 7 pn, 4 ec, 5 eg; *8275*: 47 an, 4 pn,
    5 ec, 12 eg; *8276*: 113 an, 23 pn, 105 ec, 53 eg; *8277*: 134 an, 22 pn, 15 ec, 16 eg;
    8279: 53 an, 8 pn, 21 ec, 19 eg.

Lensia sp.: *8262*: 4 pn; *8265*: 19 eb.

*L. conoidea (Kefferstein & Ehlers): *8264*: 6 an; *8265*: 9 an; *8272*: 66 an; *8274*:
    6 an; *8275*: 1 an; *8276*: 6 an; *8279*: 6 an.

*L. multicristata (Moser): *8262*: 95 an; *8263*: 119 an; *8264*: 76 an; *8265*: 125 an, 1 pn;
    8270: 48 an; *8271*: 43 an; *8272*: 157 an; *8274*: 53 an; *8275*: 25 an; *8276*: 73 an;
    8277: 31 an; *8279*: 29 an.

L. cossack Totton: *8264*: 3 an; *8265*: 1 an; *8270*: 5 an; *8271*: 7 an; *8272*: 1 an; *8274*:
    9 an; *8275*: 4 an; *8276*: 10 an; *8277*: 8 an; *8279*: 6 an.

L. subtilis (Chun): *8262*: 2 an; *8264*: 1 an; *8279*: 1 an.

L. meteori (Leloup): *8263*: 3 an.

L. achilles Totton: *8262*: 8 an; *8263*: 1 an; *8264*: 5 an; *8270*: 1 an; *8271*: 1 an; *8272*:
    4 an; *8274*: 6 an; *8275*: 7 an; *8276*: 12 an; *8277*: 7 an; *8279*: 6 an.

L. lelouveteau Totton: *8263*: 1 an; *8270*: 1 an; *8271*: 2 an; *8274*: 1 an.

*L. fowleri (Bigelow): *8262*: 1 an; *8264*: 10 an; *8265*: 14 an; *8270*: 79 an, 6 eb; *8271*:
    44 an, 5 eb; *8272*: 43 an, 19 eb; *8274*: 73 an; *8275*: 174 an; *8276*: 31 an; *8277*:
    28 an; *8279*: 62 an.

L. exeter Totton: *8263*: 1 an; *8264*: 1 an; *8276*: 1 an.

L. hostile Totton: *8262*: 7 an; *8264*: 2 an; *8265*: 2 an; *8270*: 2 an; *8271*: 3 an; *8272*:
    2 an; *8275*: 2 an; *8276*: 5 an; *8277*: 5 an; *8279*: 3 an.

L. sp. nov.: *8264*: 1 an.

L. hotspur Totton: *8277*: 1 an; *8279*: 1 an.

Dimophyes arctica (Chun) (small): *8262*: 2 an; *8263*: 10 an, 1 ec; *8264*: 10 an; *8265*:
    5 an; *8270*: 1 an; *8271*: 1 an; *8272*: 1 an; *8276*: 1 an; *8279*: 1 an.

D. arctica (large): *8262*: 1 an; *8264*: 1 an; *8272*: 1 an; *8275*: 2 an; *8276*: 1 ec; *8277*:
    2 an.

*Chelophyes appendiculata (Eschscholtz): *8262*: 453 an, 364 pn; *8263*: 229 an, 103 pn;
    8264: 159 an, 51 pn; *8265*: 97 an, 33 pn; *8270*: 103 an, 18 pn; *8271*: 66 an, 15 pn;
    8272: 105 an, 26 pn; *8274*: 71 an, 35 pn; *8275*: 91 an, 25 pn; *8276*: 104 an, 38 pn;
    8277: 122 an, 28 pn; *8279*: 60 an, 13 pn.

*Eudoxoides mitra (Huxley): *8262*: 1 an; *8263*: 32 an, 1 pn, 1 ec, 14 eb, 9 eg; *8264*:
    31 an, 2 pn, 12 eb, 16 eg; *8265*: 68 an, 3 pn; *8270*: 105 an, 7 pn, 13 eb, 11 eg;
    8271: 218 an, 19 pn, 88 eb; *8272*: 196 an, 3 pn, 66 eb; *8274*: 229 an, 10 pn, 25 eb;
    8275: 195 an, 7 pn, 5 eb; *8276*: 161 an, 4 pn, 31 eb; *8277*: 244 an, 3 pn, 27 eb;
    8279: 335 an, 12 pn, 7 eb.

*E. spiralis (Bigelow): *8263*: 38 an; *8264*: 51 an, 1 eg; *8265*: 41 an; *8270*: 27 an; *8271*:

72 an; *8272*: 58 an; *8274*: 22 an; *8275*: 26 an; *8276*: 164 an; *8277*: 72 an; *8279*: 36 an.

*Clausophyes ovata (Kefferstein & Ehlers): *8262*: 48 an, 49 pn; *8263*: 47 an, 43 pn; *8264*: 56 an, 43 pn; *8265*: 43 an, 38 pn; *8270*: 23 an, 34 pn; *8271*: 11 an, 17 pn; *8272*: 14 an, 16 pn; *8274*: 13 an, 9 pn, 2 eb; *8275*: 8 an, 10 pn; *8276*: 3 an, 3 pn; *8277*: 5 an, 9 pn; *8279*: 1 an, 2 pn.

C. massiliana Patriti: *8265*: 4 pn; *8270*: 3 an, 2 pn; *8271*: 3 an, 1 pn, 1 eb; *8272*: 3 an, 5 pn, 1 eb; *8274*: 5 an, 4 pn; *8275*: 9 an, 7 pn, 2 eb, 1 eg; *8276*: 5 an, 4 pn, 5 eb, 4 eg; *8277*: 5 an, 3 pn, 2 eb, 3 eg; *8279*: 2 an, 1 pn, 2 eb, 1 eg.

*Chuniphyes multidentata Lens & Van Riemsdijk: *8262*: 45 an, 16 pn, 5 eg; *8263*: 58 an, 25 pn, 2 eg; *8264*: 72 an, 27 pn, 1 eb, 5 eg; *8265*: 57 an, 34 pn, 5 eg; *8270*: 97 an, 60 pn, 2 eg; *8271*: 155 an, 98 pn, 4 eg; *8272*: 48 an, 21 pn, 6 eg; *8274*: 35 an, 21 pn, 6 eg; *8275*: 16 an, 11 pn, 2 eg; *8276*: 46 an, 30 pn, 1 eb, 2 eg; *8277*: 10 an, 10 pn, 2 eg; *8279*: 25 an, 19 pn.

Heteropyramis maculata Moser: *8271*: 2 an.

Thalassophyes crystallina Moser: *8276*: 1 eb.

Ceratocymba leuckartii (Huxley): *8270*: 2 an; *8274*: 1 an.

*C. sagittata (Quoy & Gaimard): *8262*: 6 an, 5 pn, 51 eb, 59 eg; *8263*: 5 an, 2 pn, 37 eb, 48 eg; *8264*: 1 an, 2 pn, 44 eb, 83 eg; *8265*: 2 an, 1 pn, 14 eb, 12 eg; *8270*: 1 an, 2 pn, 51 eb, 28 eg; *8271*: 3 eb, 7 eg; *8272*: 2 an, 8 eb, 11 eg; *8274*: 2 an, 2 pn, 14 eb, 26 eg; *8275*: 1 an, 17 eb, 21 eg; *8276*: 1 pn, 1 eb, 2 eg; *8277*: 1 an, 1 pn, 12 eb, 34 eg; *8279*: 10 eb, 22 eg.

C. dentata (Bigelow): *8264*: 2 eb, 3 eg; *8270*: 3 eb, 6 eg; *8272*: 1 an, 1 pn.

Abyla sp: *8265*: 1 eb; *8270*: 5 eb; *8272*: 2 eb, 3 eg; *8274*: 1 eb, 1 eg; *8276*: 1 eb, *8277*: 1 eb; *8279*: 2 eb, 1 eg.

A. trigoma Quoy & Gaimard: *8270*: 2 an, 1 pn; *8277*: 1 an.

*Abylopsis tetragona (Otto): *8263*: 2 an, 2 pn, 1 eb; *8265*: 4 an; *8270*: 31 an, 5 pn, 6 eb; *8271*: 94 an, 45 pn, 45 eb; *8272*: 34 an, 27 pn, 18 eb; *8274*: 56 an, 46 pn, 17 eb; *8275*: 11 an, 7 pn, 11 eb; *8276*: 48 an, 27 pn, 13 eb; *8277*: 30 an, 38 pn, 8 eb; *8279*: 28 an, 34 pn, 6 eb.

*Abylopsis eschscholtzii (Huxley): *8262*: 5 an, 4 pn, 4 eb; *8263*: 20 an, 12 pn, 19 eb, 1 eg; *8264*: 18 an, 10 pn, 27 eb; *8265*: 23 an, 11 pn, 2 eb; *8270*: 20 an, 15 pn, 64 eb; *8271*: 67 an, 52 pn, 50 eb; *8272*: 49 an, 29 pn, 29 eb; *8274*: 51 an, 46 pn, 17 eb; *8275*: 97 an, 49 pn, 57eb; *8276*: 228 an, 175 pn, 196 eb; *8277*: 13 an, 9 pn, 18 eb; *8279*: 16 an, 17 pn, 15 eb.

*Bassia bassensis (Quoy & Gaimard): *8262*: 48 an, 62 pn, 86 eb; *8263*: 81 an, 81 pn, 94 eb; *8264*: 85 an, 65 pn, 31 eb; *8270*: 11 an, 14 pn, 2 eb; *8271*: 99 an, 81 pn, 5 eb; *8272*: 19 an, 14 pn, 3 eb; *8274*: 19 an, 18 pn; *8275*: 9 an, 12 pn, 3 eb; *8276*: 113 an, 93 pn, 15 eb; *8277*: 13 an, 17 pn, 4 eb; *8279*: 40 an, 52 pn, 3 eb.

Enneagonum hyalinum Quoy & Gaimard: *8262*: 1 eb; *8263*: 1 eb, 1 eg; *8264*: 1n, 1 eb, 1 eg; *8265*: 5 eb; *8270*: 4 eb, 1 eg; *8271*: 3 eb, 1 eg; *8272*: 4n, 11 eb, 8 eg; *8274*: 1n, 4 eb; *8275*: 3 eb, 1 eg; *8276*: 1n, 2 eb, 2 eg; *8277*: 1n, 2 eb, 2 eg; *8279*: 3n, 6 eb, 5 eg.