*SOME OBSERVATIONS ON THE VERTICAL MIGRATION AND GEOGRAPHICAL DISTRIBUTION OF SIPHONOPHORES IN THE WARM WATERS OF THE NORTH ATLANTIC OCEAN

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Recent observations of siphonophores and other gelatinous animals *in situ*, using SCUBA diving techniques, have shown that these animals play a much greater role in the oceanic ecosystem than had previously been suspected. Siphonophores are efficient predators, searching large volumes of water with their tentacle nets, and their frequent predominance in the macroplanktonic catches in the top 500 m of the ocean must mean that their impact on the ecosystem is highly significant.

This paper deals with two aspects of siphonophore ecology, namely their diel vertical migration patterns and their zoogeography. From a series of one-hour hauls made over a 24 hr period at 250 m depth it was found that most migrant siphonophores underwent slow diel vertical migrations in a daily sinusoidal pattern. Only a few species migrated rapidly through the 250 m zone at dawn and dusk; one of which, the physonect *Halistemma rubrum*, may be associated with the Deep-Scattering Layer. The factors which may possibly initiate these vertical migrations are discussed and consideration is given to the mechanisms which may be involved in the accomplishment of the migrations.

Although siphonophores were one of the first groups to be used as so-called "indicator" species, it appears that the consideration of indicator communities or assemblages in oceanic waters is a more useful technique for correlating biological data with the physically defined water masses. The preliminary statistical analysis of the data for the depth distributions of siphonophores at various stations in the North Atlantic Ocean shows that broad zones of species assemblages can be drawn and these can to some extent be associated with the known water masses. At any station several siphonophore faunal zones and water masses are present in the top 2000 m depth of water. Thus account should be taken in any zoogeographical study of siphonophores not only of the geographical distribution of the faunal assemblages but also of their distribution with depth.

INTRODUCTION

THE IMPACT OF GELATINOUS MARINE ORGANISMS ON THE ECOSYSTEM

Over the past fifty or so years there have been relatively few studies of the ecology and zoogeography of siphonophores in comparison with a number of other marine planktonic and nektonic taxa. However, recent investigations have shown that the role which siphonophores, and other gelatinous organisms,

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*Invited paper.

play in the general oceanic ecosystem is very important and demands greater attention. The work of Harbison's group at the Woods Hole Oceanographic Institution is particularly relevant as they have looked at gelatinous organisms *in situ* using SCUBA diving techniques. For instance, Biggs (1976) investigated the *in situ* feeding mechanisms of various siphonophore species and found that not only do they feed on a wide size range of zooplankton,, from copepod nauplii to decapods and small fish, but by careful and often complicated disposition of their tentacles they can search relatively large volumes of water for their prey. A. *Forskalia* species with a total body protein of only 2-3 mg can expand its tentacles and tentilla to a length of more than 4-5 m, while the individual tentacles of *Physalia physalis* can be over 10 m in length.

Biggs (personal communication) also found that the feeding response of siphonophores did not level off at high prey densities, as is often seen in copepods for instance, and that a large species like *Rosacea cymbiformis* could consume 200 copepod nauplii every minute. Thus, although copepods may be more than four hundred times more abundant than siphonophores, the feeding potential of these siphonophores must mean that mere abundance is no criterion for impact on the ecosystem. In certain regions siphonophores can totally dominate the net catches of macrozooplankton such that they comprise more than 90% of the total catch volume (Pugh, unpublished data). Barham (1963) also comments on the importance of siphonophores during his osbervations from submersibles, and considers their presence in the deep-scattering layers as a living net stretched across the world's oceans which must play a key role in the overall economy of the oceans.

Similarly, Madin and Harbison (1976) concluded that salps, even when not numerically abundant, were amongst the most important consumers of nannoplankton in the open oceans. They suggest that one chain of an "aggregate generation salp..., in 1000 m³ of water could, like a single large vacuum cleaner, have the same impact as a hundred thousand copepod whisk brooms, yet the chance of catching such a chain in a plankton net would be extremely remote".

Other gelatinous taxa, such as ctenophores, which are often destroyed in net catches, have been observed by Harbison's group to be abundant in the open ocean and these observations further illustrate the fact that the impact of many gelatinous organisms on the oceanic ecosystem is often greatly underrated. In this paper two aspects of siphonophore ecology, namely diel vertical migration patterns and zoogeography, will be discussed in an attempt to illustrate further the contribution which these gelatinous organisms make to the general oceanic ecosystem.

DIEL VERTICAL MIGRATIONS OF SIPHONOPHORES

During the latter part of 1965 a detailed sampling programme was carried out from RRS DISCOVERY in the region off Fuerteventura, in the Canary Islands, to obtain information on the sonic-scattering layers and the day/night depth distributions and diel vertical migration ranges of the zooplankton and micronekton. Details of this cruise are given by Currie *et al.* (1969). In the paper on the vertical distribution of the siphonophores (Pugh, 1974) it was noted that the depth distributions of certain species, as derived from the two data sets for the IKMT and N113 net haul series, were different. As there was often a difference in the time of day (or night) during which a particular depth range was sampled by each net, it was suggested that this depth distribution anomaly could be explained if the siphonophores were undergoing slow continuous vertical migrations in a daily sine-wave pattern. To investigate

further this pattern of diel vertical migration a series of one hour hauls, using the RMT 1+8 combination net, was made over a 24 hr period at 'DISCOVERY' Station 7856 (30°N, 23°W). The opening/closing combination net system was maintained during each haul at a depth as close as possible to 250 m depth. This depth was chosen to be a reasonable compromise for the analysis of the diel migration behaviour of a wide range of zooplankton taxa. The sampling and a summary of the results for eight zooplankton taxa are presented in the paper by Roe (1974) and reference should be made to Baker *et al.* (1973) for a detailed description of the RMT 1+8 combination net and its operation. A further series of one-hour hauls, each made over 48 hr at depths of 100, 250, 450 and 600 m, has been carried out on a station at 44°N, 13°W, but the analysis of the siphonophores has not been completed.

Patterns of diel vertical migration:

Of the siphonophore species identified during the 24 hr series of hauls at 250 m, thirteen were found to be sufficiently abundant to allow an interpretation of their patterns of diel migration. These patterns can be clarified into three basic groupings as follows:-

1) Those species which were apparently non-migrant, e.g. *Dimophyes arctica, Lensia multicristata* and *L. meteori.* The number of anterior nectophores of *D. arctica* (Fig. 1) in each haul varied somewhat randomly throughout the 24 hr period, with no obvious peaks or troughs. The SOND Cruise data (Pugh, 1974) also indicated that this species was present in the 200-250 m depth range at all times.

2) Those species which underwent slow vertical migrations. This pattern of migration can be subdivided into various groupings for at any depth the abundance of a species will vary with time and be regulated by the overall vertical distribution of the species, the timing of its vertical migration and the range of this migration. Thus at 250 m there are those siphonophore species which are present throughout most of the day and migrate upwards out of. the zone at night, and those species which live below the 250 m zone by day and migrate up into or through the zone at night.

Two examples of species present during the day are *Hippopodius hippopus* and *Chelophyes appendiculata* (Fig. 1). It appears that *H. hippopus* migrates to a depth just below 250 m during the day as its peaks of abundance in the 250 m zone were found in the hauls made during the early morning and late afternoon. The SOND Cruise data for this species, in the IKMT net catches, showed a peak daytime abundance at 250 m, but as the hauls in the 200-300 m depth range were all carried out at approximately the same time, in the mid-afternoon, it was conjectured that the majority of the population had already begun its upward migration and that the actual maximum daytime depth was closer to 300 m. The 24 hr series results, therefore, confirm this conjecture. At night, *H. hippopus* was found to migrate into the 50-100 m depth range. The pattern of migration for *Chelophyes appendiculata* is very similar to that for *Hippopodius hippopus* (Fig. 1) except that *C. appendiculata* reaches its peak abundance in the 250 m zone during the middle part of the day, and so this depth probably represents its maximum daytime level.

Vogtia glabra is one example of the siphonophore species which remain below the 250 m zone during the day and migrate into or through it by night. *V. glabra* reaches a maximum abundance in this zone shortly after sunset, but then continues its upward migration and remains above 250 m for most of the

night, only reappearing on its downward migration shortly before dawn. Thus the idea that many species of siphonophore undergo slow cyclical diel migrations, as conjectured from the SOND Cruise data, is borne out by this 24 hr series of hauls at 250 m. This pattern of diel migration is illustrated diagrammatically in Fig. 2 for the three species, *Chelophyes appendiculata*, *Hippopodius hippopus* and *V. glabra*. Although this sort of approach may be too simplistic there is evidence from the series of 1 hr hauls made over a 48 hr period at 44°N 13°W that other siphonophores are carrying out the same pattern of diel vertical migration. For instance, Fig. 3 shows the variation in the numbers of anterior nectophores of *Lensia conoidea* found at 100 m over this 48 hr period.
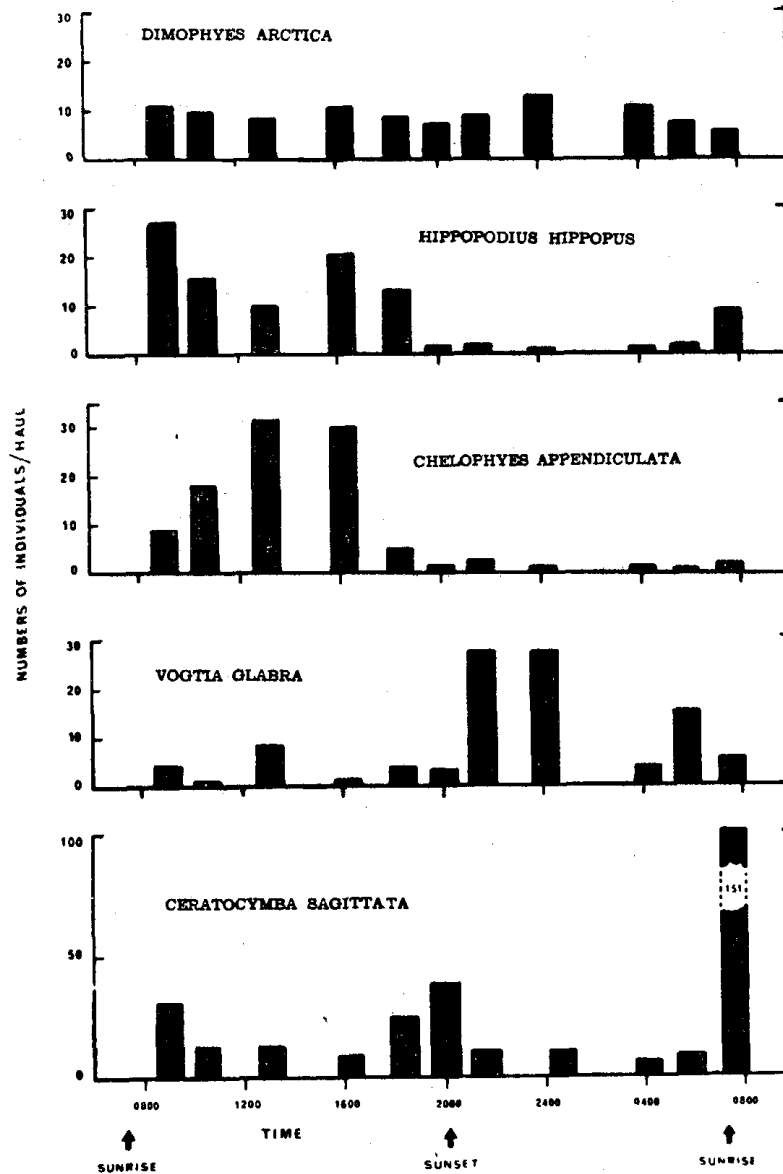

Fig. 1. Histograms for the numbers of individuals of certain siphonophore species in each of the eleven hauls taken over a 24 hr period at 250 m depth
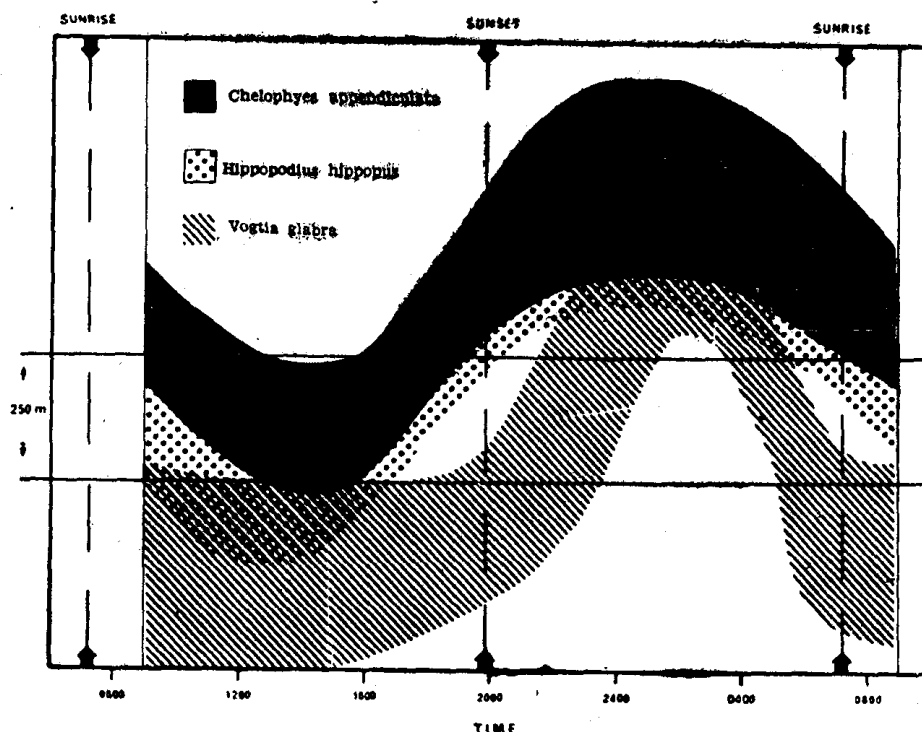
Fig. 2. Possible pattern of diel vertical migration in three species of siphonophore

It is always difficult to estimate from net samples the numerical abundance of physonect species, since they tend to break up into numerous pieces, many of which become lost through the netting. However it appears from the 24 hr series of hauls that one such species, *Halistemma rubrum*, has a similar diel migratory behaviour to *Vogtia glabra*. *H. rubrum* is absent during the day at 250 m, but appears in this zone at night. The highest numbers of nectophores of this species were found in the hauls just after sunset and before sunrise and so it is probably migrating above the 250 m depth zone for the middle part of the night. The significance of diel migrations of siphonophores with gas bladders, the physonects and cystonects, will be discussed later.

3) The third pattern of vertical migration in siphonophores is shown by those fast-moving species which migrate rapidly through the 250 m zone at sunset and sunrise. Only the eudoxid stage of *Ceratocymba sagittata* was found to fit this pattern (Fig. 1). This species is present between 300 and 400 m depth during the day and migrates a substantial distance into the 10-25 m depth range at night.

Most of this section has been concerned with data obtained at a station at 30°N which may be considered to be on the fringe of the range of warm water plankton. The distribution of siphonophores in the warmer waters of the North Atlantic Ocean will be dealt with in the section on zoogeography, but it is worth noting that the average temperature of the water column down to 1000 m, is higher at 30°N that at any of the more southerly stations considered. Although there may well be latitudinal variations in the degree and extent of diel vertical migrations the data collected at other, more southerly stations indicate that many siphonophore species have depth distributions similar to those found at 30°N.
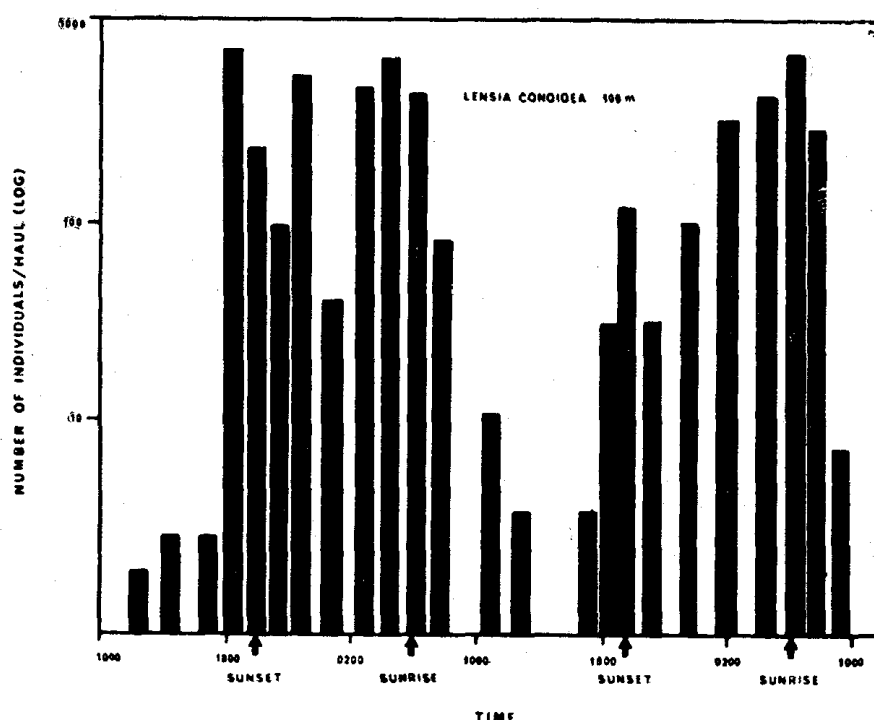
Fig. 3. Variation in the numbers of anterior nectophores of *Lensia conoidea* at 100 m over a 48 hr period at 44°N, 13°W

Factors which may initiate the diel migrations of siphonophores:

Longhurst (1976) states that the proximate stimulus for diel vertical migrations is the level of ambient illumination, while physiological condition, light adaptation and endogenous rhythms probably all interact in a complex manner but still with light as the controlling factor. If light is the primary initiator of siphonophore vertical migrations then the question arises as to how they are able to sense changes in the light intensity. Mackie (1962) has shown that the physonect species, *Nanomia cara*, has pigment spots, possibly ommochromes, on its nectophores and which have a peak absorbance between 465 and 470 nm. These might be ideal sites for a system sensitive to blue wavelengths of light but in a later paper Mackie (1964) showed that only the siphosomal or stem regions were sensitive to sudden light flashes. These flashes were, however, of an intensity several orders of magnitude higher than the light levels which siphonophores react to *in situ* if light is the proximate stimulus for vertical migration. Moore *et al.* (1953) showed that the vertical difference in the daytime distributions of some siphonophores in the Florida Current could be correlated with light intensity at the shallower end of the range, and with temperature at the deeper end of the range. Similarly Moore (1949) found that the surface abundance of some siphonophore species at night was correlated with the phases of the moon.

Siphonophores have often been recognised as contributors to Deep Scattering Layers, and the vertical movement of these layers in response to the rapidly changing light conditions at dawn and dusk is well established. For instance, during the SOND Cruise, Boden and Kampa (1967) showed that the depth of the Deep Scattering Layer changed in relation to the vertical movement of the $5 \times 10^{-4} \mu W/cm$ isolume (474 nm). These studies were continued by McCartney

(1976) who compared the depth distribution of several Sonic Scattering Layers with the vertical distribution of the mesopelagic fishes (Badcock, 1970). The siphonophore data were not included in this analysis for, as discussed earlier, it is difficult to make quantitative studies of the distribution of physonect siphonophores collected in nets. However, the data for the depth distribution of *Halistemma rubrum* (Pugh, 1974) indicate a possible relationship with the 10 kHz Sonic Scattering Layer, while the 24 hr series of hauls at 250 m suggest that *H. rubrum* can undergo fairly rapid vertical migrations.

The observations of Moore *et al.* (1953) and the evidence of Barham (1963) for an association of Deep Scattering Layers with physonect siphonophores would suggest that siphonophores are reacting directly to the ambient light level. The mechanism by which this is accomplished does not appear to have been established, and it is hoped that some work will be done to investigate how siphonophores respond to changes in light intensity at such low levels. It might also be conjectured that the diel migrations of siphonophores are not a direct response to changing light intensity, but are a secondary response initiated, for example, by the migrations of other zooplankton. Many copepods and ostracods, whose response to light is quite well documented, undergo similar migratory patterns to the siphonophores (Roe, 1974), but can the siphonophores follow these migrations, and how are they able to sense the direction of the migration?

The processes involved in the diel migrations of siphonophores:

Many siphonophores, ranging from the slow moving prayid species to the faster moving diphyids and physonects, can undergo diel vertical migrations of 200 m or more (Pugh, 1974). The question arises as to whether this process is entirely due to active swimming or are other factors involved? The association of the Deep Scattering Layers with physonect siphonophores would mean that these species must migrate vertically at speeds of up to 10-13 cm/sec to keep pace with the depth changes of this layer at dawn and dusk. Biggs (1976) reports that undisturbed physonects swim at rates of 2-7 cm/sec , but can increase these to 10-25 cm/sec if an escape response is invoked. This latter rate, if sustained, would then be sufficient to attain the necessary vertical migration rates, but it is also possible that these siphonophores control their buoyancy by regulating the volume of gas in their pneumatophores. This point is discussed by Barham (1963), and the release of gas from the pneumatophore was studied in detail by Pickwell (1967). From Pickwell's data, it appears also that the gas gland can secrete within one minute a volume of gas, at atmospheric pressure, equivalent to the volume of the pneumatophore. Assuming that the pneumatophore is not a rigid structure then the ability to rapidly secrete into or vent gas from the pneumatophore thereby effecting changes in its volume, would alter the buoyancy of the animal and so greatly assist in the vertical migration process.

The use of gas to alter the buoyancy of the animal only applies to the cystonect or physonect species of siphonophores for the calycophorans, which are the most abundant siphonophores, do not possess a pneumatophore. Biggs (1976) has measured the undisturbed swimming rate of the slow moving prayid species, *Rosacea cymbiformis,* as being 1-3 cm/sec . At such a rate it would require up to 6 hr to migrate over a 200 m depth range, assuming the animals swam continuously and only in the vertical plane. Normally the swimming phase is relatively short in comparison with the fishing phase, and so the time taken over the vertical migration range would be considerably longer. Perhaps then buoyancy regulation is again used to assist in these vertical migrations, but in this case the regulation is accomplished by adjustments to the ionic or biochemical composition of the animals.

Denton and Shaw (1962) have shown that the specific gravity of the body fluids of gelatinous organisms is less than that of seawater and is sufficient to balance the density of the remainder of the animal so that they are neutrally buoyant. Although these authors did not study any siphonophores, they found that medusae and ctenophores contained very low concentrations of the heavy ion, sulphate, equivalent to about 40% of that in sea water. Sulphate is only a minor constituent of sea water and so is it possible that the cellular control of the concentration of this ion, in association with a lighter ion such as chloride, could produce sufficient changes in the specific gravity of the animal to assist in its vertical migration? The actual change in specific gravity required to produce a rate of vertical movement of 1 cm/sec is very small and it seems that fairly small changes in the sulphate concentration could cause this. Observations by Hamner (personal communication) have shown that neutrally buoyant medusae, when placed in seawater of a different density, can readjust their specific gravity to equal that of the medium and thereby become neutrally buoyant again, within a space of 6-24 hr. Thus gelatinous organisms clearly can control their specific gravity, but can this be carried out in a rhythmical manner on a daily basis?

Another method of buoyancy control may be biochemical. Ceccaldi and Daumas (1967) have found that siphonophores contain relatively large amounts of free amino acids, which may make some contribution to the buoyancy of the animals. Again it is not known whether the biochemical composition of the animals can be regulated on a daily basis thereby playing some part in the control of the diel vertical migrations. Since such a large part of gelationous organisms like siphonophores can be considered to be a solution isosmotic with seawater it is likely that the regulation of the ionic composition of the animals would be more important than biochemical regulation, although some of the ions involved may well be organic. Thus, it is not possible to say definitely what actually initiates the diel migrations of siphonophores or what factors may be involved in their accomplishment, but it is hoped that in the future more physiological work will be done on these animals.

THE ZOOGEOGRAPHY OF SIPHONOPHORES

In many of the early works on the geographical distribution of planktonic animals attention was drawn to the fact that certain species might be used as "indicators" of the prevailing hydrological conditions. Thus, Gough (1905) considered that the presence of the siphonophore, *Muggiaea atlantica* in the English Channel indicated the influx into that area of water from the southeast. Several other authors, including Moore (1953), have discussed the use of siphonophores as "indicators" of such water movements, but, as Briggs (1974) concluded, in the case of oceanic populations there are very few species which are entirely restricted to one water mass and that the idea of looking for a distinct fauna is probably outmoded. In more recent studies on zoogeography attention has been given to species assemblages for, as Banse (1964) summarised, "... ecological groups... may be a more desirable, basis of animal geography than the species themselves".

Such work has been carried out by Backus and his co-workers in connection with the zoogeography of meso- and epipelagic lantern fishes in the Atlantic Ocean. Backus and Craddock (1975) have subdivided this ocean into several faunal zones and provinces the boundaries of which are consistent with physical changes in the large-scale oceanic circulatory patterns. Similar information is also appearing about the zoogeography of various other planktonic taxa, but so far

there are few papers which deal with the factors which affect the distributions of siphonophores. In her monograph on the distribution of siphonophores in the Pacific Ocean, Alvarino (1971) considered that the geographical distribution of the siphonophores did not correspond with water masses but was related to the depth of certain isotherms. Margulis (1972) has drawn up distributional maps for the siphonophores in the Atlantic Ocean but only delineated groups of species associated with the boreal, tropical or equatorial regions. However, Margulis did conclude that either water productivity or a combination of hydrographical conditions within one particular water mass might be important in controlling the distribution of individual species. Similarly, Stepanyants (1967) divided the North Pacific Ocean siphonophore species into groups associated with the climatic regions, but neither paper has considered the various water masses which are present in a single water column, each of which may have an individual assemblage of siphonophores.

The distribution of siphonophores in the warmer waters of the North Atlantic Ocean:

The Biology Section at the Institute of Oceanographic Sciences has carried out a concerted sampling programme in the North Atlantic Ocean, particularly along the meridian of 20°W approximately, to obtain data on the spatial distribution of various groups of zooplankton. The positions of the stations where work has been carried out are shown in Fig. 4. At each station the RMTI+8 combination net was fished, both during the day and the night, over depth ranges of 100 m, so that a series of samples from 100-1000 m depth of water were obtained. The top 100 m was usually subdivided into depth ranges of 0-10 m, 10-25 m, 25-50 m, and 50-100 m while more widely spaced depth ranges were fished between 1000 and 2000 m, namely 1000-1250 m, 1250-1500 m and 1500-2000 m. A detailed description of the nets used and the general sampling regime is given by Baker *et al.* (1973) From these day and night series samples the depth distribution of the zooplankton species at each station could be assessed together with some indication of the magnitude of their diel vertical migrations. By comparing the results from all the stations the geographical ranges of the individual species and any variations in their depth distributions were ascertained.

From these series the ostracod distribution data have been analysed using multivariate statistical analyses (Fasham and Angel, 1975) in order to clarify into various groups the faunal composition of ostracods found in each haul, on the basis of their component group loadings obtained from the statistical matrix. When these groups were plotted on the meridional section it was found that the hauls which had their highest loading in one particular group could be associated together into zones. These zones can be considered as areas where the fauna is made up of certain species with charactristic relative numerical abundances. It is quite possible for an individual species to be found in another zone but there it would be associated with different species or have a different relative numerical abundance. Fasham and Angel (1975) also compared these zones of distribution of ostracods with the presence of the physically characterisable water masses, several of which can be present in any one water column. From the analyses it was apparent that several faunal zones were present at each station and the depth distribution of some of these showed close agreement with the distribution of the water masses. Not all of the water masses contained individual faunal assemblages and probably temperature and salinity were not the only factors affecting the distribution of the ostracods. However, the results do exemplify the fact that there is little point in drawing faunal boundaries on oceanic maps unless the depth of the boundary is indicated.
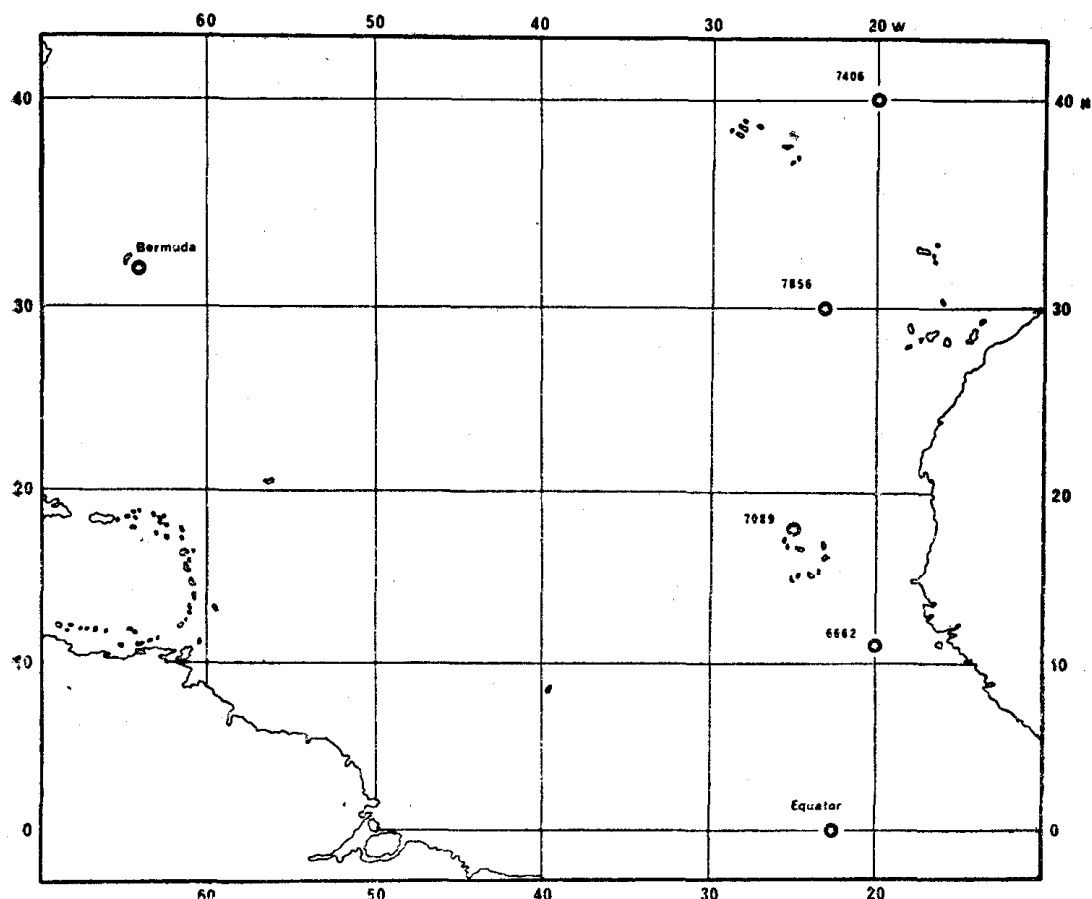
Fig. 4. Distribution of the stations in the North Atlantic Ocean.

From my studies, preliminary evidence for the association of siphonophores with broadly defined water masses was found in a series of twelve oblique (0-1000 m) RMTI+8 combination net hauls made in a transect across the North Atlantic Ocean at 32°N (Pugh, 1975). Using principle component statistical analyses it was shown that there were two major siphonophore assemblages, one in the Sargasso and the other in the eastern North Atlantic, but with a gradual transition between them centred around the mid-Atlantic ridge. The correlation coefficient matrix for the nineteen most abundant siphonophores species showed that their distributional patterns could be represented by extracting six factors, each factor having certain species associated with it. Of these factors the most important was factor 2 which showed the most marked east-west trend in the distribution of eight species, four being found more frequently in the Sargasso and four in the eastern North Atlantic water. These eight species were also shown to have the greatest differences in abundance in the two stations towards each end of the transect (Fig. 4), where the analysis of the vertical distribution of the siphonophores was made from the series of discrete depth hauls. All but one of the nineteen species considered in the analyses were found at both these stations (i. e. 30°N 23°W and Bermuda) so again it is clear that the differences between faunal zones depends more on the relative abundances of the species rather than on their presence or absence.

This work on the zoogeography of siphonophores is now being extended

with the completion of the identification of the siphonophores from the discrete depth hauls taken at the stations in the eastern North Atlantic, approximately on the 20°W meridian and at Bermuda (Fig. 4). It is not intended to go into any detail on the distribution of the individual species but an attempt will be made to summarise some of the preliminary results which have been obtained from the statistical analyses of the data, although these analyses are, as yet, incomplete. From a total of 230 hauls about 96 species of siphonophores have been identified, being divided amongst the sub-orders as 73 Calycophorae, 21 Physonectae and 2 Cystonectae. Some taxonomic problems are still to be resolved and there are also some new species present. Daniel (1974) in her excellent review of the siphonophores, lists the presence of 93 species in the Atlantic Ocean, from a world total of 144. Of these 93, twelve were not found in the present DISCO-VERY collections, while an additional fifteen species were identified. All but two of the species had wide geographical distributions and the number of species found at each station in the warmer waters of the North Atlantic are shown in Fig. 5.

The largest number of species was found at 18°N, 25°W, which agrees with the results for the ostracods (Angel and Fasham, 1975), but in contrast with the later results there are almost as many species present at 11°N, 20°W. Fasham and Angel (1975) showed that the station at 18°N was in a frontal zone where the North and South Atlantic water masses mixed with the consequent mixing of their populations of ostracods. However, many siphonophore species live in both of these water masses and so it is not surprising that the latitudinal changes in the siphonophore species abundance are not as marked as in the case of the ostracods. Another feature of the results was the high average number of species
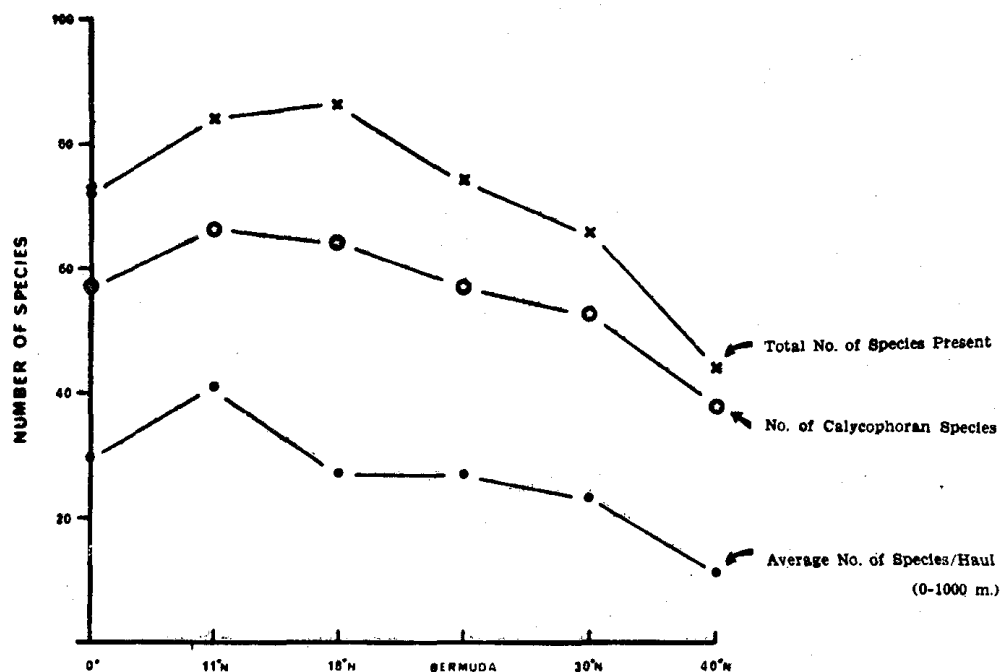

Fig. 5. The total number of species and of calycophoran species in the day and night hauls at six stations in the North Atlantic Ocean, and the average number of species per haul

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per haul in the top 1000 m of water at 11°N (Fig. 5) which is due to the fact that many species have broader vertical depth ranges at this station in comparison with those found at the other stations.

The zonation of siphonophores and their relationship with water masses:

The statistical multivariate analyses were carried out with the intention of identifying zones of assemblages of siphonophores, and thence to compare these zones with the distribution of the physically-defined water masses in the North Atlantic Ocean. The statistical methods used are described by Fasham and Angel (1975). Only preliminary results of these analyses are available and unfortunately it has not been possible to include the data for the station on the equator. From the similarity matrix, derived from the analysis of the siphonophore population present in each of the daytime hauls, nine groups were extracted which contain hauls with similar faunal assemblages. These groups are plotted in Fig. 6 on a meridional section approximately through 20°W, and the results for the Bermuda station are appended.

It can be seen that those hauls which fell into the same statistical grouping are associated together in zones which are broadly similar to those found for the ostracods (Fasham and Angel, 1975, Fig. 2). Thus:-

1) Siphonophore Zone 2 is approximately the same as ostracod zones 5 and 10. (The numbering of the zones is arbitrary). Physically this zone represents the hot, saline surface water which is found between 18 and 40°N, 20°W and in the Bermuda area. Unlike ostracod zone 5, this siphonophore zone is extended southerly to include the haul in the top 100 m at 11°N. This is probably because the siphonophores have been identified only from a 0-100 m haul, as this depth horizon was not subdivided, using the TMT net, during the DISCOVERY station 6662 sampling programme. Thus some of the finer distributional detail may have been observed. A later sampling programme at the same position (DISCOVERY Station 7824) did subdivide this 0-100 m zone in the usual way, as described earlier, but these samples have not yet been examined.

Fasham and Angel (1975) originally suggested that the lower boundary of the ostracod zones 5 and 10 was demarcated by the depth of the 17.5°C isotherm but in the case of the siphonophores the boundary appears to be deeper than this isotherm. This boundary is probably better characterised by the depth of the permanent thermocline, although on this basis the boundary at 30° N for the siphonophores should be somewhat deeper. Also, as the permanent thermocline is very shallow at 11°N, the boundary should occur within the top 100 m, but, as explained above, until the later samples of siphonophores are examined, its presence cannot be assessed properly. It should be noted that the lines drawn around the zones do not necessarily represent abrupt faunal boundaries and often the hauls on either side of a line have a faunal assemblage which is intermediate between the two zones, only differing in the slightly higher factor loadings for one or the other grouping.

2) Siphonophore zone 6 is similar to ostracod zone 7. Physically this zone appears to represent the area of mixing between the North and South Atlantic Central water masses, with temperatures between 11.5 and 18°C. This mixing is probably most intense at the more southerly station, giving rise to the large number of species present at these stations (Fig. 5).

3) Siphonophore zone 4 is comparable with ostracod zone 4. The water in this zone is mainly North Atlantic Central Water which appears to have a gyral
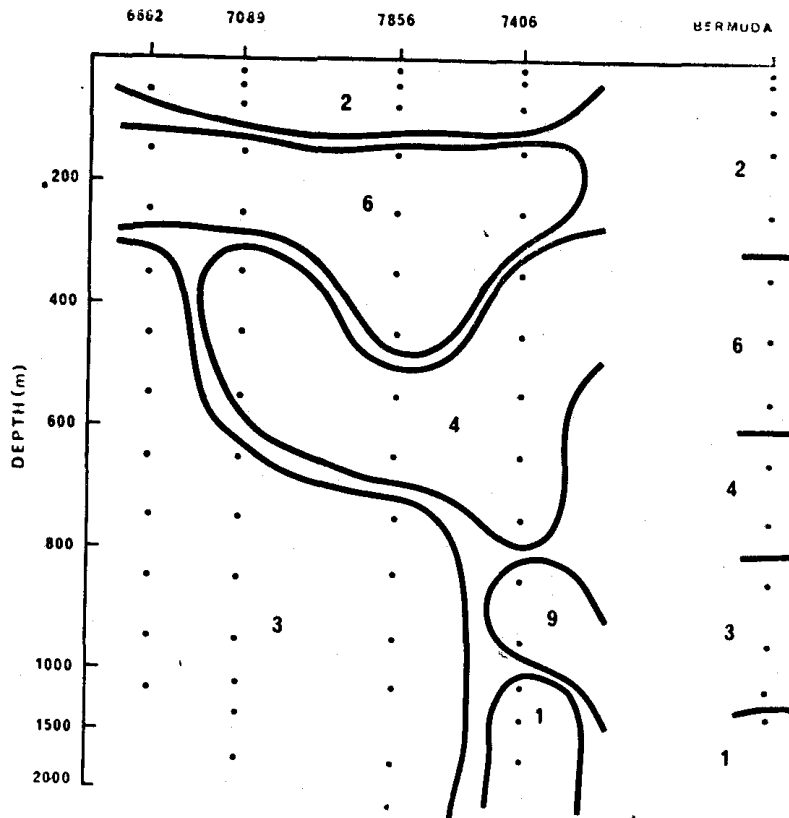
Fig. 6. The distribution of the factor groupings in the day-time hauls

circulation keeping it somewhat distinct from the surrounding water masses. It is bounded to the north at the point of influence of the North Atlantic Drift which causes a divergence.

In this zone there is some influence of Mediterranean water which diffuses into the deeper depths, and this may have some effect on the siphonophore population as is possibly shown when:-

4) Siphonophore zone 3 is compared with ostracod zones 2 and 6. Fasham and Angel (1975) thought that their more southerly zone (zone 2) was associated with the presence of Antarctic Intermediate Water, as characterised by its salinity minimum, although there was some mixing with South Atlantic Central Water at the shallower depths. They were not able to relate their zone 6 with any of the physical properties of the water although it contained certain ostracod species with unusual depth distributions. Analysis of the decapod data (Fasham and Foxton, in preparation) has shown that this latter zone is again present and it is suggested that this zone possibly represents a region of mixing between the Mediterranean and Antarctic Intermediate waters which gives rise to a characteristic faunal assemblage. However, this zone is not separated off from the more southerly one in the analysis of the siphonophore data. To the south of the Straits of Gibraltar the Mediterranean water diffuses very slowly into the other water masses, although its temperature/salinity characteristics are still sufficiently distinct for its presence to be detected. It may require up to two years for this water to penetrate as far as the area of the station at 30°N, 23°W and possibly in that time any endemic siphonophore fauna may have died out,

such that the population in the deeper waters at 30° and 18°N is not distinguishable from that found in the Antarctic Intermediate Waters.

5) The two other zones in the warmer waters of the eastern North Atlantic Ocean, zones 1 and 9, only comprise five hauls in the deeper waters at 40°N. In general these hauls have low factor loadings for these two groups, and the faunal assemblages can be considered to be influenced by one of the other groupings. In fact three of the hauls at 30°N, 23°W have quite high secondary loadings for group 9 and the appearance of this zone at about 1000 m at 40°N, 20°W may indicate the influence of Mediterranean water at these two stations.

The distribution of siphonophore zone 1 is difficult to explain as it is more generally associated with the surface waters at the more northerly cold-water stations, although it is also present in the deep waters at Bermuda. This zone at 40°N, is dominated by two species *Lensia conoidea* and *Chuniphyes multidentata*, the former of which is also numerous in the more northerly surface waters and the deeper waters off Bermuda. *L. conoidea* is also an important species in the Mediterranean and so its presence in the deep waters at 40°N may be some relic of this population carried to the area in the outflow current.

6) A comparison of the eastern North Atlantic zones with those at Bermuda shows that the same four zones found at 18°N 25°W and 30°N 23°W are present in the top 1000 m of water in the Sargasso Sea. However, the preponderance of the 18°C water in the latter area has pushed the permanent thermocline much deeper than in the eastern North Atlantic and this is reflected in the greater depth of the boundary between zones 2 and 6.

The other important boundary is between zones 4 and 3 which is close to the level of the 8°C isotherm or the oxygen minimum layer. Above this is the North Atlantic Central Water. Analyses of the depth distributions of the individual siphonophore species show that there is often a boundary around 400-600 m depth, with certain species, usually diel migrants, above and other non-migrant species below this depth. Thus the division of the North Atlantic Central Water mass into two zones with a boundary in the 400-600 m depth region probably reflects this change over in population.

Below 800 m at Bermuda siphonophore zone 3 reappears. In the eastern North Atlantic it was thought to be influenced by Antarctic Intermediate and Mediterranean waters, but in the western North Atlantic the Antarctic Intermediate Water does not appear to penetrate as far north as 32°N (Bermuda). Mediterranean water can still be detected in the deeper waters off Bermuda although it must have taken a considerable time to diffuse so far across the North Atlantic Ocean. Thus the similarity between these deep zones on either side of the North Atlantic Ocean probably indicates that there is a widespread bathypelagic population of siphonophores which is unaffected by the physical characteristics of the water masses. Nonetheless the siphonophore assemblages in the top 1000 m of water on either side of the North Atlantic Ocean have been shown to be different (Pugh, 1975). This exemplifies the earlier conclusion that the differences between these populations are not necessarily due to there being different species present in each area but to the proportional contribution of the various species.

It is difficult at this early stage in the analyses of the results to draw any major conclusions. However, there are some clearly defined zones which contain distinctive siphonophore assemblages, and broadly these can be associated with the known physical characteristics of the water. For instance, there is an assem-

blage of siphonophores above the permanent thermocline in the warmer waters of the North Atlantic Ocean and this association can be used to predict that the surface population at the equator should be quite different. This is because of the extreme shallowness of the permanent thermocline on the equator and the presence of complex convergent and divergent zones in that area. Although the equator station results have not been analysed statistically it is apparent from the raw data that the surface fauna is different from that present at the stations further north. *Ceratocymba leuckartii* is the most important species in the surface waters at the equator, whereas further north other species such as *Hippopodius hippopus, Diphyes dispar, D. bojani, Chelophyes appendiculata* and *Bassia bassensis* play a dominant role.

As there appears to be some relationship between the boundaries of the faunal zones and those of certain water masses it is interesting to establish how much of the total sample variance can be explained by the physico-chemical properties of the waters. Fasham and Foxton (in preparation) have erected an hypothesis, based on the known physico-chemical properties of the various water masses, and have tested to see how well this fits the established distributions of various zooplankton taxa. Preliminary results using this technique have shown that a substantial proportion of the total sample variance can be attributed to the water masses, thereby indicating that the geographical distribution of many planktonic animals is affected to some extent by the physico-chemical properties of the seawater.

Although the statistical analyses of the siphonophore data are incomplete some points do emerge from the preliminary results. Many siphonophores have widespread distributions in the Atlantic Ocean (Margulis, 1972) and in the open ocean there is little evidence that "indicator" species of siphonophores can be associated with certain water masses. Instead characteristic assemblages of zooplankton should be sought after. The pattern of distribution of the siphonophores in the North Atlantic Ocean can be split into several zones each of which contains a separate faunal assemblage. It has been shown that these zones have certain similarities to the distribution of the water masses in the Ocean and it is apparent that the physico-chemical properties of the waters are playing some role in affecting the distribution of the siphonophores. Thus there is little point in studying the zoogeography of siphonophores without taking into account the fact that any one water column may contain several faunal zones, the boundaries of which may to some extent be affected by the physico-chemical properties of the various water masses present.

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