Co-occurrence of hippopodiid siphonophores and their potential prey

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Abstract

It is a truism that the distribution of a predator should reflect that of its potential prey, but this is not well established for marine plankton communities. Purcell (1981) found that many siphonophore species were selective feeders and that one, *Hippopodius hippopus*, fed exclusively on ostracods. Pugh (1986) speculated that if such a dietary specificity also applied to other hippopodiid species, then a distributional relation between them and ostracods might be expected. This premise is examined using data from 'Discovery' stations in the N.E. Atlantic Ocean. A clear relation is found between the abundance of ostracods and hippopodiids, while copepods have a better relation with other calycophoran siphonophores.

Introduction

Nets have been used extensively over the past century to establish patterns of distribution of various zooplankton/micronekton populations. Statistical analyses of such data have shown that there are various faunal zones which can be related to the prevailing hydrological conditions (Fasham & Angel, 1975 – for ostracods; Pugh, 1977; Mackie *et al.*, 1987 – for siphonophores). However, since no 2 species, at least within a given taxon, have exactly the same distributional pattern, and since rarely is an individual species wholly confined within one of these statistically derived faunal zones, it is apparent that behavioural factors also are important in determining the characteristics of a given population. Thus, in zooplankton, as Isaacs (1977) concluded, the size structure of the potential food items is the foremost factor determining the structure of the pelagic food web. However, physical processes, particularly those determining seasonal and latitudinal variations in the depth of the thermocline, ultimately will determine the intensity of primary production and the size structure of the near-surface phytoplankton population.

Purcell (1981) found that in siphonophores there was a general relation between the size of the feeding polyps (gastrozooids) of a given species and the size of the prey it consumed. Pugh (1986) used this information to suggest that the species composition of the siphonophore population at a given locality or depth was influenced greatly by the size-structure and abundance of the local prey population. Thus the abundance of small, actively swimming siphonophores above the permanent thermocline at lower latitudes in the N.E. Atlantic Ocean could be linked with the preponderance there of small prey species, particulary copepods and ostracods. At greater depths, the lesser abundance but probably larger size of the prey population could be related to the presence there of larger, less active siphonophore species. However, detailed comparisons were made difficult by the dearth of information on the size-structure of the potentially important prey populations.

Purcell (1981) also showed that prey selection is not always simply size-related, and that some siphonophore species actively select for certain prey types. One such species, *Hippopodius hippopus* (Forskål), was found to feed exclusively on ostracods, despite the fact that these animals represented only 18.6% of the potential prey population. Pugh (1986) noted that such a dietary preference might explain the presence of *H. hippopus* at one station, where ostracods were abundant, and its absence at another, where the ostracod population was sparse. The family Hippopodiidae (Siphonophora, Calycophorae) comprises 5 closely related and morphologically similar species. Pugh (1986) hence conjectured that if the dietary preference of *H. hippopus* applied to the other hippopodiid species there might also be a relation between their zoogeographical distribution and that of their ostracod prey. This possibility is addressed here. Although such a relationship would seem axiomatic, as Greene (1985) stated 'the role of selective predation in structuring marine plankton communities remains to be resolved'.

Methods

The data used here have been derived from specific identifications carried out on net samples collected over discrete depth horizons, usually 100 m, in the top 1000 m of the water column, at latitudes ranging from 11° to 60° N in the N.E. Atlantic Ocean, approximately on the 20° W meridian (20° W series). Each depth horizon was fished by day and night to allow some assessment of diel vertical migration patterns, using the Institute of Oceanographic Sciences RMT1 + 8 (Rectangular Midwater Trawl) combination net (Baker et al., 1973). Thus the distributional pattern of the small zooplankton groups, for example ostracods, caught by the finer mesh RMT1 net (mesh size 0.32 mm) could be compared directly with that of the larger micronekton groups, such as hippopodiid siphonophores, caught by the coarser RMT8 (mesh size 4.5 mm). The one exception to this was the samples collected at 11° N,

where the nets were fished separately and the finer mesh net was a modified Indian Ocean Standard net of similar mesh size and mouth area to the RMT1.

Comparable ostracod (identified by Dr M.V. Angel) and siphonophore data exist from 6 of these 20° W series stations. Initial analyses were carried out on all the data. However, only 3 stations (at 11°, 30° and 60° N) will be considered in detail here, as the data represent the extremes of the distribution patterns, while the others fall in between. The data on ostracods, on the asexual stages of all calycophoran siphonophores, and on hippopodiid nectophores, all normalized to unit volume of water filtered, were extracted from the Institute's computerized biological database, which contains records of over 60 000 specific identifications from a variety of pelagic taxa. Comparisons are also made with some copepod data available from the 30° and 60° N stations.

Results and discussion

Feeding

Purcell (1981) collected 5 specimens of the epipelagic species, *H. hippopus*, that had migrated into the SCUBA diver's depth range at night. Examination of the contents of 100 gastrozooids, 94% of which contained prey items, showed that this species had fed exclusively on ostracods of carapace-length 0.4–1.4 mm (mean = 0.86 mm). The mean length of the gastrozooids was 3.3 mm. With such a specialized diet it is unlikely that *H. hippopus* is also size selective, especially since the size of the vast majority of the ostracod population lies within the 0.5–1.5 mm carapace-length range (Angel, 1979).

Since the gastrozooids of siphonophores are usually lost or detached during net collection the only means by which the diet of the deeper living species can be established is to examine material collected by submersibles. The 4 deeper living hippopodiid species should probably be considered congeners of *H. hippopus* but 'for the sake

of maintaining stability in nomenclature' (Totton, 1965) are currently referred to the genus *Vogtia*. Nine species of *Vogtia* species were collected by the submersible 'Johnson-Sea-Link' (P.R. Pugh, unpubl.) and the gastrozooids of all of these have been examined. Unfortunately only one gastrozooid was found to contain any recognizable remains, but this was a carapace of the ostracod *Conchoecia curta* Lubbock. The carapace was 0.8 mm long, while the gastrozooids of the *Vogtia* species were up to 3.5 mm long. Nonetheless, this single piece of evidence at least indicates that ostracods are eaten by deeper living hippopodiids. The absence of remains in these deep living specimens is not necessarily surprising, and need not reflect a scarcity of potential prey items. Probably it is a reflection of the delay between capture and preservation, during which time any undigestible fragments would have been egested from the gastrozooids. Mackie & Boag (1963) found crustacean exoskeletons to be egested within 1 h.

Depth distribution

Figure 1 shows the depth distribution of hippopodiid siphonophores and ostracods, by day and night, at the 3 selected positions in the N.E. Atlantic Ocean. The ostracod totals are subdivided, where practicable, into females, males and juveniles (all stages), while the hippopodiid nectophore totals are subdivided by species. It is clear that, with one notable exception, there is a close similarity in the overall depth distribution of the 2 taxa and, moreover, that a relationship exists between the density of each taxon within a given depth range.

At 11° N ('Discovery' St. 6662 and 6665; February 1968) the 2 populations were concentrated mainly in the top 300 m of the water column, with little difference between day and night. The 4 *Vogtia* species were well represented, but less abundant than *H. hippopus*. *V. spinosa* Kefferstein & Ehlers and *V. pentacantha* Kölliker occurred mainly in the top 200 m, particularly the 100–200 m depth zone, while *V. glabra* Bigelow was found mainly between 100 and 300 m by day.

The deeper-living hippopodiid population was dominated by *V. serrata* (Moser).

Equal numbers of adult and juvenile ostracod stages were present in the top 100 m of the water column at 11° N, while at greater depths they were present in a 2:1 (adult:juvenile) ratio. Although 63 species of ostracods were identified most were relatively rare, and 65% of the total population was made up of just 5 species. Of these *Conchoecia elegans* Sars (28% of the total) was the most abundant, with maximum numbers in the top 100 m. Still, its long distributional 'tail' meant that it was found in most of the samples. *C. giesbrechti* Müller (14% of the total) was the second most abundant species and again showed a population maximum in the top 100 m. The carapace length range of the predominant ostracod species was 0.6–1.65 mm (Angel, 1979 and unpublished data).

In contrast to the 11° N station, where there was little indication of a diel vertical migration, such a migration was clear for several of the species found at 30° N ('Discovery' St. 7856, April 1972). These regional differences in migration pattern were almost certainly related to differences in the thermal structure of the water column (Fasham & Angel, 1975). The populations of both ostracods and hippopodiids were considerably more abundant at 30° N than at the other 2 stations considered here. *H. hippopus*, as at 11° N, was the predominant hippopodiid and the data indicate a pattern of diel vertical migration resulting in a fairly widespread depth distribution, between 50 and 400 m by day, with a concentration of the population in the top 200 m at night. *V. glabra* also was most abundant at 30° N, and had a deeper depth distribution than at 11° N. During the day most of the population occurred in the 300–600 m depth range, with a possible migration into the 200–500 m depth zone at night. However, as discussed by Pugh (1984), it is likely that for each individual animal such a migration was only on a small scale. *V. serrata* was present in similar numbers to those found at 11° N and again had a widespread depth distribution, from 400 to > 1000 m.

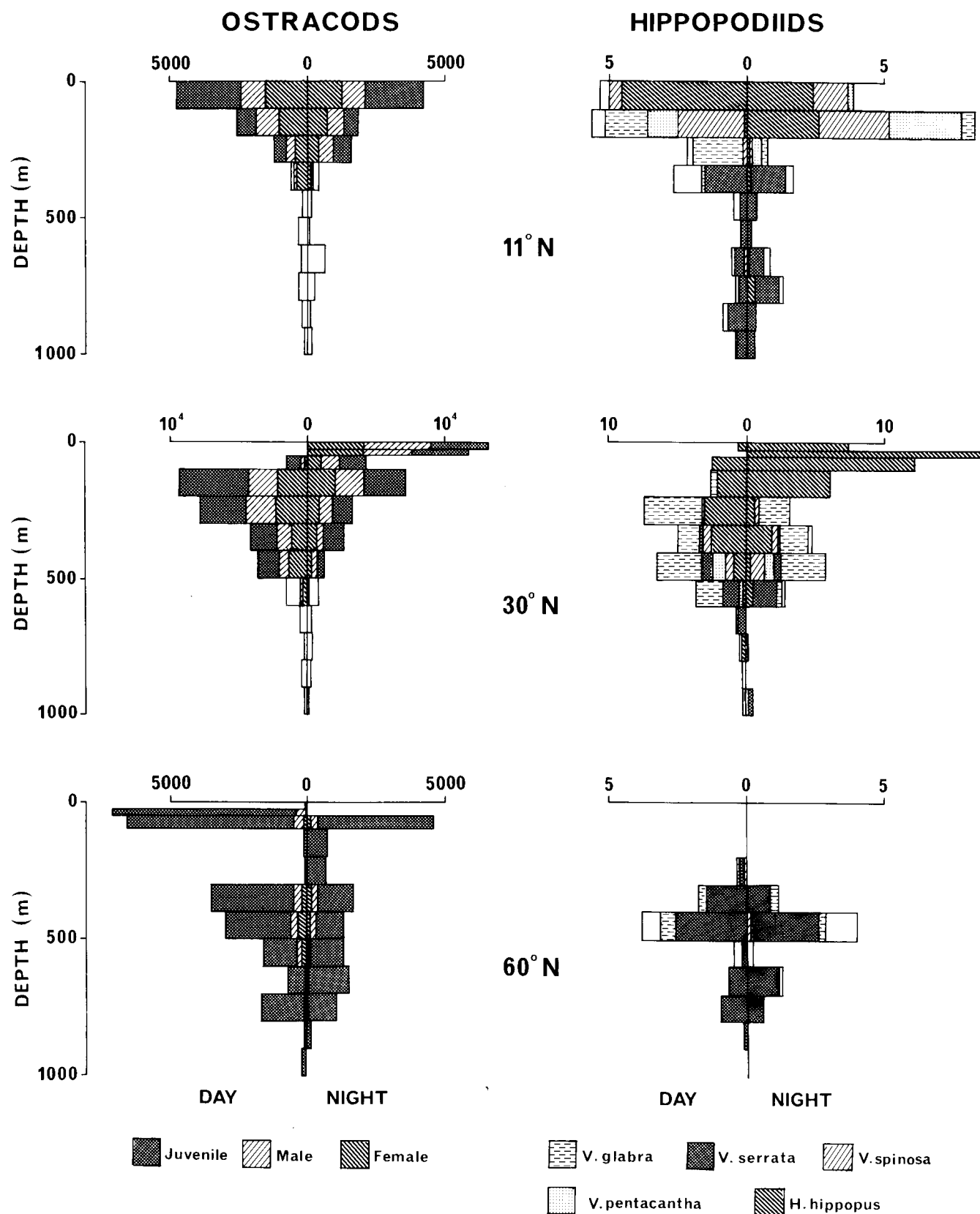The number of ostracod species (67), and the

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Fig. 1. The depth distribution, by day and by night, of ostracods (number.10^3 m^{-3}) and hippopodiid species (necto-phores.10^3 m^{-3}) at 3 'Discovery' stations in the N.E. Atlantic Ocean.

overall ratio of adults to juveniles (3 : 2), at 30° N was similar to that at 11° N, and many species were common to both stations. However, their order of dominance was quite different and there was no enhancement of the juvenile population in the top 100 m. Virtually no ostracods were found in the top 50 m of the water column during the day, while the main population was found between 100 and 300 m. Diel vertical migrations brought a large portion of this population into the top 50 m at night; a pattern that was reflected accurately by *H. hippopus*. A single species, *Conchoecia curta*, which Angel (1979) described as 'one of the most abundant species in tropical and subtropical waters', dominated the ostracod population, contributing *ca* 43% to the total numbers. This species has a carapace length range of up to 0.8 mm, depending on the developmental stage, and was the one found in the gastrozooid of *V. serrata*, as noted above. By day this species was found mostly in the 100–500 m depth zone; but there was a stage separation with the maximum number of adults occurring between 300 and 400 m, while the juveniles were concentrated in the 100–200 m depth range. At night both juveniles and adults migrated into the top 50 m. The second most abundant species, which represented *ca* 12% of the total numbers, was *C. procera* Müller. By day all stages of this species were confined mostly to the 100–300 m depth zone. A substantial diel migration was undertaken by only a proportion of the females; although the remainder of the population was concentrated in the 100–200 m depth zone at night. The carapace length range of this species was 0.9–1.2 mm.

Despite the differences between the diel vertical migration patterns of the ostracod populations at 11° and 30° N, it was clear that their overall depth distributions were reflected closely by those of the hippopodiid siphonophores. This was also true at 60° N ('Discovery' St. 7709, April/May 1971) at depths below 200 m. However, at shallower depths no hippopodiids were found although a relatively large ostracod population was present there. The relative contribution of each species to the total hippopodiid population

was very different from that found at the more southerly stations. The population was dominated by the deep living species *V. serrata*, whose numbers were approximately double those found at the other 2 stations. In contrast *V. glabra* and *V. spinosa* were relatively rare, while *H. hippopus* and *V. pentacantha* were absent.

The ostracod population at 60° N also differed from those at more southerly stations, both in the order of dominance of the 38 species present and in the proportions of juveniles and adults. Clearly seasonal effects were an important controlling factor at this station, and the ostracod population was in the process of reacting to the onset of the spring bloom. Juveniles made up almost 90% of the total population, and more than 95% of the specimens wee found in the top 100 m, where a single species, *Conchoecia obtusata* Sars, predominated. The carapace length range of the juveniles of this species was 0.6–1.0 mm. In the 300–800 m depth range, where the bulk of the ostracod and hippopodiid populations occurred, *C. obtusata* remained an important contributor to the ostracod population together with *C. elegans*, *C. hyalophyllum* Claus, *C. haddoni* Brady & Norman, *C. teretivalvata* Iles and *C. borealis* Sars. Again, the juvenile stages of these species predominated, although the adults were more common than in the near-surface waters and contributed about 22% to the total. Although data are not available on all species, the carapace length ranges of the juveniles were similar to that of *C. obtusata* (M.V. Angel, pers. comm.).

Density relations

The close relations between the relative abundances of ostracods and hippopodiids within a given depth horizon are demonstrated further in Fig. 2, where the density data from all 6 stations in the 20° W series are compared. This figure shows that when the 2 taxa co-occurred, there was a highly significant ($p \ll 0.001$) correlation between their population densities. Similar comparisons have been made between the densities of ostracods and other calycophoran siphono-
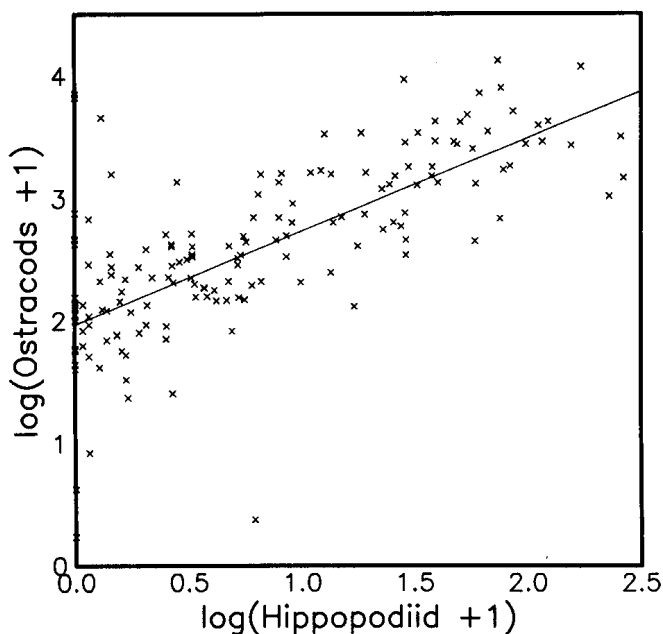
Fig. 2. Density relations between ostracods (log(number.10^3 m^{-1} + 1)) and hippopodiids (log(nectophores. 10^4 m^{-3} + 1)) at 6 'Discovery' stations in the N.E. Atlantic Ocean. Additional data from 'Discovery' St. 7711, 53° N 20° W; St. 7406, 40° N 20° W; and St. 7089, 18° N 25° W.

phores; and between copepods and hippopodiids or other calycophores. These show that although there was a correlation between ostracods and other calycophores, its significance ($p < 0.01$) was much less than that for hippopodiids. Comparable copepod data are available from only two stations. At the 60° N station the only statistically significant correlation was between hippopodiids and ostracods. However, at the 30° N station ostracods were highly significantly correlated ($p \ll 0.001$) with hippopodiids, but not with other calycophores; while copepods were highly significantly correlated with other calycophores ($p \ll 0.001$) and less so with hippopodiids ($p < 0.01$).

Despite the overall correlation between ostracods and hippopodiids it is clear, particularly from the 60° N station data, that these 2 taxa did not always co-occur and that other factors were determining the observed distribution patterns. The distribution of the epipelagic species *H. hippopus* can be related to the presence and/or depth of the thermocline. In the N.E. Atlantic,

considerable numbers of this species occurred above the permanent thermocline at latitudes south of *ca* 40° N; but its presence north of 40° N appeared to be dependent on the development of the seasonal thermocline. Thus, it has been found to spread as far north as 50° N 14° W (P.R. Pugh, unpubl.) and to occur around the British Isles during late spring and summer (Kirkpatrick & Pugh, 1984).

Such high correlations between ostracods and hippopodiids, and between copepods and other calycophoran siphonophores, were unexpected, particularly in view of the suggested difficulties in quantifying siphonophore data from net collections. In most calycophoran species such quantification problems are unimportant (Pugh, 1984), but hippopodiids may be an exception. Each hippopodiid specimen comprises several, often 8–10, nectophores of varied sizes, which usually become separated during net collection. Thus there is a difficulty in estimating the number of individuals caught from the number of nectophores present, compounded by the fact that some of the smaller ones may be lost. However, loss or extrusion of material through the meshes of a net is not a problem unique to siphonophores, nor is it the only problem associated with the quantification of net-derived data. Net avoidance is another, as Angel (1979) discussed in relation to ostracods. Since the same net design was used throughout the sampling programme from which the present data were derived, it is probable that there was some consistency with regard to the problems associated with net collection. Thus it does not seem unreasonable to make direct comparisons between the data on hippopodiid nectophores and those on other taxa.

Conclusions

The present comparisons support the premise that if all hippopodiid species feed exclusively on ostracods, then a close relation between their distribution patterns would be expected. Although the existence of such an exclusive diet has yet to be fully substantiated for *Vogtia* species, the lack

of a highly significant correlation between the distribution of these species and the other major potential prey animals, copepods, is indicative. The significant correlation between copepods and other calycophoran siphonophores, which according to Purcell's (1981) data would be expected to feed extensively on them, gives further support to the worthiness of the present comparisons.

Assuming that hippopodiid siphonophores do feed exclusively, or even predominantly, on ostracods, then how has such a prey selectivity evolved? Siphonophores are 'entangling predators' (Greene, 1985; Madin, 1988) and generally adopt 'ambush strategies' to ensnare their prey. Since passive planktivory depends primarily on the swimming behaviour of the prey, do ostracods display a particular swimming behaviour that the hippopodiids, by some morphological or behavioural adaptation, have come to exploit? Lochhead (1968) likened ostracod swimming, a zigzag series of darts, to that of copepods, but he noted that the overall course of the former was more irregular and, for equivalent sized animals, faster. Although faster swimming would increase the encounter rate, this should be offset against the fact that copepods generally occur in higher densities than ostracods. Another behavioural characteristic of ostracods is that occasionally they stop swimming and sink at species specific rates between 0.5 and 2 cm sec^{-1} (Gooday & Moguilevsky, 1975). The sinking rate can be controlled and neutral buoyancy can be achieved. Angel (1969) suggested that the frequency and duration of sinking of a particular ostracod species might be related to the magnitude of its diel vertical migration. This would argue against this behaviour being of significance for prey encounter with hippopodiids, as the magnitude of the diel vertical migration of the epipelagic populations of both ostracods and hippopodiids was low at the 11° N station but considerable at the 30° N one (Fig. 1).

Hippopodiid siphonophores possess several distinctive morphological features, not least of which is the possession of 10 or more nectophores instead of the usual 2. However, only 2 are used

in locomotion (Mackie & Boag, 1963). Another feature is the absence of bracts on the stem, resulting in the stem hanging down vertically from the nectophore region. Neither of these features, nor some of the interesting behavioural responses of *H. hippopus* reviewed by Mackie *et al.* (1987), would appear to be relevant to the present discussion. However, the tentacles and their numerous side branches are comparatively very long (Totton, 1965). Thus, they would be expected to define a relatively large 'encounter zone' (Madin, 1988), although the comparatively low number of tentacles (Purcell, 1984) reduces the tentacle density. Purcell did not find anything remarkable about the morphology of the tentacles of *H. hippopus*, or of their nematocysts which were of the 4 types characteristic of most calycophoran species.

Clearly there is still a great deal to learn about the general behaviour of siphonophores and how certain species, as appears to be the case of hippopodiid siphonophores, have evolved such highly selective feeding strategies.

Acknowledgements

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