TROPHIC FACTORS AFFECTING THE DISTRIBUTION OF SIPHONOPHORES IN THE NORTH ATLANTIC OCEAN

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INTRODUCTION

In spite of the general lack of consideration given to siphonophores and the significant role that they play in marine ecosystems, there is a reasonable amount of information on their geographical distribution in the World's oceans, particularly for the North Atlantic. Much of the earlier data has been summarized by Margulis (e.g.1972), who drew up distributional maps of 'total ranges', and broadly divided the species into boreal, tropical and equatorial forms. The patterns of distribution were considered to be consistent with those established for other planktonic/nektonic organisms and were related to the basic division of the oceans into various water masses. However, these 'total range' maps give no information on regional differences in the relative abundance of an individual species, nor do they take into account vertical distribution patterns (see Pugh, 1977). The latter situation partially was rectified by Margulis (1984), but again the conclusion were based on first and last capture principles.

Fasham & Angel (1975), using data on ostracods, demonstrated that it was necessary to consider all aspects of the regional, vertical and numerical distribution of the various species in order to establish faunal zones. They found that such zones, several of which could be present in any water column, were typified by the presence of certain species that had characteristic relative numerical abundances, and that it was rare for an individual species to be wholly confined to one zone. Many of these zones could be associated with hydrographical features, but for others the correspondence was not so apparent. A similar conclusion was reached by Pugh (1977) for siphonophores, and Fasham & Foxton (1979) for decapods. The general conclusion from all such studies, as succinctly summarized by Haedrich &

Judkins (1979), was that the faunal change was not always abrupt, even in the region of major physical boundaries (see Domanski, this volume), and that there is not necessarily an absolute response by an individual species to a change in water mass. Other more subtle reasons may be affecting the distribution of pelagic organisms. This possibility is examined in relation to the distribution of siphonophores in the N.E. Atlantic, using data from ten stations located between the equator and 60°N.

DISTRIBUTION PATTERNS

Certain underlying trends appear from these data, for example:-

1. Species diversity is highest in the warmer, more southerly waters around 18°N (Fig. 1) and declines both towards the equator, and more markedly towards the north. This is a general feature for many groups of pelagic organisms.

2. Neither the numerical abundance nor the biomass (displacement volume) of siphonophores follows the same trend. The data for the 21 most abundant calycophoran species (nectophores only), show two peaks of numerical abundance, one between 11°N and 18°N, and the other between 40° and 50°N (Fig. 1). However, biomass tends to increase with increasing latitude and, overall, gelatinous organisms are very important contributors to the total biomass of pelagic organisms at higher latitudes.

3. The great reduction in the number of species towards the north is largely accounted for by the disappearance of near-surface living forms. These species, which can occur in large numbers in warm surface waters, mainly belong to the calycophoran families Diphyidae and Abylidae, and *Diphyes bojani* is taken as an example (Fig. 2A). In contrast, the increase in siphonophore
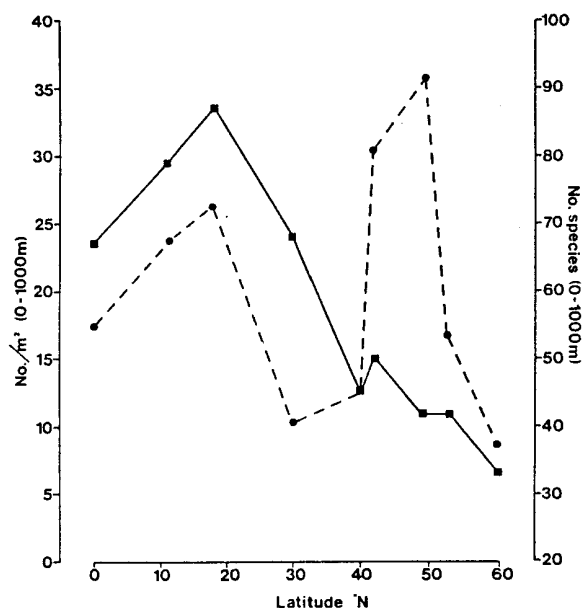
Fig. 1 The geographical distribution in the N.E. Atlantic Ocean (see Fig. 3 for exact positions) of the total number of siphonophore species (□—□) and the number of specimens m⁻² (21 commonest calycophoran species) (O--O) present in the net samples collected in the top 1000m of the water column.

numbers between 40° and 50°N is caused by large numbers of a few deep-living species (e.g. *Rosacea* spp.)(Fig. 2 B,C) that mainly belong to the calycophoran families Prayidae, Hippopodiidae and Clausophyidae. These deep-living species, although commoner at higher latitudes, generally have widespread distributions.

The change-over between the geographical distribution and numerical abundance of the major calycophoran families of siphonophores can be related directly to the regional differences in biomass. The near-surface living abylids and diphyids are mainly small, active predators; the deeper living families are generally larger and slow moving. Although these major differences in the faunal assemblage of siphonophores in warmer and colder waters can be associated with various water masses (Pugh, 1977) , there may be other factors that play more important roles. One such factor could be the dietary preferences of the individual siphonophore species.

Siphonophores are carnivorous animals, mainly feeding on crustaceans especially copepods, and undoubtedly they play an important role in the pelagic ecosystem. Recent studies by Purcell (e.g. 1980; 1981) have shown that siphonophores are selective feeders and the preferred diet of an individual species can, in general, be related to certain morphological and behavioural characteristics. Morphologically, there appears to be a direct relation between the size of the feeding polyps (gastrozooids) and the size of the prey captured. Behaviourally, although probably as a consequence of the morphology, those species with smaller gastrozooids tend to be more active and rapid swimmers*. There are also differences in feeding strategy (Biggs, 1977). Active swimmers frequently alternated between periods of swimming and 'fishing', and set, often complex, tentacular nets to ensnare their prey. Weaker swimmers tend to spend longer periods 'fishing', with their tentacles simply hanging down from the stem. These behavioural differences may be related to the fact that the swimming speed and activity of crustacean zooplankton generally increases with size (Mauchline, 1972). Thus, the larger siphonophores simply have adopted a 'sit in wait' strategy since the chances of encountering a suitable, large prey item are increased by the latter's greater activity. Similarly, the lesser abundance of such prey can be offset against the energy savings resulting from the siphonophore's lack of swimming activity.

The question thus arises as to whether these differences in dietary preference and behaviour, for the two sharply distinct siphonophore assemblages in the warmer and colder waters of the N.E. Atlantic, can be correlated with geographical and vertical differences in the distribution of their preferred prey? Although, unfortunately, a fully comparable data set for potential prey items e.g. copepods and ostracods, is not yet available, there appears to be some general evidence to support this supposition. Within a single water column there is a general trend for the mean body size both of an individual species (Bergmann's rule-see Mauchline, 1972)

*the discussion here is limited to the calycophoran species, as these are the only ones sampled quantitatively by nets - see Pugh (1984).
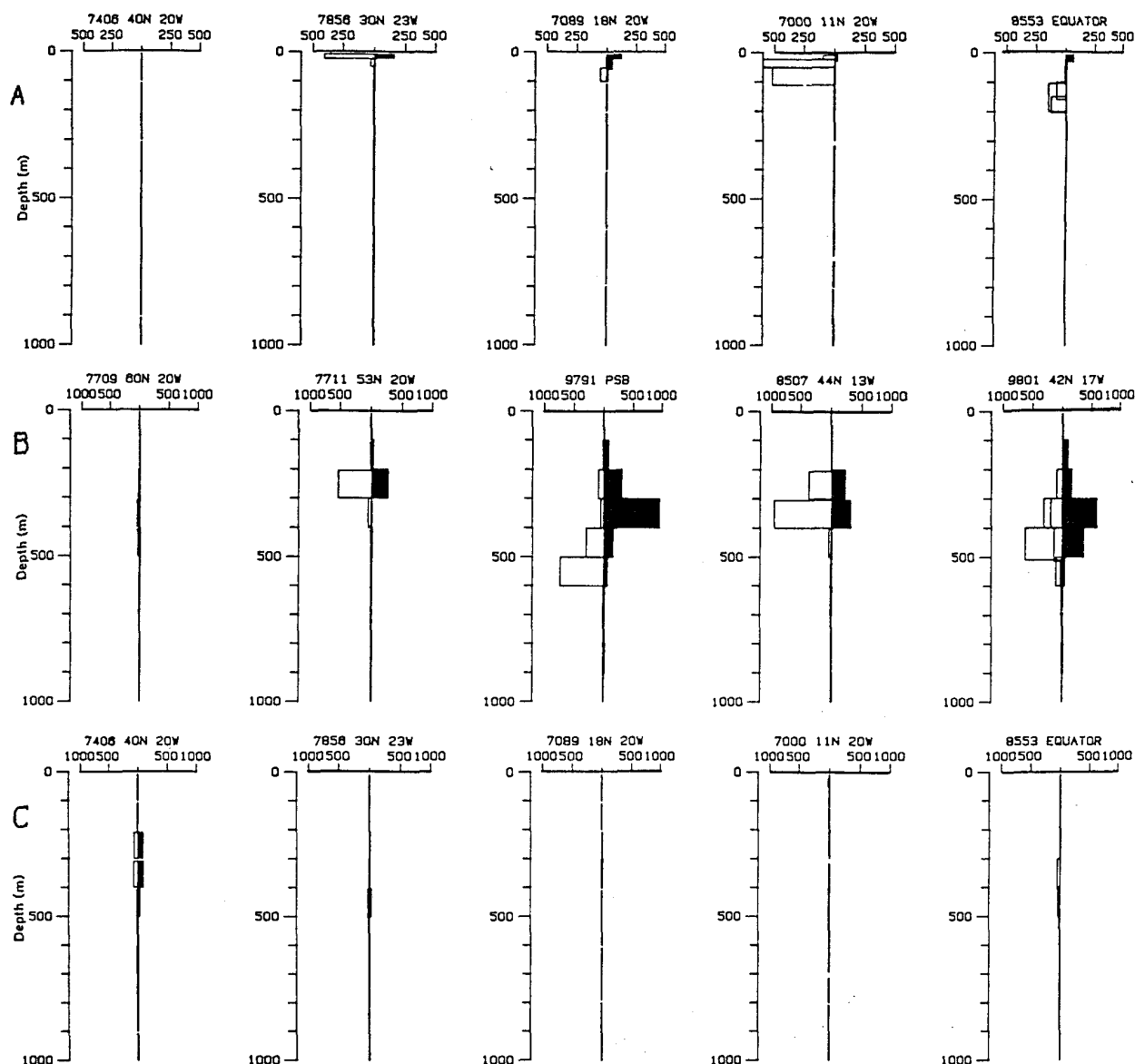
Fig. 2 **A** The vertical distribution of *Diphyes bojani*, by day and night (left and right of ordinate, respectively). Number of anterior nectophores/10^4m^3, at various localities (see headers) in the warmer waters of the N.E. Atlantic Ocean. No specimens of *D. bojani* were found north of 40°N. **B** - **C** The vertical distribution of *Rosacea* spp. at various localities in the N.E. Atlantic Ocean. Number of nectophores/10^4m^3. PSB= Porcupine Seabight ca. 49°30'N, 14°W; Equator= 0°N, 22°W. The numbers in the headers for each histogram refer to RRS 'Discovery' Station numbers, except for Sta.7000 which is an amalgam of 'Discovery' Sts 6662 and 7824.

and of a taxonomic group, particularly crustaceans, to vary inversely with temperature, at least within the top 700-1000m of that water column. Thus, Roe (1972) found, for copepods in the top 1000m of the water column around the Canary Islands, that 57% of the total displacement volume occurred within the 500-600m depth range, while ca. 30% of the total numbers were present at the shallowest depths (40 and 50m) sampled. The vertical distribution patterns of siphonophores (Pugh, 1974), and their projected dietary preferences, fit in well with this general

scheme of increasing prey size with depth. The preponderance of small items, e.g. copepods and ostracods (see Angel, 1979) in near-surface warm waters can be linked with the presence there of small actively swimming siphonophores, many of which undergo diel vertical migrations (Pugh, 1977). At deeper depths the larger mean body size, but lesser abundance, of the prey would suit the presence of larger, less active siphonophore species, and these do predominate there.

In order to explain the disappearance of small, shallow-living siphonophore species at more northerly latitudes on the same basis it would be necessary to find a concomitant decrease in small prey items. Certainly, as with depth, there is a trend for an increase in the mean body size of a population in the colder, northerly waters (e.g. Grice & Hulsemann, 1965), but in the superficial layers of such waters the situation is complicated by the moderately large seasonal changes in temperature. Thus Deevey (1960) found that, for certain copepod species, not only was there an inverse relation between body size and water temperature, but also a direct correlation between mean size and the quantity of phytoplankton material available. This might be related to the large seasonal fluctuations in primary productivity, but it is probable that a more important factor is the seasonal change in the size distribution and specific composition of the phytoplankton population itself (Holligan & Harbour, 1977). The body size of the herbivore thus being directly related to the mean size of the available phytoplankton cells. If this relation also holds between the siphonophores and their potential prey, then one might expect seasonal fluctuations in the specific siphonophore population, and its numerical abundance, but unfortunately insufficient data are available in this context. However, the northward spreading of certain shallow-living siphonophore species during the summer months (unpubl. data) would be consistent with this.

Other data also indicate a marked geographical change in the size distribution and abundance of potential prey. For instance, the ostracod population in the top 300m of the water column at 30°N 23°W and at 44°N 13°W (Angel 1977;

1979) were markedly different, with large numbers of small species being present at the former position, whereas overall numbers were very low at the latter. Below 300m depth, the population numbers at both stations were very similar. These facts can be related to the distribution of hippopodiid siphonophores, for Purcell (1981) found that the near-surface living species, *Hippopodius hippopus*, fed almost exclusively on ostracods. Thus, it was not surprising to find that *H. hippopus* was common at 30°N, but was totally absent at the 44°N site. If one can extrapolate these dietary requirements to the closely related species, of the genus *Vogtia*, then the deeper depth distribution of these means that they could exploite the larger-sized ostracod population present at all latitudes.

However, with regard to the potentially more important prey, copepods, Roe (1984) found that, at 44°N 13°W, small *Clausocalanus* spp. predominated at four depths, between 100 and 600m, whereas in the Canary Island region these species were concentrated at the shallowest depths and were less abundant (Roe, 1972). Nevertheless, the total number of copepods was far greater at 44°N than further south, the enhancement in numbers being particularly marked at the deeper depths sampled, and this could be associated with the increased number of deeper-living siphonophores found at more northerly latitudes.

CONCLUSION

Thus, despite the necessarily superficial nature of the comparisons, it is concluded that the size distribution and abundance of the potential prey population at any one locality and depth plays an important role in determining the structure of the specific siphonophore assemblage associated with it. As Headrich & Judkins (1979) concluded, it is relatively easy to establish correlations between variations in the hydrological conditions and the distributions, both vertically and horizontally, of certain species, but other underlying factors, such as trophic relations, may be playing a more immediate part in controlling these distributions.

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