I.O.S.

GREAT METEOR EAST: A BIOLOGICAL CHARACTERISATION

BY

H.S.J. ROE ET AL

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Great Meteor East: a biological characterisation

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GREAT METEOR EAST: A BIOLOGICAL CHARACTERISATION

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Abstract (100-200 words as desired) The structure and composition of the biological communities inhabiting the water column and sea bed at Great Meteor East are analysed quantitatively and qualitatively. The results are compared with previous observations. No evidence has been found to suggest that mass biological transfer of radionuclides from the sea bed to the surface will occur at GME. Some biological pathways exist whereby radionuclides could move through the water column via the biota, but the incidence of these pathways and the biomass involved is extremely low. It is emphasised that the present data are derived from a single set of observations. Further work is needed to verify the present results and to assess the effects of variability and seasonality on the biological communities at Great Meteor East.

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1. INTRODUCTION

This report describes and analyses results obtained on RRS Discovery Cruise 156 to Great Meteor East - GME (Roe, 1985a). The cruise was primarily biological and was intended to provide a biological characterisation of the site for the Department of the Environment.

Work at GME commenced on 27 June 1985 and was completed on 21 July. Sampling at GME was done in and around a 10km square centred at 31°17'N 25°24'W. This square was chosen by IOS in response to a DoE request to concentrate work at GME within a 100 km^2 area. Of necessity our trawling extended beyond this square, but both this and the physical observations were concentrated within the smallest practical area - bounded by 30°49' - 31°35'N and 24°51' - 25°37'W (Figs. 1.I, 1.II, Table 1.1).

In addition to site specific studies, shallow CTD casts with chlorophyll *a* and nutrient observations were made on passage to GME (Table 1.1), and Expendable Bathythermograph (XBT) transects were worked *en route* to and from the site.

A few parts of this report have been presented previously. An interim report on the biological sampling at GME (Roe, Domanski and Fasham, 1986) described and discussed the general physical oceanography of the area, the vertical distributions of chlorophyll *a* and nutrients, and primary production measurements and results. Tyler and Muirhead (1986a) described aspects of echinoderm reproduction based on material collected on Discovery Cruise 156. For the sake of completeness this work is all reproduced either totally or in summary in this final report (Sections 2-4, 28). Following a description of the various sampling methods and laboratory analyses the midwater and benthic faunas are discussed by individual authors. An overall discussion and summary completes this report.

2. PHYSICAL OCEANOGRAPHY M.J.R. Fasham

The GME investigations were carried out in a box contained within latitudes 30°49'N and 31°35'N and longitudes 25°37'W and 24°51'W. According to Siedler, Zenk and Emery (1985) this would put it to the south of the subtropical front (Fig. 2.I) that represents the eastwards extension of the Azores Current (Gould, 1985). This front is typified by a marked change in the depth of the isotherms and the XBT survey carried out en route to and from GME showed that the front was crossed at around 33°5'N, 23°3'W (Fig. 2.II). Note that the depth of the 16°C isotherm changes by 200m across the front. No significant change in the depth of the 16°C isotherm was observed during the work at the GME site, indicating that there was no southerly movement of the front during the cruise.

Stramma (1984) has used historical temperature and salinity data to calculate the integrated volume transport between 0 and 800m in the south-eastern Atlantic (Fig. 2.III). These show that in the GME area the prevailing current direction is likely to be south-easterly.

Deep CTD profiles down to 5424m were made on five occasions during the cruise. The profiles of potential temperature, salinity and sigma T against depth for station 11262#7 are shown in Fig. 2.IV and the potential temperature versus salinity plot in Fig. 2.V. These show the familiar water mass structure for this part of the North Atlantic with North Atlantic Central Water in the top 800m overlying Mediterranean Water which shows up as a salinity maximum at around 1100m. Below 3000m the temperature and salinity show the uniform characteristics of Atlantic Deep Water.

3. VERTICAL DISTRIBUTION OF CHLOROPHYLL AND NUTRIENTS M.J.R. Fasham

On the initial leg out to the GME site a series of vertical profiles of temperature, salinity, chlorophyll a and nutrients were made. There was a marked change in the vertical distribution of chlorophyll a on crossing the front at 33°5'N (Fig. 3.I). North of the front the Deep Chlorophyll Maximum (DCM) was at a depth of between 28 and 70m (mean = 50m, s. dev. = 17m) and had a magnitude between 0.6 and 1.2 mg m^{-3} chlorophyll a (mean = 0.68, s. dev. = 0.19). Whereas to the south of the front the DCM was at a depth between 88 and 105m (mean = 98, s. dev. = 9.7) and had a magnitude between 0.38 and 0.52 mg m^{-3} chlorophyll a (mean = 0.46, s. dev. = 0.07). A similar reduction in the magnitude of the DCM on passing southwards across the front has been observed farther west in the Azores Front (Fasham et al, 1985) and is considered to be a permanent feature of the phytoplankton chlorophyll distribution.

Shallow CTD dips to 300m were made on eleven occasions on the first leg of the cruise which provided vertical distributions of temperature, salinity, density, chlorophyll a concentrations and underwater irradiance. A typical vertical distribution of these variables for GME is shown in Figs 3.II and 3.III for station 11261#42. There was a very shallow mixed layer of approx. 6m below which the seasonal thermocline extended down to around 100m. The DCM was at a depth of 95m with a magnitude of 0.47 mg m^{-3} chlorophyll a. The 1% light level was at 86m. Good underwater irradiance profiles were obtained on six occasions and the mean depth of the 1% light level was 87m with a standard deviation of 4m. There was a significant difference at the 1% level between the depth of the 1% light level and the depth of the DCM.

Some nutrient samples were taken and showed the usual structure of high values at depth (5.5 to 6.0μM of nitrate/nitrite at 300m), decreasing through a nutricline to values of less than 1μM nitrate/nitrite within the DCM and in the surface 100m.

4. PRIMARY PRODUCTION

P.A. Domanski and M.J.R. Fasham

Primary production experiments

Four experiments were run at the GME site to estimate the daily rate of carbon fixation due to phytoplankton photosynthesis. The method used was the Carbon-14 technique (Steeman Nielsen, 1951, 1952) in which known amounts of radioactively labelled sodium bicarbonate ($^{14}CO_3^-$) are added to seawater samples containing natural phytoplankton communities. If the total amount of CO_2 in the sample water is known and a measured amount of $^{14}CO_2$ is added, then by determining the amount of ^{14}C incorporated into the phytoplankton after an incubation period the total amount of carbon assimilated can be calculated.

Sampling

Water samples for light saturation experiments were collected with 7 litre Niskin bottles using the hydrographic winch. The bottles, together with all sample water containers used during the experiment had been thoroughly cleaned prior to going to sea, first using acid washes (0.25M nitric followed by 0.25M hydrochloric) then rinses with double distilled water. This precaution was taken to remove trace metals which would have had a detrimental effect on the algal communities being measured (Fitzwater, Knauer and Martin, 1982). Most of the samples were obtained from the deep chlorophyll maximum layer (DCM) but two samples were taken about 20m above this depth. Small volumes were drawn off from the samples for the determination of chlorophyll a concentration and additional sub-samples were taken and stored in Lugols and in 2% formaldehyde solutions for qualitative analysis of the flora.

Size fractionation

Post-incubation phytoplankton cultures were removed using two types of filter. To obtain estimates of total productivity samples were filtered through Whatman GF/F glass fibre discs, these effectively remove all phytoplankton (nominally >0.4µm). Nuclepore 1µm filters were also used and in three of the four experiments estimates of picoplankton productivity (ie. cells <1µm diameter) were obtained by subtraction of Nuclepore from GF/F results.

Incubation methods

Sample water was immediately transferred from niskin bottles to darkened Nalgene carboys and all subsequent sample handling was performed in subdued lighting. The incubation chamber essentially consisted of an insulated box taking two files of culture bottles with a light source in front enabling two productivity determinations to be carried out simultaneously. A Thorn 2000W halogen lamp was used as the light source; temperature control was achieved by three separate circulating water chambers - the main one being the incubation box itself. Cooling water was obtained from the ships seawater supply. Prior to filling, 60ml transparent polycarbonate culture vessels were first rinsed with the sample water and then injected with 0.1ml of sodium bicarbonate ^{14}C solution made up to give a "spike" of 10µCi per container. The vessels were then completely filled with the sample water, shaken and placed in the incubator. 1 ml extracts of the spiked samples were then taken from a number of cultures to obtain a more accurate measure of the specific activity of the ^{14}C added. These extracts were preserved in Fisosorb 2 scintillation cocktail for later measurement in the UK.

Each experiment comprised two light saturation runs of 36 cultures, filed behind the light source. The culture vessels attenuated the light over two and a half orders of magnitude ranging from about 500W m^{-2} in front of the light to 2W m^{-2} at the back: 33 cultures of each run were used for the light uptake and the remaining three blacked out to measure the dark reaction. Each culture bottle was carefully positioned and labelled so that later, when the ^{14}C uptake had been measured for each culture, corresponding light values could be ascribed. Incubation by exposure to the light source was set at 3hrs, after which the apparatus, complete with culture vessels, was removed to a darkened laboratory. Using a filtration rack and a mild vacuum pressure (< 10kPa) the phytoplankton in the cultures were deposited on to filters as quickly as possible. The filters were placed in glassine envelopes and stored at -20°C for later measurement in a scintillation counter. The culture vessels were then refilled with more water from the same sample and replaced in the incubation chamber.

Light attentuation curves were obtained by switching back on the light source and measuring the light level behind each culture bottle with a Crump lightmeter working from the back towards the lamp.

Sample analysis

^{14}C uptake by the cultures was measured at the radiological facilities at IMER, Plymouth. Unassimilated carbonate/bicarbonate was removed from the filters by exposing them to HCL fumes for 10 minutes prior to being transferred to vials containing Fisofluor 3 scintillation cocktail. Counting was performed using a Packard scintillation counter which provided data automatically corrected for quench. Carbon uptake was calculated using the method described by Strickland and Parsons (1972) and converted to specific production by dividing by the chlorophyll concentration of that sample.

Photosynthetic parameters

From the measurements of specific production, P^B and irradiance, I, a non-linear regression technique was used to estimate the parameters in the production-irradiance curve given by the equation

$$P^B = P_s(1 - e^{-\alpha I/P_s})e^{-\beta I/P_s} \qquad (1)$$

derived by Platt et al (1981) where P_s (mg C mg chl $\underline{a}^{-1}$ h^{-1}) is the light saturated rate of specific production in the absence of photoinhibition, α (mg C [mg chl $\underline{a}]^{-1}$ h^{-1} $W^{-1}m^{-2}$) is the initial slope of the curve and β (same units as α) is a parameter characterising the photoinhibition in light saturation conditions. An example of the experimental data and a fitted curve is given in Figure 4.I. P_{max}, the chlorophyll-specific photosynthesis at light saturation, or assimilation number, can be calculated from the parameters α,β and P_s using the equation

$$P_{max} = P_s\left(\frac{\alpha}{\alpha + \beta}\right)\left(\frac{\beta}{\alpha + \beta}\right)^{\beta/\alpha} \qquad (2)$$

and I_m, the irradiance at which photosynthesis is optimal can be calculated from the equation

$$I_m = \left(\frac{P_s}{\alpha}\right) \ln \left(\frac{\alpha + \beta}{\beta}\right) \qquad (3)$$

Parametric data for all four productivity runs are given in Table 4.1. Several points emerge from these data, firstly that phytoplankton from the DCM were photoadapted to a lower light regime than those from nearer the surface; I_m for three GF/F filtered samples from the DCM (ca 90-100m) varied between 23.23 and 61.8W m^{-2} whereas values for GF/F filters from the two samples 20m or more above the DCM were 74.4 and 80.35W m^{-2}. Secondly, in the DCM, P_{max} for GF/F filtered samples (ie. all phytoplankters >0.4μm) was considerably greater than corresponding values of P_{max} for 1μm Nuclepore filters. This implies that, in the DCM, the <1μm phytoplankton fraction had a greater photosynthetic efficiency than the >1μm component. This difference in efficiency was much less marked in a sample taken well above the DCM.

A third point worth noting is that, in the DCM, we have calculated values of 62% and 70.2% for the proportion of production attributed to the <1μm phytoplankton component, this agrees well with Platt et al (1983) value of 60% for picoplankton to the west of the Azores. However, it is interesting to note that, for above the DCM, we have obtained a value of 56.6% for the proportion of productivity due to the >1μm fraction. This does indicate some difference in the relative importance of the two size fractions at different depths in the euphotic zone.

Calculation of daily production

It is obviously of interest to estimate the total daily net primary production in the euphotic zone. If the chlorophyll a concentration at depth z (measured using the in situ fluorometer) is C(z) and the chlorophyll specific net production is P(z) then, assuming that there is no net growth of phytoplankton during the day, the daily production P_T is given by

$$P_T = \int_0^{24} \int_0^{z_e} P(z,t)C(z)\,dz\,dt \qquad (4)$$

where z_e is the depth of euphotic zone. It is generally considered (Dring and Jewson, 1982) that ^{14}C primary production measurements of duration 3-4 hours are estimates of gross rather than net production. An estimate of respiration rate is required to convert this to net production and it is usually assumed that the respiration rate is one tenth of the maximum photosynthetic rate P_{max} (Steeman Nielsen and Hansen 1959). P_{max} can be calculated from equation (2).

Using equation (1) for the gross production, the net production at depth z is given by

$$P(z,t) = P_s\ (1 - \exp(-\ \alpha I(z,t)/P_s))\ \exp(-\beta I(z,t)/P_s) - 0.1P_{max} \qquad (5)$$

where I(z,t) is the irradiance at a depth z and time t. It is now necessary to determine a parameterisation for I(z,t).

Fasham et al (1983) have shown that observed irradiance-depth profiles can be very well fitted using the equation

$$I(z,t) = \gamma I_o(t)(a_1 e^{-k_1 z} + a_2 e^{-k_2 z})\ \exp(-k_c \int_o^z C(z)dz) \qquad (6)$$

In this equation $I_o(t)$ is the surface irradiance at time t and γ the surface transmittance, k_1 and k_2 are the attentuation coefficients for two main components of the visible spectrum, and it is assumed that $k_1 < k_2$. a_1 and a_2 are the proportion of these components in the total irradiance and k_c is the phytoplankton self-shading coefficient which parameterises the light absorption of the phytoplankton. The surface irradiance at time t was calculated using the methods described in Brock (1981).

Fasham et al (1983) have shown how these parameters can be estimated from an irradiance-depth profile and such estimates were made for stations 11261#49 and 11261#59 for which good irradiance profiles were available (see Table 4.2). Stations 11261#25 and 11261#42 were observed very early in the morning and so parameters could not be estimated for these stations. The parameters for station 11261#59 were used for these stations when calculating P_T.

Using the equations given and the estimated parameters of the production-irradiance curves (Table 4.1, GF/F filtered samples) and irradiance-depth profiles (Table 4.2), the total daily production can now be calculated for the four stations from the profiles of chlorophyll a concentration. The depth of euphotic zone z_e was taken to be the depth above which the total net daily production was positive. A trial integration showed that this was approx. 87m, which interestingly was the same depth as mean depth of the 1% light level, which is often taken as representing the depth of the euphotic zone.

With the exception of station 11261#59 the estimates of daily production (Table 4.3) are very similar giving us some confidence in the mean value of 227mg C m^{-2} day^{-1}. However, it is worth remembering the many assumptions implicit in this method of calculating daily production, viz.

1) The production-irradiance curve parameters measured for a sample at a single depth are assumed to apply to the total population.

2) Vertical mixing is ignored.

3) Diel changes in the production-irradiance parameters are not considered.

4) The phytoplankton population is assumed to be in equilibrium.

In view of assumption (1) it is encouraging to note that the estimates for daily production for station 11261#49 using productivity data from two different depths are not too dissimilar.

5. SAMPLING METHODS AND LABORATORY PROCESSING

Details of tows are shown in Table 1.1, track charts of tows in Figs 1.I and 1.II.

Midwater sampling

Discrete depth samples were taken throughout the water column with the IOS acoustically operated opening/closing multiple rectangular midwater trawl (RMT 1+8M - Roe and Shale, 1979; Roe, Baker, Carson, Wild and Shale, 1980). One hundred metre depth layers were fished by both day and night between the surface and a depth of 1500m (the 0 to 100m depth layer was also subdivided into 0-25, 25-50 and 50-100m layers). Four hundred metre depth layers were fished between 1500m and the bottom (ca. 5440m), irrespective of the time of day or night. Close to the sea bed a near-bottom echo-sounder (NBES) was used in conjunction with the RMT 1+8M (Roe and Darlington, 1985). Three repeat hauls were made with this system, fishing between 90 and 10m above the bottom.

Plankton is sampled by the 0.32mm mesh RMT 1 and micronekton by the 4.5mm mesh RMT 8. A multiple cod end was used on the RMT1s fished between 0 and 1500m. This cod end separates 3 size fractions - >4.5mm, >1.0mm and >0.32mm. The >4.5mm fraction is not quantitatively sampled by the RMT 1 and animals from this fraction are only of passing interest. Hang-up of smaller animals on the 4.5 mm mesh is trivial. Aboard 'Discovery' the two smaller size fractions were each divided into two with a Folsom plankton splitter; one half was preserved in 10% formalin, the other was deep frozen. The multiple cod end was not used for deeper tows and the catches of these were so small that it was impossible to subdivide them. The total catches of RMT 1 hauls made between 1500m and the bottom were therefore preserved in formalin, except for three duplicate hauls made between 3900-5100m which were frozen. Subsequent laboratory analysis depended upon the depth of the sample and the mode of preservation.

Benthic sampling

Benthic samples were taken by the IOS multiple epibenthic sledge (BN1.5 - Rice, Aldred, Darlington and Wild, 1982) and by the semi-balloon otter trawl (OTSB 14 - Merrett and Marshall, 1980).

The BN1.5 consists of a galvanised frame within which are mounted a series of nets. Three nets are mounted side by side across the width of the sledge; two outer nets, each with a mouth 0.8m wide x 0.6m high, mesh 4.5mm, flank a central net 0.68m wide x 0.6m high, mesh 1.0mm. A suprabenthic net, mouth 1.0m wide x 0.6m high, mesh 0.32mm, is mounted above the three transverse nets. The three lower nets are closed mechanically during deployment and recovery by a blind activated by bottom contact. A linkage to this system raises the suprabenthic net frame, thereby opening this net when the sledge touches the bottom. Acoustic signals from a net monitor are continuously displayed on a Mufax on board ship, (as in the RMT1+8M system), giving data on net operation and environmental parameters. A time-lapse camera system (Rice and Collins, 1981) is mounted within the sledge frame, photographing the sea floor immediately in front of the sledge at 30 second intervals (Section 23). Four tows were made with the BN1.5 (Table 1.1, Fig. 1.II), for which the distance run on the bottom was derived from the sledge odometer wheel. The two additional sledge tracks on Fig. 1.II comprised one phototransect of a manganese nodule field and one haul with a modified sledge to sample the nodules.

In addition to the photographic transects made by the sledge (Section 23) a time-lapse camera system (Bathysnap) was deployed at GME to provide long term observations of the sea floor. Bathysnap is discussed in Section 24.

The OTSB14, of 13.7m headline length and 8.6m estimated wing end spread, was fished from 50m bridles on a single warp as described by Merrett and Marshall (1980). Six tows were made, 3 in a NW by N direction and 3 in a SW by S direction (Fig. 1.II). Nominally the tows were of 3 hour duration on the seabed but the exact time was dictated by the in situ record of bottom contact given by the trawl door-mounted acoustic monitor via the shipboard echosounder. Fishing distance was then calculated using the ship's satellite navigation system. The variability in distance towed (Tables 1.1, 29.1) resulted from the difficulty experienced in keeping the net on the bottom, due, apparently, to substantial current shear in the near-surface waters. The final tow (Stn 11261#60) fouled the bottom, the net was destroyed and the usable number of tows reduced to five.

Laboratory processing

Midwater. The total RMT8 samples were volumed and the different groups counted and sorted. Individual groups were analysed and are reported on subsequently.

The RMT1 samples posed much greater processing problems than the RMT8s. They contained many more individuals (up to 50 times as many), plankton is much smaller than micronekton - necessitating sorting under a microscope, and the condition of the deep samples was poor - probably because of the high surface temperatures coupled with delays in recovering the nets.

RMT1 samples were processed as follows. Those taken below 1500m (without the multiple cod end) were passed through a 4.5mm mesh to remove large animals. These large animals were not routinely analysed and an insignificant number of small animals hung up on the mesh at this stage. The deep samples therefore consist of animals within the size range 0.32-4.5mm. Each sample was drained and the catch placed upon absorbent paper to remove any adherent surface water. The sample was then transferred to a preweighed foil boat and its wet weight determined. It was then placed in a known volume of water and its displacement volume measured. Finally each sample was sorted to individual groups and the numbers of each group in each haul counted.

The formalin preserved subsamples of RMT1 catches between 0-1500m were basically treated in the same way as the deep hauls - except that they were not passed through a 4.5mm filter. The size of these shallow samples, together with limited manpower and time, precluded complete sorting. Many of the 0.32mm size samples were fractioned with a Folsom plankton splitter after measuring wet weight and displacement volume but before sorting. Sorting was restricted to whatever fraction was deemed practical to process (Table 5.1). Practicality was assessed as containing ca 1500-3000 copepods (the most abundant group). Most fractions contained these numbers although a few were larger (Table 5.1).

Fractioning introduces errors and the effects should be borne in mind when evaluating the numbers of uncommon animals (Table 6.12 ff). It is possible, for example, that a sample contains a single specimen of a rare animal; if this single example happens to be in the, say, 1/64th fraction, then it will appear as if there were 64 animals in the total sample instead of one. In all cases the numbers of animals sorted were multiplied up by the appropriate fraction prior to correcting for volume of water filtered (see Section 6).

Sorting was carried out to different taxonomic levels, reflecting the robustness or ease of identification of particular animals. Some groups were sorted to phyla e.g. chaetognaths, whereas others were processed as far as suborder e.g. cladocerans. Several individuals carried out the sorting and inter-sorter differences were moderated as far as possible by one person (C.J. Ellis) examining their results.

The frozen subsamples of the shallow RMT1 catches, and the duplicate deep samples, were thawed and their displacement volumes and wet weights determined as previously. The samples were then dried in an oven at 100°C for 24 hours and transferred to a desiccator for a further 24 hours. They were then weighed, giving a dry weight. The dry samples were then homogenised with a pestle and mortar and the carbon/nitrogen content of a subsample determined by gas chromatography (see Hull 1985 for details). A further subsample was ashed in a muffle furnace at 450°C for 24 hours and subsequently weighed to give an ash weight. By subtracting this from the original dry weight an ash-free dry weight was determined.

Some depths were sampled twice. In many of the subsequent tables, data from repeat hauls are given, but duplicate samples were not analysed for all groups nor for the biomass measurements.

Benthic. Benthic samples were small and contained only small amounts of sediment. All organisms from OTSB catches and the larger individuals from the sledge were picked out on board and preserved separately. Residues from the coarse nets of the sledge were sieved through 4.0mm mesh and those from the fine centre net through 4.0, 2.0 and 1.0mm meshes prior to fixation. All material was fixed in 10% borax-buffered formalin for 3-5 days. Organisms with calcareous deposits, such as crustaceans, molluscs and echinoderms, were preserved in 80% ethyl alcohol and soft bodied organisms such as coelenterates and annelids were transferred to 5% formalin. Residues from the sledge were sorted under the microscope in the laboratory.

Preserved organisms were counted, drained on absorbent paper and weighed. Weights were taken to the nearest 0.01g. In general, all material of each major taxon was weighed together, but in some cases it was more appropriate to weigh material species by species. Molluscs were weighed in their shells, so the importance of gastropods, scaphopods and bivalves, in terms of organic biomass, will be overestimated.

6. MIDWATER BIOMASS AND TOTAL NUMBERS H.S.J. Roe

Introduction

Biomass data have been corrected for shipboard subsampling (shallow RMT1s see Section 5) and numerical data have been corrected for any fractioning both at sea and in the laboratory. Both sets of data have also been corrected for volumes of water filtered using the equations developed by Roe et al (1980). The RMT 1 data are expressed in terms of 1000m^3 of water and virtually all of the RMT8 data in terms of 10000m^3 of water.

Since the biomass measurements were made before sorting, the data will include animals which were sampling contaminants at particular depths and also animals which were dead before capture. Contamination can occur either as hang-up from previous hauls or as leakage into closed nets. It has been possible to identify shallow living animals as contaminants in deep hauls for some groups (e.g. copepods, euphausiids), and the numbers of copepod carcases in deep RMT1 hauls have been analysed (Section 11). However, the depth distributions of bathypelagic animals are too poorly known to allow identification of deep contaminant species, and in many groups no attempt has been made to identify contaminants. The general problem is probably insignificant except in a few hauls. The RMT1 catch at station 11261#28 was contaminated with animals caught in a previous haul (11261#24); 111261#68 also contained contaminants from a previous deeper haul and 11261#19 had a number of surface living gastropods, pteropods and ostracods. The effect of contaminants and carcases on the data sets will be small but should be borne in mind.

Biomass

The relationship between the various biomass measurements have been examined by major axis regression (Yorke, 1966; Hull, 1985). The slopes of the regression lines using $\log_{10}$ transformed values have been calculated and the significance of the difference in slope between the various lines tested according to the formula

$$t = \frac{x_1 - x_2}{\sqrt{\dfrac{(n_1-1)s_1^2 + (n_2-1)s_2^2}{n_1+n_2-2}}}$$

where x_1 and x_2 are the slopes and s_1 and s_2 are the sample variances of the independent samples of size n_1 and n_2 respectively.

Various regression coefficients for planktonic biomass are shown in Table 6.1. Volume and wet weight were available throughout the water column; dry weight was measured between 0-1500m and on the three duplicate samples taken between 3900-5100m. There was no significant difference between the volume/WW regressions for different size groups or for depths above and below 1500m. Similarly there was no significant difference in the Vol/DW, Vol/C, Vol/N, and WW/DW, WW/C and WW/N regressions between different size groups; the deep dry weight data fit well with that taken between 0-1500m. Consequently single regressions for total plankton (0.32-4.5mm) have been used, and these single regressions have been used throughout the water column.

Planktonic biomass data are given in Tables 6.2-6.5. These tables show the measured volumes for the 0.32-1.0mm, 1.0-4.5mm and 0.32-4.5mm size fractions and measured %C, %N and C:N ratios for the 0.32-1.0 and 1.0-4.5mm fractions. Wet and dry weights and the weights of carbon and nitrogen are derived data from the volume regressions (Table 6.1).

Biomass data for micronekton are limited to displacement volumes (Section 5). These volumes have been converted to wet and dry weights using the plankton regressions for volume (Tables 6.6-6.8). Several samples had very high volumes of the thaliacean Pyrosoma. For these samples separate conversions have been made, including and excluding Pyrosoma. Using planktonic regressions for micronekton is a questionable procedure. Omori's (1969) data include various micronektonic species and show that the dry weight/wet weight relationship between various crustacean groups, chaetognaths and fish are generally similar.

Gelatinous zooplankton however, including thaliaceans, have a much lower dry/wet weight relationship (Larson, 1986).

Results

Most of the biomass of both plankton and micronekton was contained within the top 1500m of the water column (Tables 6.2-6.8, Figs. 6.I-II). More than 80% of the total planktonic biomass and >95% of the total micronektonic biomass occurred between 0-1000m. The massive peaks in the micronekton data (Fig. 6.II) were caused by swarms of *Pyrosoma* which occurred between 700-900m by day and migrated to the upper 200m by night (Table 6.72, Fig. 6.XI). The peak between 500-600m at night resulted from *Pyrosoma* being sampled during vertical migration *en route* to its daytime depth.

Biomass within the upper 1500m is shown in more detail in Figs 6.III-6.VI. In the plankton, the 0.32-1.0mm size group (Fig. 6.III) had maxima within the upper 200m by day and night with an overall shoaling at night, whereas the 1.0-4.5mm group (Fig. 6.IV) had a daytime maximum between 500-600m and a marked diel migration to the upper 200m. Figs 6.III-6.VI also show the importance of the subdivided 0-100m hauls (Section 5). At night in particular the 0-100m haul undersamples this zone because of the tendency of the plankton to congregate at very shallow depths which are only briefly sampled by nets fishing wider horizons. The effect of these subdivided 100m hauls is shown in Table 6.9 where the accumulated percentages are markedly shallower in the data sets using the 0-25, 25-50 and 50-100m hauls. These subdivided 100m hauls had little influence on the micronekton which was adequately sampled by the wider horizons (Table 6.9, Fig. 6.VI). The micronekton dry weights are derived from volumes excluding *Pyrosoma*.

Biomass profiles throughout the water column, based upon day data for hauls above 1500m, are shown in Fig. 6.VII. The micronekton dry weight again exclude *Pyrosoma*. The total biomass was low. The total dry weight of plankton beneath one square metre of sea surface was 1.52g (day) and 1.25g (night); of micronekton it was 0.61g (day) and 0.52g (night). The total pelagic biomass at GME therefore amounted to ca 2g beneath each m^2 of sea surface. These figures do not include phytoplankton or zooplankton smaller than 0.32mm, neither do they include Pyrosoma nor any large pelagic animals (see discussion below).

The biomass of both plankton and micronekton decreased exponentially with depth until just above the bottom (Fig. 6.VII). Three hauls were made between 10 and 90m above the bottom. The micronekton biomass shows a fairly consistent increase with increasing proximity to the sea bed but the plankton data are rather ambivalent (Fig. 6.VIII).

Discussion

The validity of converting micronekton volumes to dry weights using plankton regressions is questionable. The absolute values obtained are therefore dubious but they do accurately reflect both the relative changes throughout the water column and the very low biomass.

The micronekton and plankton volume data for the deep hauls (Table 6.4 and 6.8) are very similar, and this results in strikingly similar biomass profiles below 1700m (Fig. 6.VII). If the micronekton were active predators, depending upon populations of living plankton, then one would expect a larger population of prey than predators - as occurs in the upper 1500m. At greater depths low populations of plankton and low populations of micronekton apparently coexist. A possible explanation is that predator/prey relationships are secondary to a more generalised omnivorous, detritivorous lifestyle - where both large and small animals depend as much upon detritius, particulates and carcases as upon encounters with living prey.

The present biomass data exclude large (and presumably rare) animals and they also exclude plankton smaller than 0.32mm. The biomass of microzooplankton can be very large in relation to net zooplankton (e.g. Endo, Hasumoto and Taniguchi, 1983; Taniguchi, 1984, 1985). The contribution of microzooplankton to the ecosystem at GME is unknown, but presumably the populations of Pyrosoma - which, in volumetric terms, dominated the mesopelagic zone, were supported by these small plankton. It is therefore possible that the total biomass at GME is larger than given here, especially within the upper 1000m (see final discussion Section 31).

Whatever effects microzooplankton may or may not have had on the present data it is pertinent to ask whether the low bathypelagic values recorded here are anomalous or whether they are typical of the depth and area. Previous bathypelagic data are scarce. Jaschnov (1961, 1962) and Grice and Hulsemann (1965) analysed plankton biomass from the same general area as GME, and Grice and Hulsemann (1967), Vinogradov (1968), Wishner (1980a) and Angel and Baker (1982) summarised and discussed data from the Atlantic, Pacific and Indian Oceans. Except for Angel and Baker (1982), the results of these previous authors are similar to the present bathypelagic data. At first sight therefore it seems that the GME biomass is not extraordinarily low. However, all the data reported by Jaschnov, Grice and Hulsemann, Vinogradov and Wishner are derived from fine mesh, small mouth area nets which sample smaller zooplankton than that taken by the RMT1. Smaller zooplankton may be expected to be more abundant than that sampled by the RMT1 but it is impossible to quantify this possibility here. Comparisons between data taken by diferent sampling gears are indirect - as Wishner (1980a) recognised. There is, however, one data set which is directly comparable with the present results - that of Angel & Baker (1982) who analysed plankton and micronekton biomass taken from the N E Atlantic with RMT1 and RMT8 nets.

To facilitate this comparison, linear regression coefficients between the logarithm of biomass and depth have been calculated for depths between 0-1000m and between 1000-5440 (the bottom) (Table 6.10). The day and night regressions for depths >1000m combine the day (or night) data between 1000-1500m with the >1500m data. These deep regressions are compared with those of Angel and Baker (1982) in Table 6.11, Fig. 6.IX - where Wishner's (1980a) N. Atlantic regression is also shown.

Compared with similar RMT1 and RMT8 data, the biomass at GME is lower than elswhere, perhaps reflecting the greater productivity further to the north and east. The effects of surface production on bathypelagic biomass are uncertain. Wishner (1980a) found little evidence for a direct relationship, but this is contradicted both by Vinogradov's (1968) observations and by recent flux studies which demonstrate a rapid coupling between the surface and the deep sea (see, for example Fowler and Knauer, 1986). Presumably bathypelagic biomass is some measure of overall surface production and reflects this plus seasonal effects. Seasonality and repeatability in general are relevant throughout this report and are discussed in the final section.

Although the intercepts differ markedly, most of the slopes in Fig. 6.IX are similar. (The major exception at 49°N was perhaps influenced by a storm). This similarity also extends to smaller zooplankton, for which Wishner (1980a) calculated similar regressions and found that all except one had slopes which were not significantly different from that shown here. This similarity strongly suggests that the processes controlling the distribution of biomass in the deep oceans are similar despite differences in the overlying surface production.

Finally the rather ambivalent results from the near bottom samples (Fig. 6.VIII) contrast with previous data. The first quantitative studies of deep-sea benthopelagic plankton were those of Wishner (1980a,b) and Boxshall and Roe (1980). The near bottom zone is now established as one where there is a marked increase in biomass, in numbers of individuals, species and groups, in particulates and biological activity (e.g. Wishner 1980a,b; Wishner and Meise-Munns, 1984; Gowing and Wishner, 1986; Boxshall and Roe, 1980; Roe, 1986; Hargreaves, Ellis and Angel, 1984; Hargreaves 1984). Previous studies, however, have all been done in shallower water or in more productive areas. There are no comparable water column/benthopelagic data from a deep oligotrophic area to contrast with the present results. It may be that the situation observed at GME is typical for abyssal oligotrophic regions.

Total numbers

The total numbers of each group of animals from both RMT1 and RMT8 catches are given in Table 6.12-87. Cirripede larvae and echinoderms are not listed in total but are discussed in Sections 12 and 19. In some of these tables the numbers of contaminants are shown in brackets. Figs 6.X-XI show the vertical distributions of the most abundant groups; they illustrate the extreme paucity of animals below 1500m and reinforce the biomass results discussed previously. Many of the individual groups are analysed in more detail in the following sections where the total numbers are broken down in varying degrees. In the time available little detailed analysis of planktonic groups was possible but many of the micronekton groups have been worked up in considerable detail.

7. SIPHONOPHORA P.R. Pugh and P.A.Kirkpatrick

Specific identifications of siphonophores were carried out on the samples from the RMT8 and RMT1 (1.0-4.5mm fraction) nets. The number of individual animals per haul was assessed according to the procedures outlined in Pugh (1984) and standardized to unit volume, and these numbers are shown in Tables 6.20-24. In addition, the total number of siphonophore 'pieces' in the RMT1 (0.32-1.0mm fraction) was assessed, and these numbers also are shown. However, since more than one piece may have originated from an individual animal, the total numbers for the RMT1 net catches are most likely overestimates. The total numbers, for the hauls within the top 1500m of the water column, are also plotted in Figures 6.X and 6.XI. The vast majority of the siphonophores caught by the RMT1 net were found in the top 400m of water, while fairly large numbers of specimens caught by the RMT8 net were found throughout the water column down to 1500m depth. There is, however, a great disparity in the numbers of siphonophores caught by the two nets, indicating that the overall population was dominated by small sized species that were not collected quantitatively by the RMT8 net. Over 90% of the total RMT1 numbers was contributed by the small 'pieces' of siphonophores, particularly in the top 400m of the water column. A visual inspection of these 'pieces' showed that they were mainly components of the eudoxid or sexual stage of the commoner epipelagic siphonophore species.

Overall the total number of siphonophores found in the top 1500m at the GME site was similar to that previously found at adjacent sites e.g. Discovery St. 7856 at 30°N, 23°W and at the West Atlantic Water Station (Discovery St. 10380) in the vicinity of the Azores Front at 32°N, 32°W (Pugh, unpublished data). At deeper depths, the siphonophore population collected by the nets was quite small and there did not appear to be any particular enhancement of the numbers in the near-bottom tows.

Depth distribution of individual species

Sixty-four species of siphonophores were identified from the samples of which all but nine belonged to the Sub-order Calycophorae. It is well known that physonect siphonophores, because of their fragility, are poorly sampled by nets and it is probable that several of these species were present in the water column but were not collected, judging by the results from other areas (Pugh and Harbison, 1986). The majority of the species found were relatively rare and half of the total occurred in low numbers in ten or less of the hauls (see Table 7.1). Only the depth distribution of the eighteen commonest species will be dealt with in any detail, but as the results from the two nets often differed considerably the species will be dealt with in systematic order rather than order of dominance.

Sub-order Cystonectae

Only one cystonect species, Rhizophysa filiformis, was found to be present in fours hauls, all of which were fished in the top 100m (see Table 7.1).

Sub-order Physonectae

Eight physonect species were found and most were relatively rare (Table 7.1). Agalma okeni, Frillagalma vitiazi and Halistemma rubrum were the more abundant species and the information suggests that they had extensive depth distributions.

Sub-order Calycophorae

Family Prayidae

Eleven prayid species were identified but none of them were abundant (Table 7.1). The three species of the genus Amphicaryon were mostly found in the top 100m of the water column, and records from deeper depths probably are due to contamination.

Family Hippopodiidae

All five species that belong to this family were present in reasonable numbers at the GME station. The individual specimens are relatively large and so were better represented in the RMT8 catches, and appeared only infrequently in the RMT1 ones (Table 7.1). Each species is comprised of between eight and fifteen nectophores, but since they are easily broken apart and losses of nectophores from the nets can be considerable, the total number of nectophores is considered here. This may, therefore, represent an overestimate of the total number of animals (see Pugh, 1984).

Hippopodius hippopus (Figures 7.IA, Table 7.2).

This was the shallowest living hippopodiid species, and the data indicate a diel vertical migration (henceforth DVM) from the 100-200m depth range by day into the top 100m at night, with 44% of the total population occurring in the 0-25m depth range. Pugh (1974), however, found this species to undergo a more substantial DVM from about 250m by day into the subsurface layers at night, at a station close to the Canary Islands. At the 30°N, 23°W station, H. hippopus was found to be present in large numbers throughout the top 400m of the water column by day, but the population became concentrated in the top 100m at night (Pugh, unpublished data). Pugh (1977) commented on the slow, sinusoidal DVM of this species through the 250m depth zone at the same station and commented on the effects that such a DVM might have on any interpretation of the depth distribution of a species as assessed from the sampling programme, such as the one carried out at the GME site. Because such species do not complete their DVM within the dawn and dusk periods, the timing of the so-called 'day' or 'night' nets at particular depths may give rise to misleading results, as vertically migrating animals may be captured or missed entirely. This factor is discussed further in Mackie, Pugh and Purcell (in press).

Hippopodius hippopus is a well-known epipelagic siphonophore species, having a widespread distribution in the warm-waters of the World's Oceans but rarely found in more temperate waters e.g. north of 40-45°N in the N. Atlantic Ocean (Pugh, unpublished data). Purcell (1981) found that this species fed exclusively on ostracods and Pugh (1986) attempted to relate the zoogeographical distribution of this species with that of its prey taxa. The absence of H. hippopus at higher latitudes, therefore, being associated with the relative scarcity of ostracods at shallow depths (e.g. Angel, 1984a).

Vogtia glabra (Figure 7.IB, Table 7.3)

The depth distributions of V. glabra showed only a slight overlap with that of

Hippopodius hippopus, and the majority of specimens were found between 200 and 600m depth. Although the population was spread out over a considerable depth range by day (Fig. 7.IB), there was an indication that the deeper part of this population underwent a DVM, as most of the nectophores were concentrated in the 200-400m depth range at night. At other similar stations the main population of this species also is found in the 200-500m depth range (Pugh, unpublished data), although Pugh (1974) found it to be concentrated between 500-600m by day but with a spreading upwards at night possibly up to 150m.

Unlike its near-surface living relative Hippopodius hippopus, Vogtia glabra has a widespread distribution throughout the World's Oceans and is abundant in temperate waters (Pugh, unpublished data). Bigelow and Sears (1937) found it to occur mainly below 400m in the Mediterranean, but it was never very abundant. The data from the 48h series of hauls at 44°N, 13°W (see Roe et al, 1984) indicated that V. glabra occurred mainly in the 450m depth zone by day, and the 250m one by night (Pugh, 1984). However, Pugh (1984) considered that this did not indicate a large-scale DVM, but a small-scale migration of the components of the total population that was spread over the 300-500m depth range by day and 200-400m by night.

Vogtia spinosa (Figure 7.IC, Table 7.4)

V. spinosa occurred over a similar depth range to that of V. glabra, but was considerably less abundant. By day this species was concentrated in the 500-600m depth range, but at night it spread upwards as far as 200m. The SOND Cruise data (Pugh, 1974) indicate a similar upward spread of the population at night but from a depth of only 350-450m by day to ca. 250m at night. However, at the 30°N, 23°W station, where the total number of nectophores was very similar to the GME site (Pugh, unpublished data), the population was concentrated in the 200-500m depth range both by day and by night. However, during the 24h series of hauls at the same station, V. spinosa was present at 250m only at sunset and during the night (Pugh, 1977) indicating that the species was undergoing a slow DVM. A similar small-scale DVM was observed around the 250m depth zone during the 48h series at 44°N, 13°W (Pugh, 1984), with 90% of the population remaining in the 200-300m depth range.

There is little published information on the depth distribution of this species (see Pugh, 1974), but Bigelow and Sears (1937) found it, in the Mediterranean, at depths greater than 300-400m. In the N E Atlantic Ocean, V. spinosa has a widespread distribution from the equator to 60°N, but is most abundant at latitudes between 40 and 50°N.

Vogtia pentacantha (Figure 7.ID, Table 7.5)

V. pentacantha was relatively rare at the GME site, but it showed a very discrete depth distribution with almost all specimens being found between 400 and 600m, with the majority in the 500-600m depth range. There were no indications of a DVM. V. pentacantha is probably the rarest of the hippopodiid species worldwide, although at the GME site V. spinosa was less abundant. It has a widespread geographical distribution and in the N E Atlantic occurs from the equator to 53°N (Pugh, unpublished data). At more northerly stations it occurs mainly in the 200-500m depth range but at lower latitudes is found slightly deeper and at the 30°N, 23°W station and in the region of the Azores Front it occurred mainly in the 400-600m depth range. At the West Atlantic Water station the number of V. pentacantha present were very similar to the GME numbers, but across the Azores Front, in the East Atlantic Water a much larger population was found.

Vogtia serrata (Figure 7.IE, Table 7.6)

V. serrata is the deepest living of the hippopodiid species and occurred mainly at depths below 500m and has a widespread distribution down to 1300m, with occasional specimens being found at deeper depths (Table 7.1). This is a well-known but uncommon species with a widespread geographical distribution in the Atlantic Ocean from the Antarctic to at least 60°N. At nearby sites the depth distribution and abundance of this species has been found to be very similar to the GME data (Pugh, unpublished data) but it is generally more abundant in temperate waters and tends to have a slightly shallower depth distribution. Thus, Pugh (1984) found V. serrata mainly in the 300-600m depth range at 44°N, 13°W, with an indication of a slight upward spreading of the shallower part of the population into the 250m depth zone at night.

Overall the five species of the Family Hippopodiidae show a degree of depth stratification, although there is some overlap (Fig. 7.I). This stratification of what may be congeneric species also was commented on by Pugh (1974).

Family Diphyidae

Twenty-four diphyid species were found in the GME samples but only seven of these were present in any number. Species of the genus *Sulculeolaria* were surprisingly rare (Table 7.1) but typically were found mainly in the top 100m of the water column. At the 30°N, 23°W station large numbers of *S. quadrivalvis* and *S. chuni* were found, but similarly low numbers of all species were found in the Western Atlantic Water close to the Azores Front (Pugh, unpublished data). *Diphyes bojani* (Table 7.1) also was surprisingly rare as a very large population was found in superficial waters at 30°N, 23°W, while in the Azores Front region reasonable numbers were present. It is not clear why these usually common epipelagic species were rare at the GME site.

Lensia subtilis (Table 7.1) is usually found in the top 100m of the water column (Moore, 1949, 1953; Patriti, 1964; Pugh, 1974) but at the GME site there are very few records in that depth zone. However, there were several records in the 300-900m and 1900-5430m depth zones. Unfortunately there are too little data to assess the main distribution range of this species or whether the deeper records were due to contamination, despite the absence of near-surface records. It is possible that a detailed analysis of the 0.32-1.00mm fraction of the RMT1 catches may provide better data on this and other small-sized siphonophore species.

Eudoxoides spiralis (Figure 7.II, Tables 7.7-12)

Overall this was the commonest species found in the GME samples, although there was a considerably disparity between the catches of the RMT1 and RMT8 nets. At shallow depths the RMT1 (1.0-4.5mm fraction) contained about forty times more specimens than the RMT8 net, while at deeper depths the ratio was ca. 15:1. The depth distribution data (Fig. 7.II) show that there are two separate populations of *E. spiralis*; one occurring mainly in the top 200m of the water column and the other much deeper, in the 1000-1500m depth range. The RMT1 data indicate that the shallower population was most abundant in the 100-200m depth zone by day and migrated into the top 100m at night. However, the nighttime numbers of this shallow population are inexplicably about twice the day numbers (Tables 7.7-8), unless the timing of a particular haul resulted in a failure to catch a large part of the migrating population, as discussed in other instances by Pugh (1977) and Mackie, Pugh and Purcell (in press). In this context, the smaller RMT8 catches indicate a clear DVM from the 200-300m depth range by day into the top 100m at night (Figure 7.II).

The deeper population of *Eudoxoides spiralis* is, for the RMT8 hauls, more abundant than the shallower one and has a very marked peak of abundance in the 1200-1300m depth range. The RMT1 data, however, indicate a greater depth distribution range mainly between 1000 and 1500m and, overall, this population is less abundant than the shallower living one. At deeper depths this species occurred sporadically.

Eudoxoides spiralis is a common siphonophore species which has a widespread geographical distributions in the warmer waters of the World's Oceans (Pugh, 1974). Although previous records indicate an extensive depth distribution for this species, it is considered generally to be mainly epipelagic, with the bulk of the population concentrated in the top 100-200m of the water column. The DVM of this population has been studied on several occasions (Moore, 1949, 1953; Pugh, 1974). However, the presence of a substantial deep living population does not appear to have been recorded in the literature, although similar situations have been found at the various stations in the vicinity of the Azores Front (ca. 32°N, 32°W), where again *E. spiralis* was the predominant siphonophore species (Pugh, unpublished data). However, at 30°N, 23°W (Discovery St. 7856) and other lower latitude stations in the N E Atlantic Ocean no deep-living population was found (Pugh, unpublished data).

The great majority of records for the eudoxid stage of *E. spiralis* at the GME site came from the top 100m of the water column (Tables 7.7-8) and it is possible that other records from deeper depths are due to contamination. There was no similar peak in eudoxid numbers in association with the deep-living population and so it is not clear as to whether this deeper living population is derived from the shallower one or has a different breeding cycle.

Eudoxoides mitra (Figure 7.III, Tables 7.13-16)

This other species of the genus *Eudoxoides* also was common at the GME site. As for *E. spiralis*, there is a marked disparity between the numbers caught in the RMT1 net by day and by night, with the latter totals being about nine times greater than the former. However, the day and night RMT8 catches were similar and indicated a distinct DVM from the 200-300m depth zone by day into the top 100m at night, with the bulk of the population concentrated very close to the surface. The eudoxid stage (Tables 7.13-16) had a similar depth distribution.

Eudoxoides mitra also is a widespread, warm-water epipelagic species and was one of the commonest siphonophores in the Bermuda region (Moore, 1949), where it undertook a DVM with a ca. 50m depth range. Pugh (1974) also considered that, in the Canary Islands region, this species underwent a small-scale DVM, with the majority of the population occurring in the top 150m of the water column. Similarly at 30°N 23°W the bulk of the population was found in the 50-100m depth range both by day and by night, but with an indication of a slight upward movement at night.

The present data, therefore, indicate a slightly deeper daytime depth distribution, but this is consistent with data from the Azores Front region (Pugh, unpublished data) where similar numbers of animals were found in the 100-300m depth zone by day, and there was an upward migration into the top 50m at night.

Chelophyes appendiculata (Figure 7.IV, Tables 7.17-18)

As with the previous two diphyid species, *C. appendiculata* was caught more efficiently by the RMT1 net, but the disparity in numbers was not so marked. The data for both nets indicate that the majority of the population was concentrated in the top 100m although, by day, part of the population spread down to deeper depths. At night most specimens were found in the 0-25m depth zone. Very few eudoxid or sexual stages were collected (Table 7.1) and most of these, suprisingly, were found in the RMT8 catches at shallow depths by day. The single instance of an eudoxid in a deep RMT1 net almost certainly was due to contamination of the sample as the net passed through the superficial waters.

Chelophyes appendiculata is one of the commonest epipelagic siphonophores in the warmer waters of the World's Oceans. Its geographical distribution is more extensive than the previous two species of the genus *Eudoxoides* and, in the N E Atlantic, has been found as far north as 53°N. Particularly high concentrations were found at 40°N, 20°W (Pugh, unpublished data). Leloup and Hentschel (1935) found that this species was most abundant in the top 100m of the water column, and Bigelow and Sears (1937) concluded that it was the commonest siphonophore species in the 0-200m depth range in Mediterranean waters. Moore's (1949, 1953) detailed studies, in the Bermuda and Florida Current regions, also confirmed the epipelagic distribution of this species and its DVM of less than 100m depth range. Pugh (1974) found evidence for a more substantial DVM, in the Canary Island region, from ca. 250m by day into the top 50m at night. Again he noted that the depth distribution pattern established for this particular species probably was affected greatly by the time at which certain depth horizons were sampled. The sinusoidal nature of its DVM was considered by Pugh (1977).

The depth distribution and abundance of *Chelophyes appendiculata* at the GME site is similar to that found previously in the Western Atlantic Water near the Azores Front (Pugh, unpublished data), but at the 30°N, 23°W site (Discovery St. 7856) this species was considerably more abundant.

Diphyes dispar (Figure 7.V, Tables 7.19-21)

Despite the relatively large size of this species, the RMT1 net caught more specimens per unit volume than the RMT8 one. The results for both nets show a considerable disparity between the total day and night numbers. This may indicate that the bulk of the population migrated into the top few metres of the water column at night and was not sampled properly. By day most of the population was found in the 0-50m depth zone. The depth distribution of the eudoxid stage was similar to that for the polygastric one (Table 7.20-21) and again, any deeper records (see Table 7.1) are probably due to contamination at the surface.

Diphyes dispar is a well-documented, but not abundant, species from the warmer waters of the World's Oceans and the Mediterranean Sea. Pugh (1974) reviewed the few earlier depth distribution records and concluded that it was mainly an epipelagic species, with most examples occurring in the top 100m of the water column. At both the 30°N, 23°W and the Azores Front sites D. dispar was less abundant than at the GME site, but in both cases the depth distribution was similar (Pugh, unpublished data).

Lensia multicristata (Figure 7.VIA, Tables 7.22-25)

L. multicristata reached greatest numbers in the 300-500m depth zone but, for the RMT8 data, there was considerable disparity in the day and night totals. A smaller, secondary population occurred between 900 and 1300m (Fig. 7.VIA) and there were occasional records for this species at deeper depths right down to the bottom of the water column. Several previous authors (e.g. Margulis, 1971; Bigelow and Sears, 1937) also have recorded this species over a wide depth range, but with the majority of specimens to be found in the region of 250-450m (Pugh, 1974). However, most authors have not noted the presence of a second, deeper-living population remininiscent of that found for Eudoxoides spiralis. Pugh (1984) noted two such populations at 44°N, 13°W, with one mainly concentrated between 200 and 300m with signs of a small-scale DVM around the 250m depth zone, and a second deeper population mainly concentrated in the 700-800m depth range. This deeper population actually was more abundant than the shallower one. In these more temperate waters, and L. multicristata has been found as far north as 60°N, the depth distribution of this species appears to be shallower, possibly associated with the change in depth of certain isotherms. Such a depth change was found in the data from the Azores Front studies (Pugh, unpublished data). In the Western Atlantic Water the shallower population of L. multicristata was found in the 400-500m depth zone, although the numbers were lower than those found at the GME site. The small deeper population occurred in the 800-900m, but overall the species had a widespread depth distribution from 200 to 1900m. Although the abundance of this species was fairly constant across the front, in the East Atlantic Water the bulk of the population was found in the 200-400m depth range, as would be expected if the distribution was related to the depth of certain isotherms.

Lensia fowleri (Figure 7.VIB, Tables 7.26-17)

The RMT1 net data indicate that almost the entire population of L. fowleri was found in the 100-200m depth zone, but twice as many animals were present in the nighttime hauls. In contrast, four times more nectophores were found in the daytime RMT8 hauls than the night ones, and the data indicate a daytime peak in the 200-300m depth range. The picture, therefore, is confused.

This diphyid species has a widespread distribution in the Atlantic Ocean from 61°N to 34°S, and usually has a peak abundance at ca. 200m depth (Margulis, 1971). Moore (1949, 1953) found mean day levels of 165 and 100m in the Bermuda and Florida Current regions. In the N E Atlantic L. fowleri was found in large numbers between 0 and 11°N, while at 30°N, 23°W numbers were lower than those found at the GME site and were concentrated in the 100-200m depth range with no obvious signs of a DVM. In contrast, although the depth distribution remained the same, the numbers of L. fowleri at the Azores Front stations were greater than at the GME site (Pugh, unpublished data).

Lensia spp. (Tables 7.28-33)

A few nectophores and eudoxids of Lensia spp. remained specificially unidentified and the depth distribution data for these are presented in Tables 7.28-33.

Dimophyes arctica (Tables 7.34-37)

The nectophores of this species were fairly rare in the RMT1 samples with most occurrences in the 100-400m depth range, particularly at night. The eudoxid stage usually occurred much deeper, and several of the hauls at depths greater than 1500m contained examples (Table 7.1). The data from the RMT8 hauls also are inconclusive with a daytime maximum between 200 and 300m, while at night most nectophores occurred in the 300-400m depth range. The small eudoxid stage was rare in these samples. Pugh (1974) also found that whereas the nectophores were commonest in the 200-250m depth range, the eudoxid stage was not found at depths shallower than 660m. However, during the 24h series at 30°N, 23°W, large numbers of eudoxids were found in the 250m depth zone (Pugh, 1977). As Totton (1954) reviewed, although this species has a widespread geographical and depth distribution, it is generally found in colder waters and is most abundant at shallower depths in high latitudes. Thus, in the N E Atlantic Ocean, peak numbers were found in the 50-200m depth range at 53°N, while south of ca. 30°S the species was rarely found (Pugh, unpublished data). Across the Azores Front there was an increase in number of D. arctica from the Western Atlantic Water, where numbers were similar to those at the GME site, across to the East Atlantic Water.

Family Clausophyidae

Seven clausophyid species were identified but only three occurred in any number and only these will be discussed here. The data for the other species are given in Table 7.1

Clausophyes ovata (Figure 7.VIIA, Tables 7.38-41)

The majority of this species was found in the 700-900m depth range according to the RMT1 catches, while the RMT8 ones indicated a more extensive range from 700 to 1100m with, in both cases, occasional records at deeper depths right down to the bottom of the water column. The RMT8 data (Fig. 7.VIIA) give the appearance that a slight DVM was taking place but, judging by the variability in results between the two nets, this is considered unlikely. Pugh (1984) similarly found the species mainly in the 600-1000m depth range, and at 600m, although it had an erratic temporal distribution, there were no clear-cut signs of a DVM.

Pugh (1974) pointed out that there was relatively little information on the depth and geographical distribution of this species, but that most previous records had come from the Atlantic Ocean. In the N E Atlantic, Clausophyes ovata has a widespread distribution from the equator to 60°N, and is generally found in the 600 to 1000m depth range although it is often found at deeper depths (Pugh, unpublished data). At the Azores Front site, the population in the Western Atlantic Water was very similar to that at the GME site, but the population was considerably enhanced in the Front and East Atlantic Water (Pugh, unpublished data).

Chuniphyes multidentata (Figure 7.VIIB, Tables 7.42-44)

This large clausophyid species was found almost exclusively in the RMT8 net catches. It had a widespread depth distribution from 400m depth to the bottom of the water column, with the majority occurring in the 1200-2700m depth range. Most previous records from similar areas have indicated a peak abundance in the 600-800m depth zone (Leloup and Hentschel, 1935; Pugh, 1974) but depths below 1000m were rarely sampled. At 30°N, 23°W peak numbers actually occurred between 500 and 600m, and there the population overall was an order of magnitude greater than at the GME site. In contrast, in the Western Atlantic Water at the Azores Front, numbers were slightly lower and the population was fairly evenly distributed below 500m depth. Across the Front numbers were considerably higher, with a widespread abundance peak in the 500-1200m range (Pugh, unpublished data). Other data indicate that this species is more common in temperate than tropical waters.

Chuniphyes moserae (Figure 7.VIIC, Tables 7.45-46)

This species was found mainly in the 1100-1500m depth zone, although there were sporadic records at deeper depths. Little is known about the geographical and depth distribution of this species, probably because most sampling programmes do not adequately sample the bathypelagic depths at which it lives. In the N E Atlantic C. moserae has been found at stations from the equator to 42°N, and further to the north it is replaced by its congener, C. multidentata (Pugh, unpublished data). At both the 30°N, 23°W station and in the vicinity of the Azores Front, similar numbers of C. moserae were found, mainly in the 1000-2000m depth zone.

Family Abylidae

Eight abylid species were found in the GME samples, but only three were present in any number. Most abylid species are epipelagic, warm-water species apparently with restricted geographical ranges, although the information in the literature is not usually sufficient to assess these ranges in detail. One species, Enneagonum hyalinum usually lives at deeper depths and has a widespread geographical distribution (Pugh, 1974). At the GME site most of the records for this species occurred in the 500-110m depth range (Table 7.1).

Ceratocymba sagittata (Figure 7.VIIIA, Tables 7.47-49)

The RMT1 data indicated that this species was found mainly in the 400-500m depth range by day but was more widely spread, between 50 and 300m at night. The RMT8 data indicate a concentration of nectophores in the 200-500m depth range by day with an apparent DVM for the deeper part of the pouplation so that, at night, it was found mainly in 200-400m depth range. The eudoxid stage had a similar depth distribution, and Pugh (1977) found, at 30°N, 23°W, that this stage underwent a rapid DVM through the 250m depth zone at dawn and dusk.

Ceratocymba sagittata is a well known, but not abundant, epipelagic species in the warmer waters of the World's Oceans (Pugh, 1974), it is well known from samples in the vicinity of the GME site; at similar depths and in the same abundance (Pugh, unpublished data).

Abylopsis eschscholtzi (Figure 7.VIIIB,C, Tables 7.50-53)

The RMT1 and RMT8 data show remarkable accord and indicate that this species is concentrated in the top 50m of the water column, with no obvious DVM although the sampling regime would be too coarse to assess any such small-scale migration. The eudoxid stage of this species was caught in large numbers (Tables 7.50-53), and had a similar depth distribution to the nectophores. It is probable that all records from the deeper samples (Table 7.1) are due to surface contamination.

Although *Abylopsis eschscholtzi* is a well-known epipelagic, warm-water species, there is not a great deal of information in the literature on its depth distributions. However, Leloup and Hetnschel (1935) and Pugh (1974) found it to be commonest in the top 100m of the water column, while (Moore 1949, 1953) found mean day levels in the top 50m, with little indication of any DVM.

The geographical distribution pattern of *Abylopsis eschscholtzi* and of its congener, *A. tetragona*, appears to be complicated. At the GME site, and indeed at 30°N, 23°W, (Pugh, unpublished data), *A. tetragona* is very rare while a fairly sizeable population of *A. eschscholtzi* exists. Similarly at the Azores Front site *A. eschscholtzi* was more abundant in the Western Atlantic Water than at the GME site, but showed a rapid decline across the front to low numbers in the East Atlantic Water. A. tetragona, again, was very rare (Pugh, unpublished data). However, elsewhere in the North Atlantic the two species do not appear to be mutually exclusive and Pugh (1975) illustrated the variations in the population of these two species in a transect across the Atlantic at 32°N.

Bassia bassensis (Figure 7.VIIID,E, Tables 7.54-57)

Bassia bassensis was found in large numbers in the top 200m of the water column, and it is probable that all records from deep nets (Table 7.1) are due to surface contamination. There is a great disparity between the day and night totals for nectophores in both nets, with more being found at night. Thus, although the population appeared to be migrating to very shallow depths at night, such a conclusion should be treated with some caution. The eudoxid stage had a similar depth distribution to the nectophores.

Bassia bassensis is a well-known, abundant, warm-water species occurring mainly in the top 100m of the water column (see Pugh, 1974). Like Chelophyes appendiculata, its geographical distribution is more extensive than other epipelagic species and it has been found in large numbers at 40°N (Pugh, unpublished data). Similar populations to the GME site were found at 30°N, 23°W and in the Western Atlantic Water at the Azores Front, but across the front and in the Eastern Atlantic Water numbers were considerably enhanced (Pugh, unpublished data).

8. **CHAETOGNATHA** K.C. Chidgey

Chaetognaths are caught by both the RMT 1 and RMT 8 but the present RMT 1 material was in poor condition and, except for the deep hauls, has not been examined in detail. Total numbers of chaetognaths in both RMT 1 and RMT 8 catches are given in Tables 6.25-6.29. The total numbers caught by the RMT 8 throughout the water column were surprisingly low and especially low in the 0-50m layer. There was an increase in total numbers caught at night in the 0-25m hauls (13: 171) and in the 0-100m hauls (176: 435 - Table 6.28), but the numbers of individual species caught by day and night were too low to obtain any specific results on diel vertical migration except for _Sagitta hexaptera_.

In the RMT 8 hauls five genera of pelagic chaetognaths were found (Table 8.1) comprising 18 species, including one new species of _Sagitta_, a single specimen of _Heterokrohnia davidi_ only recorded once before (Casanova, 1985) and another new _Heterokrohnia_ species not yet described. There was also one specimen of _H. murina_, another species only recorded once before (Casanova, 1985) in a deep RMT 1 haul. The results are compared with other unpublished IOS data previously obtained in the north east Atlantic, with the Sond Cruise results (Chidgey, 1985) and with a 24 hour series of hauls at 30°N, 23°W (Roe, 1974).

Krohnitta subtilis (Table 8.2)

K. subtilis is an epi- or mesopelagic species found between the surface and 900m in warm and temperate regions, but surprisingly few of this species were caught in these hauls considering the numbers obtained previously at 28°N, 14°W between 0 and 960m (Chidgey, 1985) and at 30°N, 23°W between 240 and 260m (Roe, 1974).

Pterosagitta draco (Tables 8.2, 8.3)

The numbers caught were again lower than expected but it probably was not adequately sampled by the RMT 8 as its maximum length is only 11mm. _P. draco_ occurs above 300m in all oceanic temperate and tropical waters and it is recorded in the Discovery Collections at 18°N, 25°W, at 28°N, 14°W, at 30°N, 23°W and at 40°N, 20°W (Chidgey, 1985; Roe, 1974 and IOS unpublished data).

Eukrohnia spp.

The genus Eukrohnia was not well represented at this site, especially in the deeper hauls; only E. hamata, E. fowleri and E. bathyantarctica were found in small numbers and virtually no specimens occurred below 1500m. No specimens of E. bathypelagica were caught although it has been found at 18°N, 25°W and at 40°N, 20°W (IOS unpublished data).

E. hamata is epipelagic at high latitudes and meso- or bathypelagic at lower latitudes. Very few specimens were caught in the night hauls or below 1200m and the maximum numbers caught were by day at 400-500m (Tables 8.2, 8.4). At 18°N, 25°W E. hamata was found between 110 and 1250m with maximum numbers at 210-290m, at 28°N, 14°W between 350 and 960m with maximum numbers at 475-570m; at 40°N, 20°W between 110 and 2000m with maximum numbers at 910-1000m and at 42°N, 21°W it was found in the 3475-3640m layer (Chidgey, 1985 and IOS unpublished data).

E. fowleri is a cosmopolitan meso- or bathypelagic species and in these series of hauls it was found below 800m, but with very few specimens below 1500m (Tables 8.5, 8.6). In the Discovery Collections it is recorded at 18°N, 25°W, at 28°N, 14°W, at 40°N, 20°W and at 42°N, 21°W with a depth range of 410-4021m (Chidgey, 1985 and IOS unpublished data).

Only a few specimens of E. bathyantarctica were found (Table 8.2) but it has now been recorded in the Discovery Collections at this site (31°N, 25°W), at 18°N, 25°W, at 40°N, 20°W and at 42°N, 21°W (IOS unpublished data), thereby increasing its geographical range from one solely in the Antarctic (David, 1958) to a more widespread bathypelagic distribution in the north east Atlantic.

Heterokrohnia spp.

Due to recent improvements in deep fishing techniques (Roe and Shale, 1979; Roe and Darlington, 1985), the known species of Heterokrohnia now number nine. H. davidi was found in an RMT8 haul at 2700-3110m (Table 8.2); H. murina in an RMT 1 haul at 4295-4720m; 15 specimens of Heterokrohnia nov. sp. were caught in the deep RMT1 hauls and a single specimen in a deep RMT 8 (Table 8.2). These three species have also been found at 42°N, 21°W between 3500 and 4000m (IOS unpublished data).

Sagitta spp.

The genus Sagitta comprised eleven species at this site; S. lyra (2009 specimens) and S. hexaptera (1985 specimens) were the most numerous.

S. lyra is an epi- or mesopelagic species with an extensive vertical distribution, although maximum numbers are usually found in the epipelagic layers. In this species there is a direct relationship between size, and therefore maturity, and depth large individuals being deepest. In the RMT 8 hauls it was not well represented in the 0-100m layer and the maximum numbers caught were between 300 and 600m (Tables 8.7, 8.8). S. lyra has been caught extensively throughout the water column at 18°N, 25°W, at 28°N, 14°W, at 30°N, 23°W and at 40°N, 20°W (Chidgey, 1985; Roe, 1974 and IOS unpublished data) but at 40°N it was also low in numbers in the 0-100m level.

S. hexaptera is an epi- or mesopelagic species with maximum numbers usually occurring between the surface and 300m in all warm and temperate oceanic waters. In the RMT 8 hauls the numbers of S. hexaptera caught in the 0-100m layer showed a slight increase at night and a corresponding decrease in the 100-300m layer indicating a small diel vertical migration (Tables 8.9, 8.10). Both juveniles and adults were caught throughout the water column whereas at 18°N, 25°W and at 28°N, 14°W there was a slight diel vertical migration of only the juvenile population within the 0-100m layer (Chidgey, 1985 and IOS unpublished data).

As with S. lyra, virtually no S. hexaptera were caught in the 0-100m layer at 40°N, 20°W (IOS unpublished data).

S. decipiens is usually described as a cosmopolitan mesopelagic species of warm and temperate waters but it was very scarce at this site; only two specimens were caught in the night RMT 8 hauls (Tables 8.2, 8.11). It has been recorded in high numbers at 18°N, 25°W, at 28°N, 14°W, at 30°N, 23°W and at 40°N, 20°W (Chidgey, 1985 and IOS unpublished data). However, it is a slender species with a maximum body length of 14mm and the previously recorded high numbers included hauls using the finer meshed N113 and RMT 1 nets.

Too few specimens of *S. bipunctata* were caught to draw any conclusions although this is a cosmopolitan epipelagic species commonly found in the north east Atlantic (Tables 8.2, 8.12). It has previously been found in quite high numbers in the Discovery Collections at 18°N, 25°W and at 28°N, 14°W, but only a small number at 40°N, 20°W (Chidgey, 1985 and IOS unpublished data).

A few specimens of *S. serrodentata* were caught (Table 8.2). This species is a common epipelagic species of warm Atlantic waters, usually below 50°N, and has been found in high numbers at 18°N, 25°W and at 28°N, 14°W. This species is often confused with *S. tasmanica* which however is generally found in colder waters than *S. serratodentata* (Chidgey, 1985 and IOS unpublished data).

Three specimens of the epipelagic *S. enflata* were caught in the RMT 8 hauls (Table 8.2). It is recorded in the Discovery Collections in low numbers at 28°N, 14°W, at 30°N, 23°W and at 40°N, 20°W, but at 18°N, 25°W it was the second most numerous chaetognath caught (Chidgey, 1985 and IOS unpublished data).

S. planctonis is considered by some authors to be a separate species (David, 1956) or it is considered, with *S. zetesios* to be a form of a polytypic species, *S. planctonis* f. *planctonis*, (Pierrot-Bults, 1969). I consider it to be a separate species but closely related to *S. zetesios* and to the deep *Sagitta* nov. sp. found at this site (Chidgey, in prep.).

S. planctonis is generally described as a shallow mesopelagic species found between 40°S and 40°N, and in these RMT 8 hauls it was found between the surface and 1500m and in an RMT 1 haul at 5132-5233m (Table 8.13). At 18°N, 25°W it was found between 49 and 900m, at 28°N, 14°W between the surface and 800m and at 42°N, 21°W between 1000 and 4031m (Chidgey, 1985 and IOS unpublished data).

S. zetesios was found below 500m in the RMT 8 day hauls and below 600m in the night hauls, and 1 specimen was caught in the 5345-5385m haul (Tables 8.2, 8.14). Its distribution ranges from 60°S to 60°N and between 40°S and 40°N it is usually described as a deep mesopelagic species. However, in the Discovery Collections it has been found at 18°N, 25°W between 300 and 1250m, at 28°N, 14°W between 400 and 960m, at 30°N, 23°W between 240 and 260m, at 40°N, 20°W between 400 ad 2000m and at 42°N, 21°W between 1000 and 4021m (Chidgey, 1985; Roe, 1974 and IOS unpublished data).

S. macrocephala is a widely distributed meso- or bathypelagic species rarely occurring above 500-600m. It was found in the RMT 8 hauls below 600m by day and 800m at night, and as deep as 5110m (Table 8.15, 8.16). At 1200-1300m the population consisted entirely of juveniles and adults were only found below 1910m. It has been recorded at all the other areas studied below 440m (IOS unpublished data).

One specimen of *S. maxima*, a cold deep water species, was found at 1100-1200m (Table 8.2). It has previously been recorded in the Discovery Collections at 42°N, 21°W and at 60°N, 20°W (IOS unpublished data).

9. GASTROPODA

C.J. Ellis

Pteropoda

These holopelagic opisthobranch molluscs swim by means of muscular footlobes which look like wings and give them the common name of sea butterflies. There are three groups of pteropods, the gymnosomes, pseudothecosomes and the euthecosomes. The gymnosomes are shell-less carnivores, their prey usually being euthecosomes. The majority of pteropods are shallow living but some species e.g. Peraclis bispinosa (a pseudothecosome) and Clio polita (a euthecosome) are deep mesopelagic to bathypelagic. Pteropods were collected by both RMT 1 (Tables 6.33-35) and RMT 8 nets.

Gymnosomata

Gymnosomes are particularly difficult to identify to species usually due to their contraction during fixation (van der Spoel 1976). They are poorly known and little information is available on their distributions or biology.

Only eight specimens were taken in the RMT 8 nets (Table 9.1). Six of these were caught below 500m and were possibly predatory on the deep-living species mentioned above.

The RMT 1 caught a great many very young juveniles about 0.5mm diameter (apparently all the same species). The data for juveniles are distinguished from the much larger adult specimens in Table 9.2. Juveniles seemed to occur principally at mesopelagic depths from 100-600m whereas adults occurred erratically throughout the water column.

Pseudothecosomata

The Pseudothecosomata includes 3 diverse families, the Desmopteridae, Peraclididae and Cymbuliidae. All have the parapodia fused to a swimming plate and the mouth is raised and projects ventrally. The pseudothecosomes use a funnel-shaped mucous sheet to trap food. Fragments of large fast moving prey can be found in the stomach contents (Gilmer and Harbison 1986) so it is not clear whether they should be regarded as carnivorous trappers or suspension feeders. Probably they exploit a wide range of food sources.

Relatively few pseudothecosomes were caught. Data for cymbuliids are given in Table 9.3 but they have not been identified to species.

Peraclids, with their distinctive shells have been specifically identified. Three species were found, of which *Peraclis bispinosa* was the commonest (Tables 9.4-9.6). This is a deep meso- to bathypelagic species. Numbers per m^2 of sea surface are low; 1.23 by day and 1.72 by night for the top 1500m, but how this compares with other areas is unknown as no comparable data are available. Pafort-van Iersel (1985) regards *P. bispinosa* as a typical inhabitant of subtropical and transitional waters up to 45°N.

A very few specimens of the shallower-living species *P. apicifulva* and *P. depressa* were found; $0.78/1000m^3$ between 300-400m (day) and $23.17/1000m^3$ between 0-100m (day) respectively.

Euthecosomata

Most euthecosomatous species are found in the top 200m of the water column, though some such as *Clio pyramidata* are commoner at mesopelagic depths and *Clio polita* is a deep meso/bathypelagic species. Specimens of species other than *Clio polita* caught below ca 800m probably represent leakage contaminants or dead/dying individuals.

Most species undertake a diurnal vertical migration. In RMT 1 hauls the peak density for euthecosomes was between 100-200m by day and 0-100m by night (Tables 9.7-9, Fig. 6.X). The number per m^2 of sea surface in the top 1000m was 47.25 by night and 59.96 by day. Most individuals (predominantly *Limacina* spp) are in the smaller (0.32mm) size fraction - $44.8/m^2$ by night and $59.0/m^2$ by day.

The larger species are better sampled by the RMT 8 (Table 9.10) which gave an estimated $6.35/m^2$ by day and $2.13/m^2$ by night in the top 1000m. These data are similar to the densities observed in June at 35°N 33°W where there were $9.08/m^2$ by day and $8.94/m^2$ by night (Ellis unpublished data). Both sites are depauperate when compared with samples taken in June in the Sargasso Sea (30°N 33°W) where there were 56.42/m^2 by day and 60.02/m^2 by night. There are no comparable data available for RMT 1 hauls. These densities are unlikely to be constant throughout the year and occasionally huge monospecific swarms occur. One such swarm was sampled at 39°30'N 15°W where *Cavolinia inflexa* reached an estimated density of 3,850 individuals per m^2 sea surface in the top 200m, (Ellis pers. obs.).

The details of vertical migration in individual species are mostly poorly known and probably differ with season and latitude. However, migration to the surface is unlikely to occur from depths greater than 600m. There is no evidence of migration in the unusually deep-living *Clio polita* and this species, which appears to be the only bathypelagic euthecosome in these samples, was not recorded from depths greater than 2700m.

Euthecosomes do, however contribute to a downward flux of material to the benthic environment. For example single *Peraclis bispinosa* shells, with fragments of the soft parts attached, were found in two near bottom samples (Stn 11261#55, 11262#25). These had perhaps been attacked and partially eaten by gymnosome predators. Also amongst the stomach contents of two species of asteroid *Styrachaster horridus* and *Hyphalaster inermis* (Billett pers. comm.) were 3 shells of adult *Cavolinia gibbosa*. Pteropod shells may provide a useful source of nutrition as their aragonite is laid down on a proteinaceous matrix and also the nutritive value of a shell may be increased by fungal hyphae which may invade during degradation (Thiel 1983a).

Limacina species

These were the commonest euthecosomes in the RMT 1 catches. They are small species which were not sampled by the RMT 8. Four species were caught, *L. bulimoides*, *L. inflata*, *L. leseurii* and a species that was not identified.

Limacina bulimoides

This species is regarded by Pafort-van Iersel (1985) as a strong vertical migrant. In these samples it congregated at 100-200m by day and moved to

50-100m by night (Tables 9.11-12). Records from deeper than 300m are probably leakage contaminants.

Limacina inflata

This is an abundant warm water species which Pafort-van Iersel (1985) has shown to be a distinct vertical migrant. Data from GME samples also indicate a migration, from 300-500m by day to the top 100m by night (Tables 9.13-14).

Limacina leseurii

The distribution and vertical migration pattern were similar to Limacina inflata (Tables 9.15-16).

Limacina sp.

These tiny patulous-shelled animals also showed a vertical migration from 100-200m by day to 50-100m by night (Tables 9.17-18).

Diacria major

This relatively large species was previously considered to be a subspecies of D. trispinosa, hence not much information on its distribution is available. However, Pafort-van Iersel(1985), using data from the AMNAPE transect, found that it occured mainly from 25°N to 30°N in the mid North Atlantic. She also suggested that the species was a non-migrant. The present depth range (50-300m) is identical to that found in the AMNAPE material (Table 9.19). The number per m^2 of sea surface in the top 500m was 0.06 by day and 0.05 by night.

Diacria trispinosa

This species has a wider geographic range than D. major in the mid North Atlantic. Pafort-van Iersel (1985) found it between 25-51°N. It also shows a clear diurnal vertical migration with peak densities at 200-300m by day and 50-100m by night in the AMNAPE material, and between 300-400m by day and 0-25m by night at GME (Table 9.19).

Juvenile Diacria trispinosa or D. major

A number of juvenile specimens were taken by the RMT 1 that could belong to either of these species: there is no known way to distinguish them prior to the development of the adult shell. Depth range was 50-100m by day and 50-200m by night (Table 9.19).

Diacria quadridentata

The adults of this species are relatively small (about 3mm high) but were sampled by both RMT 1 and RMT 8s (Table 9.19). It occurred principally in the top 100M. Bé and Gilmer (1977) suggested that it prefers boundary currents, and is a good indicator species of the Gulf Stream. Conversely however, Pafort-van Iersel's (1985) analysis of the AMNAPE material suggested that it is restricted to subtropical waters and is absent from the Gulf Stream.

Cuvierina columnella

This species is common in tropical and subtropical waters though often patchily distributed (Bé and Gilmer, 1977). Pafort-van Iersel (1985) found a marked diurnal migration which is repeated in both RMT 1 and RMT 8 material here, with a peak day time density between 200-400m and a peak night time density between 0.25m, (Table 9.20).

Cavolinia tridentata

A few specimens of this large species were collected in the RMT 8 nets (Table 9.20). All the specimens were taken by day from 50-100m. Little is known of the depth or geographic distribution of this seldom captured species in the North Atlantic, though it is generally regarded as being subtropical (Be and Gilmer 1977).

Cavolinia gibbosa

Adults were sampled by the RMT 8 and juveniles by the RMT 1 (Table 9.20). Pafort-van Iersel (1985) comments on its patchy distribution, and from the data available from the AMNAPE material and GME it is difficult to determine whether or not the species migrates diurnally.

Clio pyramidata

Specimens were taken in both RMT 1 and RMT 8 nets (Table 9.21). Both sets of data suggest a marked diurnal migration similar to that observed by Pafort-van Iersel (1985). She also records that it is a strongly seasonal species which is relatively rare in the summer. Hence the low numbers caught here may be a seasonal effect.

Clio cuspidata

A few specimens were taken by both RMT 1 and RMT 8 (Table 9.21). Diurnal migration was demonstrated by Pafort-van Iersel (1985) at 45°N 34°W and she also notes that it was absent south of 30°N in the summer collections of AMNAPE.

Clio polita

This species occurred from 1910m to 2700m in the RMT 1s and from 500m to 1910m in the RMT 8 (Table 9.21). This depth range seems to be normal for the species (Pafort-van Iersel, 1985). It does not appear to be a vertical migrant.

Styliola subula

This small, conical-shelled species was occasionally taken in the RMT 8 catches but is much better sampled by the RMT 1 (Tables 9.22-24). Most specimens pass through the 1.0mm mesh into the .32mm subsample, since although the shell length can be up to 6mm the diameter is seldom more than 1.0mm. The GME data are somewhat erratic for day hauls but at night most specimens occurred at 25-50m. Pafort-van Iersel (1985) found a diurnal vertical migration from 200-400m by day to 0-50m by night at 45°N. She also described seasonality, the species being least abundant in the summer.

Creseis sp

The shells of Creseis resemble those of Styliola subula but are longer, thinner cones. Most specimens were damaged and shell-less and had to be identified on soft characters notably the wing cusp. Identification to species was not possible. Specimens were taken mainly in night hauls (Table 9.25) and perhaps suggest a patchy distribution.

Unidentified euthecosomes

A few specimens which had lost their shells and were very badly damaged or very small could not be identified. These are listed in Table 9.25.

Heteropoda

The Heteropoda are prosobranchs highly modified for a holopelagic carnivorous existence. They are typically shallow living (see Tables 6.36-38). Occurrences of heteropods in samples below 600m are most probably leakage contaminants or dying. Heteropods fall into two main types, the gelatinous pterotracheids and carinariids in which the shell is absent or greatly reduced and the more common and less modified atlantids which can completely retract into a coiled shell. Data on seasonality in these animals is very poor but they can occur in large swarms (Taylor & Berner, 1970).

Pterotracheids and Carinariids (Table 9.26)

Three carinariids and 3 pterotracheid species were present in the GME samples. One species of carinariid, Carinaria challengeri was taken only in the >4.5mm subsample of RMT 1 11261#31, hence it is not included in the RMT 1 data in Table 9.26, but its presence at GME should be noted. This record is considerably further south than records given by Pafort-van Iersel (1983). Likewise a specimen of Pterotrachea hippocampus was found in the >4.5mm subsample of RMT 1 11261#73, which is also not included in Table 9.26. The commonest species in both RMT 1 and RMT 8 hauls was Firoloida desmaresti, the smallest of the pterotracheid species with a maximum body length of 40mm. This species was not seen in samples taken at 30°N 33°W in June 1981 (Ellis, unpublished data) whilst

P. scutata, which was common in these latter samples, was absent from GME. This is possibly due to seasonality of the species. There is some previous evidence of seasonality and Pafort-van Iersel (1984) notes that most species were commoner in the spring and summer collections of the Amsterdam mid-North Atlantic plankton expedition. The general paucity of material, as illustrated by these samples, makes an understanding of the seasonal and geographical distributions a difficult task.

Atlantids

In these shelled heteropods the shell seldom exceeds 12mm diameter. It is multispiral and flattened in one plane with the large outer whorl encircled by a keel. As with the pterotracheids and carinariids they are shallow living. The data for total atlantids is figured (Fig. 9.I). Table 9.27 lists species in the top 300m of the water column. Occurrences below 300m are either contaminants or else in the process of sinking out of the water column. Identification of species was based on Tesch (1949) and van der Spoel (1976). The separation of Atlanta gaudichaudi and A. peroni was particularly difficult as many specimens were juvenile and could not be keyed out. It was assumed that large specimens with pigment at the base of the keel were A. gaudichaudi. Juveniles were separated on the basis of a black-pigmented duct lying between the head and hepatopancreas - those with a black duct were attributed to A. gaudichaudi. There is some doubt that A. peroni and A. gaudichaudi are separate species.

Eight species were found in the samples and two main types of veliger larvae (Table 9.27). One veliger type with purple shells was ascribed to A. inflata. They are probably not A. helicinoides (also purple shelled at GME) as the rate of whorl expansion does not fit with this species. The white shelled veligers could belong to several of the other species or they could be mixed species. Most probably they are juvenile A. peroni or A. gaudichaudi - though they might also be juveniles of another species, e.g. A. leseuri which occurred at 30°N 33°W in June 1981 (Ellis unpublished data), and the possibility that they were juveniles of A. inclinata (comparatively rare in these samples) cannot be excluded.

The data are by no means conclusive, but are suggestive of a minor diurnal vertical migration over a short range, at least in A. peroni and possibly A. inflata. Examination of Table 9.27 and Figure 9.I also suggests that a diurnal migration occured in the 1.0-4.5mm fraction i.e. that the larger atlantids migrated upwards from 50-100 to 0-50m at night. In the small size class (.32-1.0mm) there is a large discrepancy in numbers by day and night with fewer by night (4.22 per m^2 sea surface - in hauls #29, #30 and #31) than by day (19.14 per m^2 sea surface - hauls #73, #74 and #75). This is likely to arise if the animals are concentrating at the surface at night and so escape being sampled effectively.

Monotocardia

Besides the holopelagic gastropods (opisthobranch pteropods and prosobranch heteropods) the juveniles of some more snail-like monotocardian prosobranchs were found. These seem to survive capture fairly well as the animals can retreat into their shells. However, the shells may become fragile in the preservative. All the specimens were small, seldom more than a few millimetres shell height and their contribution to the biomass was trivial. The great majority were tiny juveniles of a ianthinid species occurring largely in the top 100m of the water column.

The material was sent to Dr. P. Bouchet of the Museum National d'Histoire Naturelle (Paris) who identified them in collaboration with Dr. A. Waren of the Naturhistoriska Riksmuseet (Stockholm). Material from the RMT 8 and the RMT 1 nets are considered separately.

RMT 8 Samples

Eleven specimens were found, all too small for their populations to have been representatively sampled by the RMT 8 nets. However, the material included two species not found in the RMT 1 catches, viz the tonnaceans Tonna galea and Cypraecassis sp. The data are listed in Table 9.28.

All were probably the teleplanic larvae of shallow water Tonnacea. The nearest possible locality for the source community is Cruiser Seamount some 140 miles to the northwest. Decapod larvae of similarly shallow-living species have also been found in GME samples (see Section 17). Hence it can be deduced that there is some measure of horizontal flux in these communities.

RMT 1 Samples

The RMT 1 samples yielded some 596 specimens of eleven species. The majority (576 specimens) were the larvae of a Ianthina species (Tables 9.29-31). The other ten species were represented by only one or two specimens per subsample and in view of the paucity of the data it would be misleading to provide numbers per $1000m^3$ for these (Table 9.32), particularly as gastropod shells, being heavy, sink quickly so numbers are likely to be poorly estimated from fractions. The value of the data lies in illustrating the potential for vertical interchange between the benthos and the water column in the form of larval gastropods. The specimens of Benthonella, Haloceras and eulimid are all larvae of benthic species and are discussed below.

Ianthina sp. A (Taenioglossa: Ptenoglossa: Ianthinidae)

Ianthina species are holopelagic. They enclose air in bubbles of mucus to form a raft which allows them to stay floating at the sea surface where they feed largely on siphonophores, especially Velella (Fretter and Graham, 1962).

Juvenile specimens were abundant in the top 100m of the water column (Tables 9.29-9.31). They were small and of uniform size, about 0.5mm spire height, suggesting that they were recently released. The numbers were erratic, estimated numbers per m^2 for the top 100m were 16.74 by day and 47.46 by night on the basis of the three hauls subdividing the top 100m, whilst estimates based on 0-100m hauls give 104.99 per m^2 by day and 6.17 per m^2 by night. These data and the biology of Ianthina suggest that the juveniles are highly patchy in their distribution.

Specimens apparently occurring deeper in the water column are likely to be leakage contaminants in view of their small size and relatively high densities at the surface.

Ianthina sp. B (Taenioglossa: Ptenoglossa: Ianthinidae)

A single specimen of a different ianthinid species was found at 1100-1200m. This is probably a surface contaminant (Table 9.32).

Cymatiid spp. (Taenioglossa, Tonnacea, Cymatiidae)

Four species were found in the RMT 1 samples (Table 9.32). Sp. C was the commonest, with 4 specimens in RMT 1 catches and 6 in the RMT 8. Of these ten specimens nine occurred in hauls taken in the top 100m of the water column; the tenth was taken in haul 11261#19 and is probably a contaminant as this haul contains a range of shallow-living species. Cymatiids are carnivorous prosobranchs, equipped with an efficient neurotoxic saliva that they squirt over their prey which is frequently echinoderm (Fretter and Graham, 1962).

Echinospira larvae (Taenioglossa: Lamellariacea)

Echinospira larvae are found in three families, Lamellariidae, Eratoidae and Capulidae. These larvae are long-lived in surface waters with an elaborate shell which helps to keep them afloat. The single specimen caught was nautiloid - suggesting that it was a lamellariid (Table 9.32). These are carnivorous prosobranchs typically feeding on tunicates (Fretter and Graham, 1962).

Benthonella (Taenioglossa: Rissoacea)

Three specimens were taken, between 1700-2600m off the bottom (Table 9.32). There were a number of adult *Benthonella* taken in the sledge samples (see Section 30). It is known that larvae of this genus migrate to the surface and then return to the benthos after metamorphosis (Bouchet, 1976 a,b; Bouchet and Fontes, 1981). From the size of the shell it would seem likely that the present specimens were caught in the process of sinking to the bottom.

Turrid, Eulimid, *Haloceras* and unknown species

Juveniles of these were found in the near bottom samples suggesting that the larvae of these species migrate a few tens of metres off the bottom but do not make the migration to the surface seen in Benthonella.

The turrids (Stenoglossa: Conacea: Turridae) live mainly on soft bottoms feeding on polychaetes. At bathyal and abyssal depths they are usually the commonest prosobranchs both in terms of species and numbers of specimens (Bouchet and Waren, 1980). Unusually at GME the benthic fauna is dominated by echinoderms rather than polychaetes so the turrids are also likely to be less important at this site (Section 22, 30).

The eulimids (Taenioglossa: Aglossa: Eulimidae) are ectoparasitic, usually associated with echinoderms and specialising in feeding on body fluids (Fretter and Graham, 1962). This juvenile specimen could not be identified at species or even generic level.

Overall these gastropod larvae make a comparatively trivial contribution to the biomass. However the possibility exists that the larvae arising from benthic species may provide an upward pathway for flux of material off the bottom into the pelagic communities. In some species the larvae may even reach the surface.

10. OSTRACODA C.J. Ellis

Ostracods are usually the second most abundant group after copepods in plankton samples. At GME there were 1206/m^2 sea surface in the top 1000m by day and 1465/m^2 by night. This is a similar density to that seen at 35°N, 33°W where there were 1373/m^2 by day but less than observed at 30°N 33°W (1818/m^2 day) and at 49°N 14°W (2401/m^2 day) (Ellis unpublished data).

Ostracods were present throughout the water column, their density declining with increasing depth so that at about 1500m there was only about 1% of the density seen in shallow water (Tables 6.42-44; Fig. 6.X). No near-bottom increase in overall density occurred at GME, in contrast to ostracods elsewhere in the North Atlantic (Hargreaves, Ellis and Angel, 1984; Ellis, 1985). However, this general view disguises the near-bottom increase observed in one ostracod genus, Bathyconchoecia. It is probable that leakage contaminants affect the overall figures, disguising a small but real increase near-bottom. Elimination of contaminants requires identification to species and a more complete data bank on vertical distributions than is currently available.

Identification of species is particularly difficult with GME material as the condition of most of the ostracods was very poor. Most ostracod species can be recognised by carapace characters, when sex or instar is also apparent. However, many of the present specimens consisted of detached and battered carapaces, or were missing appendages that might have aided identification. The near-bottom ostracod community contains many undescribed species (e.g. Angel and Baker 1982), and the present samples had a number of new or partially described species. In very few benthopelagic species have both sexes and larval stages been fully described (Ellis, in press). Clearly nothing is known of the ecology of undescribed species and very little about described abyssal and benthopelagic species. Even within the better known meso- and bathypelagic species such aspects of the ecology as deep tails to vertical distributions (Angel, 1979, 1983a) are not properly understood. These problems make analysis of the data from this under-researched group very difficult.

Identification to genus, and in some cases to species has been possible. Eight genera were distinguished Gigantocypris, Macrocypridina, Halocypris, Halocypria, Archiconchoecia, Bathyconchoecia, Conchoecia and Thaumatoconcha. For five genera only one species occurred, hence generic numbers are equivalent to specific numbers. All Archiconchoecia and a few Bathyconchoecia were identified to species.

Gigantocypris

The features distinguishing the two species of Gigantocypris that occur in the N E Atlantic are only usable for adult undamaged specimens. The majority of specimens in these samples were battered and juvenile or were detached carapaces. Material from the RMT8 hauls could not be identified to species (Table 10.1). However 4 adults caught in the >4.5mm mesh of the RMT 1 samples, were in better condition and were tentatively identified as G. dracontovalis. Other specimens in the RMT1 samples were mostly juvenile or carapaces; they mainly occurred between 2310-4295 suggesting that they too were G. dracontovalis (Tables 10.2-3; Fig. 10.I). This species is deeper living than its congener G. mulleri. Angel (1979, 1983a) recorded it between 2100-3900 (42°N, 17°W) below 2500m (44°N, 13°W) and below 3000m (20°N, 21°W). This species is not thought to undertake any vertical migration.

Macrocypridina

There is only one pelagic species in this genus, M. castanea. It was regular but not abundant between 300-1400m in the RMT 8 catches (Table 10.1); a few specimens were also taken by the RMT 1 (Tables 10.4-10.5, Fig. 10.I). These data agree with those of Angel (1979) who found that at 30°N, 23°W the adults were deep mesopelagic (500-1500m) by day and that a substantial proportion migrated upwards at night; whilst juveniles were shallower (50-400m) by both day and night.

Halocypris

Two species of this genus were encountered in the GME samples, H. inflata and H. pelagica. They are closely related, the most obvious distinguishing character is size combined with a subtle distinction in carapace shape (Angel, 1982). Adults are relatively easy to distinguish, however juveniles are more difficult

- especially when the material is in poor condition. A single specimen of H. inflata - an adult female, was caught between 50-100m (Day). All the other specimens were identified as H. pelagica (Tables 10.6-10.8, Fig. 10.I).

Most H. pelagica were taken in the top 200m, however there was a deep tail to the population consisting largely of females which extended to between 800-2700m (Tables 10.6-10.8, Fig. 10.I). Below this, the samples appeared to contain more juveniles than adults and the relative numbers of sexes and stages seem more like those of shallow hauls - suggesting that they might be leakage contaminants. Vertical migration occurred with peak densities at 100-200m by day and 0-100m by night (Fig. 10.I).

Angel (1982) recorded the overall dominance of H. pelagica in the water column at 30°N, 23°W though H. inflata dominated a neuston net catch at this position. He also found a deep distributional tail of females at both 30°N, 23°W and 32°N, 64°W (Angel, 1979).

Halocypria

H. globosa is the sole species within this genus. Females occurred erratically throughout the water column but were taken mainly from 0-300m by day and 0-100m by night (Tables 10.9-11; Fig. 10.I). Juveniles were taken by day only in the top 200m. Only two males were caught, one at 600-700m (day) and the other at 700-800m (night).

Angel (1979) regards H. globosa as typically a centre gyre species which may be advected into peripheral regions. At 32°N 64°W, he found that females and juveniles were concentrated in the top 200m, whereas males occurred deeper, mainly between 800-900m. The female distribution showed a distinct deep tail going down to 2000m. Deevey (1968) failed to observe adult males in samples taken off Bermuda, probably because the maximum depth of her samples was 500m.

The deep distributional tail of females is a common feature of H. globosa distributions (Angel, 1979, 1983a) but has not been fully explained. Angel (1982) reported numerous adult female H. globosa at depths around 1000m in the Porcupine Seabight and suggested that the capture of H. globosa might be a function of season and depth of fishing. However, the extreme depth of females at GME is surprising, though if they were leakage contaminants then it would be expected that some juveniles would also have been seen - and this was not the case.

Archiconchoecia

The species of this genus can be split into three types, cucullata-group, striata-group and ventricosa-group. All the specimens of Archiconchoecia have been identified to species (Tables 10.12-10.14).

The largest species are in the cucullata-group. Currently only one species has been described but there are at least three others being described, (Angel, in prep.), two of which were also found here. These new species are not yet named and are designated A. sp.M and A. sp.P.

Adult A. cucullata and A. sp.M can be distinguished on size. However, many of the specimens in this group were badly damaged and juvenile, making it difficult to assign them to species. The data should therefore be treated with circumspection.

A. cucullata

This species occurred throughout the water column below 1000m, but appeared to avoid the near-bottom environment. It was not present in samples closer than 200m off the sea bed. Angel (1979) found that it occurred deeper in the water column than A. sp.M at these latitudes.

A. sp.M

This small species showed peak densities at 800-900m by day and 300-400m by night. It occurred at low densities throughout the water column and most specimens at abyssal depths are probably leakage contaminants.

A. sp.P

This is an abyssopelagic and benthopelagic species. It occurred at low densities below 2700m. Twelve specimens were taken and most were badly damaged.

A. striata

A. striata is a very small species, the female, which is larger than the male, is about 0.5mm carapace length (Deevey, 1968). Probably only the female is adequately retained by the RMT 1 mesh, and all save one of the specimens (a male taken in 11261#12) were female.

At 30°N, 23°W Angel (1979) found it between 50-400m. At GME it was most abundant at shallow mesopelagic depths though its occurrence was rather erratic.

A. bispicula and A. gastrodes

These species fall into the ventricosa-group of eleven species considered by Deevey (1978).

Two females and one male A. bispicula were taken. These were identified by the two prongs on the frontal organ and the size and setation of the claw setae of the sixth limb.

One male was tentatively identified as A. gastrodes. The identification is uncertain as Deevey (1978) described only the female, taken at 32°N 64°W in a haul from 1000-1500m. However, the size and setal characters of the present male fit the characters for this species.

Archiconchoecia spp. occurred throughout the water column. Deevey (1978) observed that the percentage contribution of Archiconchoecia to total ostracod numbers increased from 1.2% at 0-500m to 10% at 1500-2000m. A similar general increase with depth was also seen at GME (Tables 10.20-10.22).

Bathyconchoecia

The distribution of this genus is clearly abyssopelagic and benthopelagic at GME

(Tables 10.15-10.16, Fig. 10.I). The highest densities occurred within 100m of the sea bed. In the three trawls taken in the bottom 100m the highest densities were between 25 and 50m above bottom.

Identifying the Bathyconchoecia material to species was not feasible. Only 19 species of the genus have been described and probably an equal number of undescribed species are represented in Discovery Collections. Both male and female have been described in only six species, and four species have been described from juveniles only. Identification of specimens was rendered more difficult by the state of the material, and only 21 of a total of 129 specimens belonged to species with distinctive carapace characters; the remainder could not be sorted into species, described or undescribed.

The 21 specimens belonged to four species. Three specimens were of 7-spined species - two were juveniles of a species currently being described (Ellis, in press) and the other appears to be a juvenile of a closely-related but undescribed species. One specimen of an undescribed 3-spined species was caught. The other seventeen specimens were of another undescribed species, which has dramatic diagonal striation. Specimens of this species were taken mainly within 100m of the bottom but one specimen was taken in 11262#10, some 1000m off bottom, and two in 11261#68 at 1400-12500m; these two may possibly be hang-up from a previous haul. A specimen of this species was also found in the gut of the fish Echinomacrurus mollis (Section 29).

Conchoecia

The great majority of halocyprid ostracod species are classified in Conchoecia (Tables 10.17-10.19, Fig. 10.I); there are over 200 species in the genus. Some groups of similar species can be identified within the genus but distinguishing species within the groups can be difficult especially when the material is in poor condition. Time did not permit specific identification of this genus. However, Conchoecia species dominated all the samples (Tables 10.20-10.22), contributing more than 55% of the total ostracods. Any near-bottom increase in benthopelagic Conchoecia species would probably be concealed by leakage contaminants, a particular problem in this predominantly shallow living genus. Little is known of the ecology of benthopelagic species and only a few descriptions have been published (Angel and Ellis, 1981).

Thaumatoconcha

The thaumatocyprids are regarded as the most primitive of the halocyprids. They have a long fossil history dating back at least to the Permian (Kornicker and Sohn, 1976). They are generally benthic or troglodytic.

A tiny juvenile, tentatively assigned to the genus *Thaumatoconcha*, was caught in 11261#55 (5388-5415m, 24-55mob). The members of this genus are typically benthic. This specimen is of particular note as this is the deepest record for a thaumatocyprid in the North Atlantic. The previous deepest record was for *T. polythrix* at 2223m (Kornicker and Sohn, 1976).

11. COPEPODA

H.S.J. Roe

Introduction

Copepods were the most abundant planktonic group sampled at GME (Tables 6.45-47). They occurred throughout the water column but were most numerous in the top 500m. Overall there was a distinct upward vertical migration at night in the epi and mesopelagic populations (Fig. 6.X).

No detailed specific analyses of copepods could be made in the time available. However the deep RMT1 samples, including one set of near bottom tows were examined. The replicate near bottom tows were not studied and all the copepod numbers in Tables 6.45-47 are slight overestimates because they include contaminants and carcases (see below).

Methods

For each sample (Table 11.1) the calanoid and non-calanoid copepods considered to be alive when captured, and to inhabit the depth sampled, were counted.

Shallow living contaminants, principally species of *Acartia*, *Pleuromamma*, *Clausocalanus*, *Oithona* and *Oncaea* were also counted. Contamination of deep plankton samples by shallow living copepods is a common problem, see, for example Grice and Hulsemann (1965, 1967, 1968), Wheeler (1970), Roe (1972) and Harding (1972). Contaminants leak through the closed mouths of the RMT1s, usually as they are being paid out or recovered through the surface layers. The level of contamination here was apparently high, ranging from 1-78% (mean 29%) of the total numbers of copepods caught. These figures are rather misleading however; in percentage terms a small number of contaminants will be very large if the number of non-contaminants is very low - as in the deepest hauls here.

The number of copepod carcases was also counted. These comprised moulted exoskeletons and corpses with advanced degeneration of internal structure. Individuals were counted as carcases when the cephalothorax musculature (if present) appeared as undifferenciated, presumably decaying, tissue, and no trace of the gut remained. Similar criteria have been used by other authors (Farran

1926; Wheeler 1967 and Harding 1972, 1973). On the assumption that some carcases will have been contaminants, the numbers of carcases found in each haul have been corrected by the same percentage contamination observed in the "live" copepods of that haul (Table 11.2).

Results and Discussion

Below 1500m the numbers of copepods declined exponentially with increasing depth (Tables 11.1-2; Fig. 11.IA - see also Fig. 6.X for the total water column). The decline was arrested at Stn 11261#46 where there was a sharp increase in numbers (Fig 11.IA). The RMT1+8M hit the bottom during this haul and the increased numbers of copepods may reflect this. The three near bottom tows, (St 11261#63-65, fished 90-50, 50-25 and 25-10m above the bottom respectively), did not contain increased numbers of copepods but the proportion of non-calanoids increased markedly close to the bottom (Fig. 11.IC) and the proportion of carcases to "live" copepods also increased (Fig 11.IB).

Except for the two comparatively shallow hauls between 1910-2700m, the numbers of copepods below 1500m was less than 1 individual per m^3 of water (Table 11.2). These very low densities are similar to previous bathypelagic data from the Atlantic (Grice and Hulsemann 1965; Wheeler 1970, Harding 1972) the Indian (Grice and Hulsemann 1967) and Pacific Oceans (Vinogradov 1968). Only Vinogradov (1968) had data from depths greater than 5000m.

Benthopelagic plankton studies have been discussed previously (Section 6). Wishner (1980b), Boxshall and Roe (1980) and Roe (1986) refer specifically to near bottom copepods and all found increased numbers with increased proximity to the sea bed. These data contrast to the present analyses (Tables 11.1-2; Fig. 11.I) which show little, if any, near bottom increase. As pointed out earlier (Section 6) none of the previous data were from comparable depths or area and it may be that significant increases at depths of up to 100m above the bottom are restricted to shallower and/or more productive regions.

There was, however, a marked increase in numbers in the haul which hit the bottom (Fig 11.IA). Many copepods are apparently endemic to the zone immediately above the bottom (within 1m) or to the upper sediment layers. In the deep ocean these species have only been sampled by benthic trawls (Bradford 1969), by submersibles (Grice 1972) or by midwater trawls which accidentally hit the bottom (Roe 1986, unpublished data). Increasing numbers of these peculiar copepods have been found in shallow water (e.g. Fosshagen 1968, 1983) and there seems no reason why the deep-sea should not harbour many more.

Non calanoid copepods (cyclopoids and harpacticoids) were relatively more abundant within 50m of the bottom (Fig 11.IC). These data are comparable to those of Wishner (1980b) who found that adult calanoids comprised 40-68% of the total adult copepods caught between 10-100m above the sea bed.

The occurrence of copepod carcases in the deep sea, both dead animals and moulted exoskeletons, has rarely been estimated, probably because of the difficulties in distinguishing between naturally dead specimens and those killed and damaged in nets (Wheeler 1967; Harding 1972, 1973). The present data show an erratic distribution of carcases: "live" copepods between 1500m and the bottom (Fig. 11.IB). There is no obvious trend towards increased numbers of carcases with increased depth in midwater, perhaps indicating a balance between in situ production of moults and corpses and loss due to disintegration, consumption and sinking. In this context the potentially high incidence of detritivory discussed in Section 6 may be relevant - numbers of carcases do not build up in midwater because they are continously eaten.

There are few comparable midwater data. Farran (1926) concluded that the numbers of dead copepods increased with depth to at least 3658m but he analysed only five depth zones between 914-3658. Sameoto (1986) found that the numbers of both exoskeletons and corpses increased with depth between 0-1000m. It is possible that such an increase occurs at relatively shallow depths because the incidence of detritivory is relatively low. Wheeler (1967) found that more than 50% of the copepods caught between 2000-4000m in the Sargasso sea were carcases. These data are therefore similar to those given here (Fig. 11.IB).

Immediately above the bottom the proportion of carcases to "live" copepods increased (Fig. 11.IC). This near bottom increase is very similar to that observed by Wishner (1980b) who found that empty exoskeletons were 2.5-7.3 times as abundant as "live" copepods in hauls taken between 10-100m above the bottom at depths of 2400-3200m. She explained the paradox of large numbers of exoskeletons in plankton hauls with their virtual absence in sediment traps to their near neutral buoyancy, their tendency to flow with currents instead of settling out, and to resuspension and/or rapid decomposition when they do reach the bottom. There is an increase in current velocity close to the sea bed at GME (Saunders, 1985) and the large numbers of exoskeletons and corpses in this layer could reflect both a reduction in sinking rates and resuspension.

Whatever their history, copepod carcases are potentially very important food sources for the deep sea. Wheeler (1967) measured the carbon content of total carcases and chitin and concluded that copepod carcases had "a significant role in deep-sea food chains .... where the conventional primary producer - primary consumer relationship cannot exist". Detritivory would fall into this category. The biomass results (Section 6) amalgamate data from "live" animals and carcases of all types of plankton and micronekton. Copeods presumably contribute the bulk of planktonic carcases but it would be unrealistic to attempt to estimate the proportion of carbon due to live animals and that due to carcases in these samples.

Finally it should be pointed out that the biomass results (Section 6) also include contaminant species. Again most of these will have been copepods, but since the species concerned are mostly small (ca 1-2mm total length) the error in biomass due to their inclusion should also be small.

12. CIRRIPEDIA C.J. Ellis

The pedunculate goose barnacles are a frequent constituent of the oceanic fauna. In many species the adult stage is neustonic, *Lepas fascicularis* has the capability of making a spongy float and other species such as *L. anatifera* and *L. pectinata* attach to floating debris or ships' hulls etc. *Conchoderma* species specialise in settling on turtles and whales though they can also be found on ships and moorings. The larval stages of lepadids are common members of the plankton. There are six naupliar instars which are succeeded by the cyprid larva stage. Both cyprids and nauplii were sampled by the RMT 1 at GME and the data are considered below. These larval stages showed very different vertical distributions. Nauplii were found principally in the top 100m (Table 12.1; Fig. 12.I). A few specimens occurred below 300m which were probably leakage or hang-up contaminants or dying. The cyprid larvae occured deeper, principally between 400-600m (Table 12.2; Fig. 12.I). No adult goose barnacles were taken in the RMT 1+8M but a few *Lepas anatifera* were taken from a subsurface (142m) buoy at 31°28.8'N, 24°43.8'W. The mooring was deployed on the 19th November 1985 and recovered on the 24th September 1986. It had been out for 307 days and the maximum capitulum length was 50mm which indicates a minimum growth rate of 168μ per day. This is somewhat less than the 185μ recorded by Sneli (1983) from the North Sea (56°52.40'N, 02°05.12'E) and the 200μ-300μ he cites which was recorded by Evans (1958) off South Africa.

Nauplii

Cirripedes have six planktotrophic naupliar instars. The smallest stages (I & II) were not caught by the RMT 1 and stage III was probably only imperfectly sampled. Two types of nauplii were seen and these were provisionally identified as those of *L. pectinata* and *L. anatifera* on the basis of notes kindly provided by Dr. Moyse of Swansea University.

Lepas anatifera

Nauplii of all stages sampled (III - VI) congregated at 50-100m and avoided the surface both by day and night (Table 12.1). There was no indication of diurnal vertical migration though Roskell (1975) found many more larvae in night hauls at 10m than equivalent day hauls in Continuous Plankton Recorder data. This depth of peak abundance appears to correspond with the deep chlorophyll maximum (see Section 3) between 88 and 105m where these larvae were probably feeding. Their food preference seems to be for flagellate phytoplankton, (Moyse, 1984). Roskell (1975) found large numbers of these larvae in the summer from July to November.

Lepas pectinata

These are much less common than the nauplii of L. anatifera and only stage V and VI nauplii were caught. The vertical distribution pattern is rather erratic. Nauplii appeared to congregate at 100-200m depth by day but did not have a very clear pattern by night (see Table 12.1) though more were caught in the 50-100m haul by night than by day. In the CPR data Roskell (1975) found more L. pectinata nauplii between the months October to April with comparatively few in the summer.

Cyprids

The cyprid larva is the settling stage of barnacles. It is non-feeding and in lepadids has copious oil droplet energy reserves. Few lepadid species have been observed over the period of metamorphosis from cyprid to adult. Only L. pectinata and L. anatifera, which readily metamorphose in the lab, are unequivocally known at the cyprid stage (Moyse, pers. comm.). Four other types of cyprid were found at GME and these were designated A, B, C & E. A and B are thought to be Conchoderma species, C a Lepas species and E Lepas fascicularis (pers. obs.)

The greatest density of cyprids occurs at mesopelagic depths both by day and by night (see Tables 12.2-8 and Fig. 12.I). This extraordinary distribution appears to be typical for cyprids and similar distributions have been seen at 35°N 33°W and 32°N 64°W (Ellis unpublished data). Why cyprids spend time at depth when they might reasonably be expected to be spending their energy reserves seeking out a suitable settling site on floating material at the surface is an unexplained mystery.

By day the peak abundance of cyprids was at 400-500m whilst by night it was at 500-600m suggesting that a small diurnal reverse migration may have taken place, though this was not observed either at 35°N 33°W or 32°N 64°W and is probably a sampling error artifact. The increase seen in 11261#28 (1400-1500m) is due to the hang-up of material from haul 11261#24 that was later washed down into the 11261#28 catch. The 11261#6 haul may similarly have been affected by a hang-up from 11261#3 which was an unusually small catch.

Lepas pectinata

Cyprids of this species were very common at GME. *L. pectinata* is the smallest of the lepadid barnacles. Most species reach at least 40mm in length but Roskell (1975) suggested that this species reached only 13mm capitulum length; however, a specimen in the Discovery Collections measures 15mm. It occurs on *Sargassum* weed (Morris and Mogelburg, 1973) and Roskell (1975) suggested that its adult size is reduced so as not to sink its floating host. In collections made around 30°N 33°W many recently settled specimens were found on floating bits of oil, plastic and detached *Sargassum* weed floats - though none were found on ten clumps of *Sargassum* weed that were also collected (Ellis pers. obs.). Larger specimens were taken in this area which had settled onto clumps of *Lepas fascicularis*, a species which makes its own bubble float.

L. pectinata cyprids quite clearly shun the upper part of the water column (Tables 12.2-4) though at some stage they must return to the surface to settle. The majority occured between 400 and 600m. Some occured deeper in the water column, these may have been leakage contaminants or they may have been dying.

'E' type cyprids

These were the second most common cyprids at GME though an order of magnitude less abundant than *Lepas pectinata*. They followed a similar distributional pattern with peak abundances between 400 and 600m by day and night. None were found in the top 400m of the water column, (Tables 12.5-7).

A, B, C & *Lepas anatifera*

The other four types of cyprid were represented by only one or two specimens and so no comment can be made on their vertical distribution. The data are listed in Table 12.8.

13. **MYSIDACEA** P.M.D. Hargreaves

Introduction

Detailed analysis of mysids has been done mainly on RMT 8 catches. The total numbers of mysids caught by the RMT 1 and RMT 8 are given in Tables 6.48-52.

Biomass (RMT 8)

The greatest biomass (measured by displacement volume) was recorded at depths between 900m and 1300m by day and night. Maxima occurred in the 1000-1100m day and night hauls (3.4 and 2.5 ml per $10^4 m^3$ of water filtered respectively) and were accounted for by the dominant species Eucopia unguiculata (Willemoes-Suhm) and Eucopia sculpticauda (Faxon). Above 800m and below 1400m the biomass did not usually exceed 0.3ml per $10^4 m^3$ of water filtered.

The vertical distribution of the mysidacea is shown in Fig.6XI. By day and night most specimens occurred at 800-1300m with maximum numbers of 15-21 specimens per $10^4 m^3$ of water at 900-1100m. Below these depths mysids occurred in low concentrations (Tables 6.51-52).

Species (RMT 8)

Specimens were examined and attributed to ten species. Of these only two species (Eucopia) were found in moderate concentrations, other species were sparse and included two other species of Eucopia, two species of Gnathophausia and one species of Boreomysis.

Eucopia

The classification of Eucopia given by Tattersall and Tattersall, (1951) Tattersall (1955) is followed here. Specimens of Eucopia with well-developed or developing oostegites (which eventually form a brood pouch) were classified as females. Large specimens without oostegites and with well-developed pleopods or gills were classified as males; all other specimens were classified as juveniles.

Eucopia unguiculata

The most abundant species recorded was E. unguiculata, a species which is common in the North-eastern Atlantic mainly between 500m and 1500m (Mauchline and Murano, 1977; Hargreaves, 1985a, 1985b) and which may undertake limited diel migrations (Roe, 1984). At the GME position this species occurred by day and night mainly at 800-1200m (Tables 13.1-4; Fig. 13.I) and hardly any diel migration occurred. The majority of juveniles occupied the 800-1200m zone (Table 13.4). The ratio of males to females was 1:2. In addition there were several occurrences of single specimens in deep hauls extending to the sea floor. Previously this species has been found in low numbers in the bathypelagic zone to depths of about 2500m (Mauchline and Murano, 1977) but it seems likely that the few occurrences in the deep bathypelagic zone below 2500m were contaminants. Generally specimens were as abundant at the GME position as those previously recorded at 30°N, 23°W in Aril 1972 but less abundant than those recorded at 40°N 20°W in October/November 1970 (Hargreaves, in prep.).

Eucopia sculpticauda

This species is common in the North-eastern Atlantic and has been previously recorded in low-to-moderate numbers at 30°N 23°W, 40°N 20°W and 42°N 17°W at varying depths of 600-1800m (Hargreaves, 1985a, 1985b, in prep.). At the GME position it occurred in low concentrations by day and night mainly at depths of 900-1400m and there was no evidence for diel migration (Tables 13.1-3). In addition several large specimens occurred in a deep haul at 1910-2300m. The ratio of males to females was 1:2.

Eucopia grimaldii (Nouvel)

This species is common in the north-eastern Atlantic but tends to be sparse at mid-latitudes. Only eight specimens occurred by day and night. The depth range at GME was 1200-1500m (Tables 13.1-2) and this observation is consistent with previous data for 30°N 23°W (Hargreaves, in prep.).

Other *Eucopia* species

Several specimens of the previously rarely recorded deep-living species *Eucopia australis* (Dana) occurred mainly between 1200m and 3500m by day and night (Tables 13.1-3). The adults of this species tend to be large and fragile and are distinguishable by somewhat subjective features such as the size and maturity of the specimen, shape of the eye and by the formation of spines on the telson (Tattersall, 1955). Moreover, their fragility often made them difficult to identify with certainty and indeed several damaged or immature specimens found between 1100m and 3500m, although probably *E. australis*, could not be distinguished easily from the usually smaller, shallower-living species *E. unguiculata* or *E. grimaldii*. Their occurrences are marked with an asterisk in Tables 13.1-3.

Gnathophausia species

Two species occurred both in very low concentrations. Three specimens of *G. ingens* (Dohrn), all juveniles, occurred (800-1000m by day, 300-400m by night). Previous data suggest that this species occurs in relatively low numbers in the north Atlantic and is rarely found to the north of 40°N. Adults have previously been recorded at about 900-1100m but rarely below this depth, and there is also evidence of diel migration up to approximately 200-400m (Mauchline, Pers. comm.; Hargreaves, in prep.). Only three specimens of *G. gracilis* occurred (1200-1400m day) and all were juvenile. Previous data suggest that this species is relatively sparse and usually occurs to the south of 30°N at depths below 1000m and possibly deeper than 1500m (Hargreaves, in prep.).

Boreomysis species

Previous data suggest that specimens of the genus *Boreomysis* are common in mesopelagic and bathypelagic zones in the Atlantic, occurring to at least as deep as 4000m (Mauchline and Murano, 1977; Hargreaves, 1985a). However, at GME only a few specimens of *Boreomysis* occurred in the RMT8, including one specimen of *B. inermis* (Willemoes-Suhm) in each of three repeated near-bottom hauls between 5340m and 5430m. Other specimens of *Boreomysis* occurred in deep hauls but the latter was damaged and were impossible to identify.

Other species

Only three other species were identified. One specimen of Euchaetomera typica (G.O. Sars) occurred at 500-600m by day. One specimen of Siriella cf. thompsoni (Milne-Edwards) occurred at 1300-1400m by night and this was probably a contaminant from nearer the surface. One specimen of Lophogaster spinosus (Ortmann) occurred at 600-700m by day.

RMT 1 hauls

As expected relatively few mysids occurred in the RMT1 hauls. Of the twenty specimens examined, nine were larval forms mostly of the genus Eucopia, two were of the genus Siriella, three were of the genus Eucopia and six small specimens were unidentifiable due to damage in the net. Distribution of species was similar to that occurring in the RMT8 hauls except that the Siriella were present in near surface hauls, as expected from previous data.

Discussion

Generally species occurrences were consistent with previously recorded geographic and vertical distributions, (Fage, 1942; Tattersall and Tattersall, 1951; Tattersall, 1955; Mauchline and Murano, 1977; Hargreaves 1985a, 1985b, in prep.). Eucopia was by far the dominant genus with E. unguiculata the dominant species in the lower mesopelagic zone. Specimens recorded deeper - at 1200-3500m - were mainly Eucopia of the 'australis' group rather than E. unguiculata or E. grimaldii thus implying discontinuity in the vertical distribution of the Eucopia species between the upper mesopelagic zone and 3500m. However, because of the fragility of these deeper-living Eucopia and the absence of morphological characters in specimens on which identification could be based objectively, some uncertainty remains as to the extent of this discontinuity. The scarcity of specimens of the genus Boreomysis, particularly in the deep hauls, was unexpected in view of their previously recorded abundance in the mesopelagic and bathypelagic zones of the Atlantic, (Mauchline and Murano, 1977; Hargreaves, 1985a).

14. ISOPODA M.H. Thurston

Isopoda may be both abundant and diverse in the deep sea (Hansen, 1916; Wolff, 1956, 1962; Menzies, 1962; Hessler, 1970; Menzies et al., 1973; Wilson and Hessler, 1980). Although they can form a significant part of the fauna at slope and abyssal depths, most species are benthic or epibenthic in habit. Wolff (1962) surveyed records of isopods taken in the pelagic realm, and found the group to be very poorly represented. With the exception of larval Epicaridea, only a few Flabellifera and Parasellota can be considered as belonging to the plankton or micronekton.

The rarity of planktonic isopods found by previous workers was reflected by the GME catches. Over 130 specimens have been recovered from RMT1 hauls (Table 3.53), but, because few species exceed 10mm in length, the RMT8 catches provided only eight individuals. Seven of the RMT8 specimens were parasellotes belonging to species found in RMT 1 catches, and were confined to the bottom 100m of the water column. The eighth specimen, a flabelliferan, Eurydice cf. caeca Hansen, 1916, was taken at 1910-2315m.

The RMT1 catches comprised 30 parasellotes and 104 epicarids (Tables 14.1-3). At least five species of parasellotes were present, but only one, Paramunnopsis oceanica (Tattersall, 1905) could be identified with certainty. Two entities are close to, if not identical with Acanthocope galatheae Wolff, 1962 and Munneurycope murrayi (Walker, 1903), and two represent undescribed species. The two remaining entities may be identical to their congeners, but damage precluded certain identification. P. oceanica has been found in the Atlantic Ocean and over wide areas of the South Pacific and Southern Oceans (Schultz, 1977), at depths to at least 3000m (Menzies, 1962). The two specimens taken at 1400-1520m fell into this depth range, but other material caught within 100m of the bottom indicated a much wider depth range. A single specimen from one of the near-bottom hauls has been referred, with some doubt, to M. murrayi. M. murrayi has been recorded throughout the Atlantic and Indian Oceans, and in the north Pacific at depths in the range 550-3000m (Wolff, 1962). Thus the present specimen lies within the geographical range of M. murrayi, but was taken at a much greater depth than has been recorded previously. Species of Munneurycope and Paramunnopsis are among the very few parasellotes thought to be pelagic as

1982) or more can be distinguished. Material in the GME samples collected by day appeared to be concentrated almost entirely in the 50-100m layer. No specimens were taken in night hauls (Table 15.1.1). It is tempting to interpret these data as showing a migration into the neuston at night, as the top few tens of centimetres of the water column would be sampled inadequately by the RMT1. The apparently high density at 50-100m may have been due to patchiness a phenomenon known to occur widely among the hyperiids (Hardy and Gunther, 1935; Nemoto, 1959; Kane, 1966; Gray and McHardy, 1967; Nair, 1972; Everson and Ward, 1980; Bowman et al, 1982; Boden, 1985; Lobel and Randall, 1986), but equally may be an artefact of sampling as only small fractions of the 0.32-1.0mm elements of the RMT1 catches were sorted. Clearly, however, Lycaeopsis is an epipelagic entity, thus agreeing with previous reports of species of the genus (Thurston, 1976b; Shulenberger, 1977).

Four species of Eupronoe have been recognized by Vinogradov et al (1982), but other undescribed species exist (Shulenberger, 1977). The present material suggests a distribution between 50 and 200m by day and by night (Table 15.1.1). This conforms to previous findings that species of Eupronoe are epipelagic. Interpretation of migratory behaviour are contradictory (Thurston, 1976b; Shulenberger, 1977).

Parapronoe and Streetsia occurred in low but significant numbers in RMT8 hauls. Species of both genera are relatively large, and in Parapronoe at least, are rapid swimmers (Bowman et al, 1982; personal observations). Small numbers of both genera were found scattered through the top 1000m of the water column (Table 15.1.9) suggesting a mesopelagic and epipelagic distribution, but offering no clues as to migratory behaviour. Juvenile specimens of Streetsia were taken close to the surface in RMT1 hauls (Table 15.1.5).

Occurrences of genera and species other than those mentioned above have been listed in Tables 15.1.4, 15.1.5 and 15.1.10. In most cases these entities were rare in the GME area, and little can be gleaned from the records. The presence of scinoid and lanceoloid genera at meso- and bathypealgic depths conforms to previous findings. Most Vibilia specimens taken by day were caught at 500-900m, whereas night-caught specimens were confined to the top 100m. This pattern is in agreement with that found for Vibilia armata Bovallius, 1887 off the Canary Islands (Thurston, 1976b), although no evidence for migration in this species

Schultz, 1977. This situation is not unprecedented. Oceanic epicarids have been studied hardly at all. Schultz (1977) working on bathyal Southern Ocean material felt constrained to describe all his entities as new, to assign each to a new genus, and for all species, except those placed in the Dajidae, leave the familial placement open.

Little can be said regarding vertical distribution of the epicarids in this collection. Most entities were represented by very few specimens (Tables 14.1-3), and occurred in only one or two hauls. The only exceptions were Cryptoniscid C found in 13 hauls from 1400m to the near-bottom layers, and Dajid D in four hauls from 3300m to the near-bottom layers. Cryptoniscid C was found also in suprabenthic net hauls (see Section 26).

None of the epicarids in the present collection were found in association with a host organism. Nothing can be said about likely associations of any of the cryptoniscins. Adult female Dajidae parasitize mysids and euphausiaceans almost exclusively. As Dajid B and Dajid D were taken at depths below the maximum penetration of euphausiaceans, there is some likelihood that they are associated with mysids. The wide bathymetric range occupied by Cryptoniscid C suggests that it is associated with a host with an equally wide range. An ontogenetic migration is a possible but less likely explanation. If the former is true, there are limited possibilities for potential host species. Only decapods have depth ranges of 3000m or more (Section 6, 17), and at GME only two species, *Hymenodora glacialis* Buchholz, 1874 and *Acanthephyra microphthalma* Smith, 1885, had wide vertical ranges and were other than rare. At GME *H. glacialis* was taken at 1910-5233m (Section 17) but has been recorded at shallower depths (Hargreaves, (1985a),and *A. microphthalma* was taken from 2700m down to the bottom at 5440m although elsewhere has been caught at shallower depths (Domanski, 1986; Section 17).

Knowledge of food preferences and feeding habits of bathyal and abyssal isopods is fragmentary, and has been summarized by Wolff (1962). Gut contents of *Munneurycope* and *Paramunnopsis* - mainly coccolithophores, diatoms and radiolarians etc. - suggested a microparticulate diet, but this does not accord with mandibular structure, at least in *Paramunnopsis*. Occasional crustacean fragments in *Munneurycope* guts, and a greatly reduced molar process in

Paramunnopsis make it probable that both genera are, to some extent at least, carnivorous. *Acanthocope* cf. *galatheae* may well be an omnivore, by analogy with *A. spinosissima* (Menzies, 1956). Cryptoniscins have highly modified mouth parts with styliform mandibles and strongly reduced maxillae (Nielsen and Strömberg, 1965). Clearly the mandibles have a piercing function, so probably the animals feed on host fluids.

Isopods are very rare in the water column, but a few species (*P. oceanica* , ?Munnopsidae gen. nov., Cryptoniscid C) have wide vertical distributions, and therefore could contribute, albeit on a minute scale, to an upward vertical flux of material from the sea floor. When epicarids infect their host they take on the potentially greater mobility of that host.

15. **AMPHIPODA** M.H. Thurston

Chevreux (1900, 1935), Stephensen (1915, 1918, 1924, 1925), Pirlot (1929a, b) and Thurston (1976a, b) have made significant contributions to the knowledge of pelagic amphipods of the eastern warm-temperate Atlantic Ocean. Further information has come from major expeditions passing through the area (Stebbing, 1888, 1904; Vosseler, 1901; Behning, 1925, 1927; Schellenberg, 1926; Wagler, 1926, 1927; Mogk, 1927; Spandl, 1927; Woltereck, 1927; Barnard, 1930, 1932; Pirlot, 1939; Reid, 1955; Fage, 1960).

Perhaps because amphipods tend to form a relatively small proportion of the overall plankton and micronekton biomass, rather few intensive investigations of vertical distribution and migration have been undertaken. Such studies as have been reported include those in the Bay of Biscay (Stebbing, 1904), off Bermuda (Shoemaker, 1945), Southern California (Brusca, 1967), Hawaii (Brusca, 1973), Canary Islands (Thurston, 1976a, b) and in the North Pacific gyre (Shulenberger, 1977, 1978, 1979, 1980). Extensive studies by Birstein and Vinogradov (1955, 1958, 1960, 1962, 1963, 1964, 1970) and Vinogradov (1956, 1957, 1960, 1962, 1964, 1970) have provided considerable data on vertical distributions of amphipods in the Pacific, Indian and Southern Oceans. Only the studies of Stebbing (1904), Thurston (1976a, b) and Shulenberger (1977, 1978, 1979, 1980) used opening/closing nets routinely.

Generally, amphipods contribute a rather small proportion towards the total of zooplankton organisms from extensive oceanic sampling programmes. In the SOND collections taken off the Canary Islands (Currie _et al_, 1969), they formed about 2% of the total zooplankton (Thurston, 1976a, b), which is about average. Murano _et al_ (1976) found amphipods to represent only 0.8% of their catches, whereas Shulenberger (1977) reported amphipods as forming 4-7% of collections taken in the North Pacific gyre. This higher than average figure may have resulted from a predominantly epipelagic sampling programme.

Amphipods were present throughout the water column at GME, but in common with most other groups discussed in this report, they showed a very strong reduction in numbers with increasing depth. The pattern of decrease with depth varied from group to group. In contrast to taxa such as the mysids, euphausiaceans and decapods which had peak densities at meso- and bathypelagic depths, amphipods, and particularly hyperiids, were typically epipelagic in habit. Both by day and by night amphipod densities in the 0-200m layer were an order of magnitude greater than in the 200-500m layer (Tables 6.54, 6.55). Peak densities occurred by day at 50-100m with high numbers at 100-200m, while at night individuals were most abundant at 25-50m with substantial numbers at 0-25m and 50-100m. Amphipods were rare at depths below 1500m (Table 6.56) with average densities only 0.76 individuals/1000m^3, a value nearly four orders of magnitude less than that for the 0-200m horizon. There was no evidence of an increase in numbers in the near bottom layers.

15.1 Hyperiidea

Over 230 species of the entirely marine and mainly oceanic group Hyperiidea are recognised currently in more than 70 genera (Bowman and Gruner, 1973; Vinogradov et al, 1982). In common with many other groups of organisms, the Hyperiidea have gone through periods of 'splitting' when many new species were raised, often on scant material (Bovallius, 1887, 1889, 1890; Stebbing, 1888), and 'lumping' when many earlier species were reduced to synonymy (Pirlot, 1929a, 1930, 1938, 1939; Shoemaker, 1945). In the light of critical modern treatments of several genera and families (Shih, 1969; Bowman, 1973, 1978; Harbison and Madin, 1976), the total of 230 species is likely to be increased substantially. In this sort of climate, it is hardly surprising that many taxonomic problems exist at all levels, nor that the two schemes of classification for the Hyperiidea which have been proposed recently (Bowman and Gruner, 1973; Vinogradov et al, 1982) should be to some degree at variance one with the other. The scheme of Bowman and Gruner has been followed here.

The present material, although identified in part to the genus level only, conforms to previously determined patterns of high diversity in warm surface waters where phronimoids and platysceloids are most abundant. In cooler deeper layers scinoids and lanceoloids assume greater importance but never achieve the diversity found near the surface (Thurston, 1976b). By analogy with the SOND collections (Thurston, 1976a, b) from the Canary Island region, the GME material might be expected to contain in excess of 80 species.

Scina is the most speciose hyperiidean genus with more than 30 species accepted currently (Vinogradov et al, 1982), and was the most speciose genus in the SOND collections. The GME material was speciose also, and occurred throughout most of the upper 1500m by day and night (Table 15.1.1). *Scina borealis* (Sars, 1882) was the most abundant *Scina* in the SOND collections, and the peaks of abundance (300-600m by day, 0-50m by night) at GME correspond to those found for this species off the Canary Islands (Thurston, 1976b). The *Scina* population as a whole showed clear evidence for a substantial upward migration of 300-400m at night. RMT8 catches were numerically far less abundant, but showed a similar range of occurrence. Penetration to depths greater than 1500m was minimal for both larger and smaller species (Tables 15.1.6, 15.1.11).

Paraphronima, probably represented by two species, clearly was epipelagic, and showed little evidence for any vertical migration (Table 15.1.1). Thurston (1976b) and Shulenberger (1977) found *Paraphronima* species to be epi- and mesopelagic non-migrants.

Hyperietta contains five species (Bowman, 1973) of which three or possibly four occur in the Atlantic. *Hyperietta* species formed the third ranking entity at GME (Table 15.1.2), were confined almost entirely to the top 200m, and showed evidence of an upward migration from 50-100m by day to 0-50m by night. Shulenberger (1977) recorded all five species in the North Pacific gyre and found them to be epipelagic and mostly non-migrants. The two species found in the SOND collections occupied the epipelagic zone (0-200m) (Thurston, 1976b). Both these authors found *Hyperietta stephenseni* Bowman, 1973 to be a small-scale reverse migrant, ie the species occurred deeper at night than during the day.

Hyperioides longipes Chevreux, 1900 was the most abundant amphipod at GME (Table 15.1.2), and showed clear evidence of a migration from 100-200m by day to 0-50m at night. This upward movement confirms the migration deduced from numerically disparate day and night catches in the SOND collections (Thurston, 1976b). Shulenberger (1977, 1978) found *H. longipes* to be a non-migrant in the North Pacific gyre, but that its congener, *H. sibaginis* (Stebbing, 1888) moved upward at night. Shulenberger (1978) has postulated that differences in migratory behaviour or preferred depths could help similar or closely related species to avoid competition. In this context it is interesting to note that in the Pacific where both species occur, *H. longipes* is a non-migrator which avoids the top 75m, precisely the layer occuped by *H. sibaginis*. At GME, where *H. sibaginis* does not occur, *H longipes* is a migrant rising into the top 50m at night.

Of the six species of Lestrigonus known (Bowman, 1973), five have been found in the Atlantic Ocean, and four were recorded in the SOND area. At GME Lestrigonus species formed the sixth most abundant entity. Specimens were confined to the top 200m and showed no sign of migratory behaviour, although numbers taken during the day were three times the night total (Table 15.1.2). Lestrigonus schizogeneios (Stebbing, 1888) showed evidence of migration in the SOND area (Thurston, 1976b) and the North Pacific gyre (Shulenberger, 1977). An apparent lack of migration by Lestrigonus species at GME may indicate that L. schizogeneios was not a dominant species in this area.

Eight or nine species of Phronima are recognised (Shih, 1969; Laval, 1970; Vinogradov et al, 1982). Phronima taken at GME occurred from the surface down to 1300m but were absent at 300-500m by day and night (Table 15.1.3). A somewhat similar pattern was shown by material from RMT8 catches (Table 15.1.8), although here the break in vertical distribution occurred somewhat deeper. In contrast to many physocephalatan hyperiids, some Phronima attain an appreciable size. Three large species reach a length of 25mm or more, and the remaining smaller species have maximum length of 9 to 17mm. In most cases males reach about half the length of adult females. RMT1 catches will have contained mainly juveniles and smaller individuals of all species present, whereas RMT8 catches will have retained only the larger specimens, particularly of the smaller species. Based on the SOND results, the different sized species of Phronima have different bathymetric ranges (Thurston, 1976b). The two large species taken in the SOND samples, P. atlantica Guerin, 1836 and P. sedentaria (Forskål, 1775) were taken throughout the top 1000m. The former species showed a marked bimodality, being rarer between 250 and 600m than shallower or deeper. The smaller species are epipelagic. The epipelagic species showed some tendency to migrate into the top 50m by night. The large species also showed some migratory tendency, but the situation was not clear cut, and may have depended, to some extent at least, on degree of maturity. The pattern of distribution of the GME material (Table 15.1.3) would suggest that both large and small species were present, and that some migration occurred in the epipelagic layer.

Phronimella elongata (Claus, 1862) was confined to the epipelagic zone, being found at 50-200m by day and mostly shallower than 25m by night (Table 15.1.3). The RMT8 catches showed a similar pattern (Table 15.1.8). The day time concentration at 100-200m is deeper than was found in the SOND area or the North

Pacific gyre, where the population was confined essentially to the top 100m of the water column. Evidence for vertical migration at GME was more clear cut than in either of the previously studied areas.

Phrosina semilunata (Risso, 1822) ranked fourth in abundance at GME and was found almost exclusively in samples from the epipelagic zone (Table 15.1.3). A very considerable size disparity exists between the sexes in P. semilunata. Adult females have been reported to reach over 30mm in length, whereas adult males do no exceed 6mm. As a result, the RMT1 hauls would have taken juveniles, males and small females, whereas RMT8 hauls would contain only immature and adult females. Small individuals were confined to 50-200m by day and 0-100m by night, indicating a small magnitude migration towards the surface at night. This situation agrees with that found off Fuerteventura (Thurston, 1976b). Evidence for non-migration was found in the North Pacific gyre but the vertical range corresponded with that found at GME.

Bowman (1978, 1985) has recognized five species of Primno, three of which occur in the warmer parts of the Atlantic Ocean. In the SOND area only Primno johnsoni Bowman, 1978 (as P. macropa) was found, and it was the most abundant hyperiid, accounting for 44% of all specimens taken. Similarly, in the North Pacific gyre Shulenberger (1977) found Primno latreillei Stebbing, 1888 (as P. rectimanus) the most abundant species present, providing 25% of all specimens. At GME, Primno formed 19% of the hyperiid population, but was just outnumbered by Hyperioides longipes. RMT1 catches (Table 15.1.3) took peak numbers of Primno at 100-200m by day and 50-100m by night, indicating a smal-scale normal migration. Although occurring mainly in the epipelagic layer, there was a deep tail to the distribution, with specimens being taken at depths down to 1500m. The small-scale migration and deep-tailed distribution are at variance with the situation found in the SOND area where the P. johnsoni population was markedly bimodal, and some elements underwent extensive migrations. This very different pattern of distribution and migration suggested that part at least of the GME population belonged to a species other than P. johnsoni. A closer examination of several GME samples showed that at least two species were present, P. johnsoni and an undescribed entity close to P. brevidens Bowman, 1978.

In common with many other genera in the Hyperiidea, the number of species which should be recognized in Lycaeopsis is in doubt. Two species (Vinogradov et al,

1982) or more can be distinguished. Material in the GME samples collected by day appeared to be concentrated almost entirely in the 50-100m layer. No specimens were taken in night hauls (Table 15.1.1). It is tempting to interpret these data as showing a migration into the neuston at night, as the top few tens of centimetres of the water column would be sampled inadequately by the RMT1. The apparently high density at 50-100m may have been due to patchiness a phenomenon known to occur widely among the hyperiids (Hardy and Gunther, 1935; Nemoto, 1959; Kane, 1966; Gray and McHardy, 1967; Nair, 1972; Everson and Ward, 1980; Bowman et al, 1982; Boden, 1985; Lobel and Randall, 1986), but equally may be an artefact of sampling as only small fractions of the 0.32-1.0mm elements of the RMT1 catches were sorted. Clearly, however, Lycaeopsis is an epipelagic entity, thus agreeing with previous reports of species of the genus (Thurston, 1976b; Shulenberger, 1977).

Four species of Eupronoe have been recognized by Vinogradov et al (1982), but other undescribed species exist (Shulenberger, 1977). The present material suggests a distribution between 50 and 200m by day and by night (Table 15.1.1). This conforms to previous findings that species of Eupronoe are epipelagic. Interpretation of migratory behaviour are contradictory (Thurston, 1976b; Shulenberger, 1977).

Parapronoe and Streetsia occurred in low but significant numbers in RMT8 hauls. Species of both genera are relatively large, and in Parapronoe at least, are rapid swimmers (Bowman et al, 1982; personal observations). Small numbers of both genera were found scattered through the top 1000m of the water column (Table 15.1.9) suggesting a mesopelagic and epipelagic distribution, but offering no clues as to migratory behaviour. Juvenile specimens of Streetsia were taken close to the surface in RMT1 hauls (Table 15.1.5).

Occurrences of genera and species other than those mentioned above have been listed in Tables 15.1.4, 15.1.5 and 15.1.10. In most cases these entities were rare in the GME area, and little can be gleaned from the records. The presence of scinoid and lanceoloid genera at meso- and bathypealgic depths conforms to previous findings. Most Vibilia specimens taken by day were caught at 500-900m, whereas night-caught specimens were confined to the top 100m. This pattern is in agreement with that found for Vibilia armata Bovallius, 1887 off the Canary Islands (Thurston, 1976b), although no evidence for migration in this species was found by Shulenberger (1977) in the North Pacific gyre. *Anchylomera blossevillii* Milne-Edwards, 1830 was confined to the top 100m, thus confirming previous reports of its distribution. Evidence for migration is equivocal. At GME there is no evidence that migration had occurred, whereas Thurston (1976b) found evidence of a small upward migration at night, and Shulenberger (1977) postulated a reverse migration. Patchiness and swarming tendencies could have a profound effect on resultant patterns of apparent diel movements. Thus it is significant that this species has been recorded in very high density but extremely short-lived swarms at the surface (Lobel and Randall, 1986). Most of the platysceloid records from GME came from depths of 200m or less (Tables 15.1.5, 15.1.10). Exceptions were *Brachyscelus*, *Pseudolycaea pachypoda* Claus, 1879, *Platyscelus* and *Hemityphis*. *Brachyscelus* is a genus of relatively large, fast swimming species. RMT8 catches of adults suggested an epi- and mesopelagic distribution, whereas juveniles in RMT1 catches were confined mainly to epipelagic hauls. Thurston (1976b) suggested that *Brachyscelus crusculum* Bate, 1861 might be a non-migrant, a status confirmed by Shulenberger (1977). Although present in small numbers only, *P. pachypoda* was consistent in occurring at 600-800m by day and within 200m of the surface at night, suggesting an extensive diurnal migration. The deep records of *Platyscelus* (Table 15.1.10) may be genuine (cf. Thurston, 1976b for *Platyscelus ovoides* (Risso, 1816)) but that of *Hemityphis* perhaps should be regarded as contamination.

Very little information is available on the distribution of hyperiid amphipods at depths greater than 1500m. Although many of the earlier expeditions (see above for references) fished nets to considerable depths, almost without exception non-closing nets operated through very broad depth horizons were used. Some generalities on scinoid and lanceoloid vertical distribution in the Pacific Ocean are available (Vinogradov, 1957, 1970). Hyperiids taken in GME samples from depths greater than 1500m have been listed in Tables 15.1.6 and 15.1.11. Most records are based on single specimens. Species of *Lanceola* appear to ocur throughout the deeper water column, but other entities were too spasmodic to give any real indication of distribution. It is possible that some of these apparent deep records were the result of contamination.

Hyperiids have been regarded as parasties on morphological grounds for many years (Milne-Edwards, 1830; Pirlot, 1932; Laval, 1965; Bowman and Gruner, 1973). Direct observation of associations between hyperiids, particularly Hyperiidae and Phronima have been reported on many occasions, and have been summarized by Harbison et al (1977), Thurston (1977) and Laval (1980). Recent work using SCUBA diving techniques has established that most epipelagic hyperiids are associated with gelatinous zooplankton (salps, siphonophores, medusae, ctenophores, radiolarians) for part or all of their lives (Madin and Harbison, 1977; Harbison et al, 1977). Direct evidence for the nature of such associations has been forthcoming in some cases, and by inference most if not all of these associations are a result of substrate, protection and feeding requirements of the hyperiid. Hyperiid eggs hatch in the marsupium of the female, and in some cases the resultant hatchlings are incapable of swimming due to the rudimentary condition of the abdomen and its appendages (Laval, 1963, 1965, 1968; Harbison, 1976; Thurston, 1977). Although some hyperiids are predators of other zooplankton organisms (Sheader and Evans, 1975; Bowman, 1978), most appear to prey on host tissue or host prey (Laval, 1980).

At epipelagic and shallow mesopelagic depths, hyperiids are relatively abundant and undergo vertical migration. However, their near absence deeper in the water column means that hyperiids could not by themselves be involved in a recycling of material from the seafloor to the upper layers of the ocean.

Despite partial identification only of some entities, the present collection is in basic agreement with previous findings. However, it does highlight the need for further extensive, carefully planned sampling programmes in different geographic areas if a fuller understanding of the bathymetric range, vertical migration and biology of most hyperiids is to be gained. This is particularly true at depths below 1000-1500m. Such investigations will require much basic taxonomy as a precursor in order to delineate more clearly the extent of speciation in the Hyperiidea, and the geographical ranges of the entities involved.

15.2 Gammaridea

The Gammaridea is a far more speciose group than the Hyperiidea. Over 6000 species have been described, a total rising currently by several hundreds a year. In contrast to the hyperiids which are essentially organisms of the ocean plankton, gammarids are widely distributed throughout the aquatic environments, both marine and continental, and in some areas have invaded the land to become animals of forest litter (Barnard, 1959, 1969; Hurley, 1968; Bousfield, 1982; Barnard and Barnard, 1983). Of the 6000+ species, only 100-200 can be considered pelagic (Barnard, 1962, 1969). These species range from neustonic to hadopelagic, and some have, to a greater or lesser degree, an association with the seafloor. In most oceanic areas, and in all but abysso- and hadopleagic depths pelagic gammarids are heavily outnumbered by hyperiids. In terms of numbers of species and individuals, gammarids formed about 10% of the total SOND amphipod collection. In the largely epipelagic and shallow mesopelagic samples taken during the International Indian Ocean Expedition, only 3.3% of the pelagic amphipods have gammarids (Nair et al, 1973). Gammarids constituted about 3% of the GME material.

As might be expected over such a depth of water all gammarids taken in the day and night series down to 1500m belonged to species considered truly pelagic (Tables 15.2.1 , 15.2.3). Cyphocaris anonyx Boeck, 1871 occurred in rather low numbers in RMT1 and RMT8 catches. The depth ranges shown by the two nets are not in precise agreement one with the other, but the upper limit is shallower at night in both cases, perhaps indicating some degree of vertical migration. This species was relatively abundant in the SOND collections (Thurston, 1976a). That material suggested that juvenile specimens occurrred at shallower depths than did adults, and that they undertook a diel vertical migration which adults did not. The present data, although too sparse for unequivocal interpretation, fits this pattern. Specimens in hauls taken in the 1000-1500m range, together with specimens at 1500-1900m (Tables 15.2.2, 15.2.4) confirmed the conclusions of Thurston (1976a) that adults of this species were taken in small numbers only off the Canary Islands because the sampling programme covered no more than the top 1000m of the water column.

Based on the present samples, Cyphocaris challengeri Stebbing, 1888 would appear to be a mesopelagic species possibly showing a migratory tendency. Similar conclusions based on rather more specimens were reached by Thurston (1976a). His comparison with previous results showed that this widely distributed species occupied different depths in different parts of its geographical range, and that there was some evidence to suggest that these differences were mediated by physical parameters and water mass boundaries.

A few specimens of Parandania boecki (Stebbing, 1888) were caught between 700 and 1100m. This species, although widespread in occurrence has never been recorded in other than very small numbers, and little is known of its depth preferences and possible migration. There is some degree of consensus that P. boecki is a deep mesopelagic species, usually found between 500 and 1500m (Thurston, 1976a), although Birstein and Vinogradov, 1970 indicated a vertical range of 500-4000m based on their work in the northwest Pacific Ocean. In common with a number of other cosmospolitan species, P. boecki occurs at shallower depths in the Southern Ocean, where it is one of the commonest gammarids at 200-500m (Thurston, unpublished data).

Stenopleura atlantica Stebbing, 1888 is a relatively small species, reaching sexual maturity at a length of 4-5mm, and, as a consequence, was sampled only in RMT1 hauls (Table 15.2.1). The depth ranges occupied, at least 100-700m by day and 25-300m by night, suggest that the species is a migrant. The overall distribution found here is comparable with that demonstrated by the SOND collections. Data from that source seemed to indicate that a reverse migration occurred, but the present results suggest that part of the population was not sampled, thus justifying the reservations on migratory behaviour expressed by Thurston (1976a).

The gammarid material taken at depths exceeding 1500m is characterized by a high diversity (21 species in three superfamilies) and very low numbers (Tables 15.2.2, 15.2.4). It is noteworthy that only one species (C. anonyx) occurred both above and below the 1500m horizon. Based on scattered literature reports (see references in the preamble to Section 15) and unpublished observations, it is possible to divide these deep-dwelling species into two groups. In one group are those species which are truly pelagic, and in the other those which, although making perhaps considerable excursions up into the water column, are dependent to a greater or lesser extent on the bottom.

The first group contains nine species of which C. anonyx has been referred to above. Cyphocaris richardi was represented in hauls taken between 1500 and 2700m. This depth range agrees with data given by Chevreux (1935) and Birstein and Vinogradov (1964, 1970) who reported the species from through hauls from 1500m or deeper, with a single shallow occurrence in a haul from 890m. In Antarctic waters, this species which is bathy- and abyssopelagic in low latitudes, is among the most abundant pelagic gammarids, and reaches high densities at 200-600m (Andres, 1979, 1983; Thurston, unpublished data). *Paracyphocaris praedator* Chevreux, 1905 was found in the RMT1 haul at 1910-2315m, a depth in keeping with the bathy- and abyssopelagic depth range reported for this rarely taken species (Chevreux, 1935; Birstein and Vinogradov, 1960, 1964). The *Eusirella* specimen taken at 2700-3100m appears close to *E. valdiviae* Schellenberg, 1926, a poorly described species known only from a 0-3000m haul in the South Atlantic. Various attempts have been made to synonymize this species with other in the genus. However, the status of some entities described in *Eusirella* is open to doubt (Barnard, 1964) and probably it is better to regard *E. valdiviae* as a distinct entity pending further material. The Pardaliscidae is a deep-water polar emergent family whose members appear to be pelagic or epibenthic. Three species of *Halice*, *H. aculeata* Chevreux, 1912, *H. macronyx* (Stebbing, 1888) and *H. secunda* (Stebbing, 1888), were found in GME hauls taken at 2300-4700m. All these species have wide geographical ranges and have been captured in midwater nets at depths mostly exceeding 1000m and usually well above the bottom (see references in Karaman, 1974, but beware erroneous data). Unidentified pardaliscids were taken in RMT1 hauls at 2310-2700m and 3330-3900m. One entity is an undescribed species and genus, and the other was too damaged for generic placement.

Twelve species taken in deep midwater or near-bottom hauls have been recorded previously from benthic samples. Three of these species are eusiroids belonging to the genera *Cleonardo*, *Eusirus* and *Rhachotropis*. All these genera are ubiquitous in the deep sea and typically are long-legged members of the epibenthic community. A few species, particularly in *Cleonardo* and *Eusirus*, are planktonic in habit. The remaining nine species are lysianassoids. The four species which have been identified fully (*Eurythenes gryllus* (Lichtenstein, 1822), *Orchomene gerulicorbis* Shulenberger and Barnard, 1976, *Paralicella caparesca* Shulenberger and Barnard, 1976 and *P. tenuipes* Chevreux, 1908) together with *Cyclocaris* sp. nov. are known to be necrophages, ie they feed on large, dead food sources such as fish carcasses, and can be attracted to baited traps (Thurston, 1979). It is very probable that the undescribed species of *Hirondellea* are necrophages also, as other species, both described and undescribed, of this genus have been taken in traps (Chevreux, 1935; Ingram and Hessler, 1983; Desbruyeres *et al*, 1985). The ninth lysianassoid, *Eucallisoma* sp. nov. is only the second specimen of the genus to be recorded. *Eucallisoma* belongs to a number of closely related genera, the *Scopelocheirus*-group, assigned tentative familial status by De Broyer (1985). Species of several genera in this group have been taken in traps (Chevreux, 1935; Thurston, unpublished data), so *Eucallisoma* sp. nov. may also be a necrophage.

Obligate necrophagy in the abyss, even under oligotrophic surface waters, clearly is a viable life style, as amphipods appear rapidly at baited cameras and can be trapped in large numbers (Shulenberger and Hessler, 1974; Hessler *et al*, 1978; Thurston, 1979). If, as is likely, suitable food falls are not abundant under central ocean gyres, a successful necrophage must be well equipped to make full use of such food falls as do occur. This implies an acute sensory ability to detect the food fall, a strong locomotary ability to reach the food fall in the minimum possible time, and efficient mouthparts to ingest the maximum amount of food prior to the dispersal of the food source. In terms of the present discussion, the second attribute is of most importance. Amphipods arrive rapidly at bait (Hessler *et al*, 1978; Thurston, 1979; Lampitt *et al*, 1983) and direct estimates of swimming speed (Smith and Baldwin, 1984; Laver *et al*, 1985) show that early arrival is not due simply to the proximity of amphipods to a food fall at the moment of impact.

Early evidence that *E. gryllus* was not confined to the bottom came from records of this species in bird stomachs (Mandt, 1822; Stephensen, 1933, 1949; Chevreux, 1935). It should be noted also that the supergiant amphipod *Alicella gigantea* Chevreux, 1899, another necrophage and trapped not far from the GME area (De Broyer and Thurston, in press), has been recorded from a seabird stomach (Barnard and Ingram, 1986). Direct evidence for excursions high above the sea floor by *E. gryllus* has come from Smith *et al* (1979), and subsequent investigations have found this species up to 1400m above the bottom under the North Pacific gyre (Smith and Baldwin, 1984a). *E. gryllus* is a coldwater stenotherm (Bowman and Manning, 1972) and thus is confined to great depths in low latitudes. In common with other gammarids, *E. gryllus* lacks larval stages. Despite occupying what amounts to an abyssopelagic habitat, dispersal must be to some extent limited as the species shows morphological variation in different parts of its range, implying that gene exchange is limited (Bowman and Manning, 1972). Smith and Baldwin (1984a) found that the minimum depth of occurrence on a transect across the warm temperate North Pacific was governed more by distance from the surface rather than absolute water depth. Extensive vertical trap sets operated by Ingram and Hessler (1983) have showed that all other necrophages, which are much smaller than E. gryllus, were confined within the Ekman layer (4m under the North Pacific gyre), and thus are components of the near bottom fauna identified by Wolff (1971). However, Ingram and Hessler quote K.L. Smith as having taken P. caperesca at 610 and 951m above the water-sediment interface. The GME data summarized in Table 15.2.5, are comparable with results of near-bottom hauls taken by I.O.S. near 20°N, 21°W in 1976 and 1977 (Thurston, unpublished data). Thus it is clear that E. gryllus and other necrophage species can and do make extensive migrations into the water column, and thus provide a pathway for upward transport of material from the sea floor.

16. **EUPHAUSIACEA** P.T. James

Introduction

Euphausiids mainly inhabit epi- and mesopelagic depths and few species occur deeper than 1500m. Individual species and stages vary widely in size, those greater than 15mm in body length are more quantitatively sampled by the RMT8 whereas smaller species (and stages) are better sampled by the RMT1. In this section, data for species/stages >15mm in length are taken from RMT8 catches, for those <15mm from the RMT1s. Specimens caught in the "wrong" net have been excluded. In the RMT1 samples both the 0.32-1.0 and 1-4.5mm size fractions were combined.

Results and Discussion

The total numbers of euphausiids caught by both nets are summarised in Tables 6.59-63. The population sampled by the RMT1 was comprised mainly of larval stages, maximum abundance occurred in the upper 200m by both day and night (Fig. 6.X). In contrast, the larger species sampled by the RMT8 showed a marked diel migration from 800-900m by day to 300-400m by night (Fig. 6.XI). Euphausiids are notorious for avoiding nets during the day (e.g. Brinton 1967); this, combined with their habit of forming large swarms, makes interpretation of their diurnal behaviour difficult and accounts for the day/night discrepancy in numbers seen here.

Twenty seven species were caught at GME. Tables 16.1-16.5 show the depth range, depth of maximum abundance and numbers caught for each species and stage. Generally speaking the depth distributions of most species and stages were 50-200m deeper than those found previously at a position 30°N 23°W (James In press). Conversely a few species e.g. N. boopis were slightly shallower.

Eighteen species were sampled by the RMT1. T. parva was the most abundant species, comprising 30.3% of the total population, E. hemigibba formed 26.7%, S. longicorne 11.1%, S. suhmii 9.9%, E. brevis 6.3% and T. aequalis 1.9%. Twelve species were sampled by the RMT8, T. obtusifrons was most abundant forming 38.5% of the total numbers, followed by T. microphthalma (16.6%) and N. boopis (13.6%). Weigmann (1974) analysed euphausiids from the GME area and found that E. brevis, S. suhmii, E. hemigibba, S. longicorne and T. aequalis were the dominant species. Surprisingly she did not record _T. parva_, possibly because it has a patchy distribution or perhaps her samples were too shallow. In the present samples _T. parva_ occurred mainly around 1000m and its distribution at GME seems to coincide with that of Mediterranean water (Section 2; Badcock and Merrett, 1976; Saunders, 1983).

17. DECAPODA

RMT 8 and benthopelagic species. P. Domanski and P.M. Hargreaves.

Introduction

This section primarily considers decapods taken in midwater trawls. However, this group shows a marked near-bottom increase in abundance of some abyssal species, some of which were caught by the OTSB. In this section therefore reference is made to natant decapods caught in midwater and on the bottom.

Results

Maximum numbers of decapods occurred by day within the surface 100m and at 700-1200m (up to 40 specimens per 10^4m^3, Tables 6.67-68; Fig. 6.XI). By night greatest numbers occurred in the surface 200m (up to 44 specimens per 10^4m^3. Below 2700m the numbers of decapods were very low, not exceeding 1.5 specimens per 10^4m^3, and indeed in four hauls between 3900m and 5110m numbers ranged from nil to 0.5 specimens per 10^4m^3. However numbers in hauls taken 10-90m above the bottom, although relatively sparse in comparison to those in the mesopelagic zone, showed an increase in abundance with proximity to the bottom (Fig. 17.I).

Tables 17.1-17.5 list species occurrence by day and night at given depths. Mesopelagic species were found mainly at depths <1000m. The range of bathypelagic species extended down to ca. 2500m or so; whereas abyssopelagic species such as Hymenodora glacialis extended to 3000m or below. Some species appeared to be benthopelagic in habit spending at least part of the time just above the sea-floor. To what extent species vertically migrate between the sea-floor and the upper part of the water column is discussed below.

Mesopelagic and bathypelagic species

The vertical distribution of the most frequently occurring species within the surface 1500m are listed in Tables 17.1 (day) and 17.2 (night). Infrequently occurring species are listed in Table 17.3. The most dominant species in the mesopelagic zone included the carids Oplophorus spinosus (Brulle), Parapandalus richardi (Coutiere) Acanthephyra purpurea A. Milne Edwards and Systellaspis debilis (A. Milne Edwards). The penaeids included Funchalia villosa (Bouvier) and Gennadas valens (Smith). There were several species of Sergestes H. Milne Edwards which were easily identifiable but also relatively large numbers of larval and juvenile Sergestes which it was not possible to identify (see also section on RMT 1 Decapoda). Sergia species were common. Contamination resulting from net leakage was generally minor.

The distributions of the commonest mesopelagic species are shown in Fig. 17.II. These species all showed varying degrees of vertical migration.

Bathypelagic species were deeper living, extending their depth range to below 2000m. Sergia japonicus Bate was at 800-2315m with a maximum at 900-1300m and showed evidence of limited diel migration up to 500m by part of the population. However, in deep-living species generally, there was little evidence of diel migration. For example, Bentheogennema intermedia (Bate) occurred mainly at 900-1500m by day and night (Fig. 17.III) and Petalidium obesum, Acanthephyra stylorostratis (Bate) and Hymenodora gracilis Smith all had restricted depth ranges of only 800-1000m by both day and night.

Abyssopelagic and/or benthic or benthopelagic species

In contrast to the considerable amount of existing Atlantic data on pelagic and bathypelagic decapods there are few data on abyssopelagic, benthopelagic and benthic decapod communities. However bottom and near-bottom decapods have been examined at a site centred at 41°30'N 30°W, to the south of King's Trough, at a depth of ca 4040m (Domanski, 1986). These data are very important for comparison with the GME results, and the present data are supplemented with observations made at King's Trough. Profiles of decapod abundance near-bottom at King's Trough are given in Fig. 17.IV; these should be cmpared with the GME profile (Fig. 17.I). Decapods were more abundant at King's Trough than at GME but there was a similar increase in numbers in hauls closest to the bottom at both stations.

Abyssopelagic and benthopelagic decapods are of potential importance to vertical transport mechanisms within the deep water column. Thus, although scarce when compared with mesopelagic decapods, these species are considered in detail below. Dominant species are listed in Table 17.4; infrequently occurring species in Table 17.5. Species occurring in OTSB hauls are given in Table 17.6.

Caridea

Hymenodora Sars 1887

Hymenodora glacialis (Buchholz) was common. It has a wide geographic distribution but is rarely found above 1500m (Sivertsen and Holthuis 1956; Hargreaves, 1985a). At GME it occurred in relatively low numbers at 1910-4720m with a single specimen at 5132-5233m (Table 17.4, Fig. 17.III; it did not occur in near-bottom hauls. However, this species was found close to the sea-floor at King's Trough, where there was a two-fold increase in abundance near-bottom; it was absent in benthic hauls, (Domanski, 1986). At King's Trough individuals of all sizes were present in near-bottom hauls but immature individuals were dominant. Hargreaves (1985a) found that at 42°N 17°W the largest specimens occurred towards the maximum of its depth range and that juveniles and small adult stages were at all depths within a 1000-4000m range. There was some evidence of ontogenetic migration.

H. glacialis is predominantly carnivorous. Its diet includes small crustaceans, chaetognaths and gelatinous animals. Absence of sedimentary material in the gut indicates that it is unlikely to feed at the sediment surface (Domanski 1986).

There was considerable variety of form among the near-bottom *Hymenodora* species. In *H. glacialis* the shape of the rostrum varied considerably and some specimens had slender abdomens closely resembling those of the little known species *Hymenodora acanthitelsonis* Wasmer, 1972.

H. acanthitelsonis occurred in several pelagic hauls at both King's Trough and GME in relatively low numbers (Table 17.4). These records are the first from the Atlantic (Domanski 1986). At GME this species occurred below 5000m, predominantly in near-bottom hauls (Table 17.4). In the Pacific *H. acanthitelsonis* extends to greater depths than *H. glacialis* and is not confined to a benthopelagic habitat (Domanski 1986). Wasmer (1972) described this species from two specimens collected in a beam trawl which failed to reach the bottom in a depth of 2560m. Kikuchi and Omori (1985) recorded a single specimen in the Pacific at 5041-5591m over a sounding of ca. 6200m. Gut contents indicate that its diet may be similar to that of *H. glacialis*.

Acanthephyra microphthalma Smith, 1885.

This species has been recorded from the western Atlantic (Smith 1885, 1886), off Portugal (Coutiere 1911), near to the Azores (Silvertsen and Holthuis, 1956), in the Indian Ocean (Alcock, 1901) and in the Pacific (Wasmer, 1972) *Acanthephyra microphthalma* was taken at GME in both RMT and benthic catches (Tables 17.4, 17.6. The largest specimen was taken in a benthic sample (male, 24.1mm carapace length). Each of the RMT hauls at about 10-25m above the bottom contained at least one specimen out of a total of six specimens caught near-bottom. Several specimens also occurred in the water column, the shallowest being at 2700-3110. This species was not caught at King's Trough.

Like *H. glacialis*, *A. microphthalma* occurs in the water column at abyssal depths. However, it tends to concentrate near-bottom and, unlike *H. glacialis*, on the bottom - where it was probably most abundant although it is impossible to make accurate quantitative comparisons between data collected with two different sampling gears. The presence of the largest individuals in the benthic samples infers that adults tend towards a benthic existence.

Examination of the foreguts of four specimens revealed a varied diet. Two specimens seemed to have fed on the bottom - their foreguts contained ingested sediment and foraminiferan tests. Three of the foreguts contained well-masticated crustacean parts (mainly copepods) and two contained a mixture of unidentifiable softer tissues.

Acanthephyra brevirostris Smith, 1885

A. brevirostris is a bathypelagic shrimp which has been caught at a few wide-ranging locations. Most records are from the Atlantic (Smith, 1885; Chace, 1940, 1947; Sivertsen and Holthuis, 1956; Springer and Bullis, 1956; Kensley, 1968). It has also been found in the east Pacific (Faxon, 1895) and in the west Indian Ocean (Bate, 1888). Recently a number of juveniles have been taken in RMT hauls between 1000m and 2000m to the southwest of the Azores (Domanski, unpublished). The previous depth record for this species was 5394m (Smith, 1885).

Several specimens were caught in the 3,500m RMT hauls at King's Trough. A few individuals were caught in RMT 1 hauls in the water column at GME but only a single specimen in the RMT 8 (Table 17.5). No specimens occurred in the benthic catches. There are insufficient data to deduce whether this species aggregates near the bottom but the data confirm that its depth range extends to over 4000m.

Penaeidae

Three of the most notable deep or bottom-living species were Benthesicymus spp., Plesiopenaeus armatus (Bate) and Hepomadus tener Smith. The latter two species occurred only in benthic trawls (Table 17.6).

Benthesicymus spp.

Specimens of this genus are difficult to identify because they are soft bodied and usually suffer considerable damage during sampling, (Roberts and Pequegnat, 1970; Gore, 1985a). All specimens taken at GME and King's Trough belong to Burkenroad's (1936) Benthesicymus brasiliensis complex. Most were B. iridescens Bate, but there were several B. brasiliensis Bate.

These two species had different vertical distributions. B. brasiliensis is mainly pelagic, occurring in near-bottom tows at GME (Table 17.4) and in both near-bottom and deep pelagic tows at King's Trough. A single adult was caught 600m above the bottom at King's Trough. Conversely B. iridescens is primarily benthic, most specimens occurring in OTSB samples (Tables 17.5, 17.6).

The size frequency distributions for B. iridescens in OTSB hauls at GME are shown in Fig. 17.V. Possible explanations for this curious distribution are discussed later.

Most of the specimens examined from King's Trough and GME had empty foreguts. However, where contents were found, these consisted mainly of setae and ground-up crustaceans. In addition several foreguts contained white amorphous tissue possibly of coelenterate origin. In a few instances the foreguts were gorged with grey sediment rich in foraminiferan tests and shell-like fragments.

One specimen was full of brown-red material resembling the faecal material described by Honjo (1980) from sediment traps set at about 5300m. There were insufficient data to determine whether the diets of the two species differ.

Pleisiopenaeus armatus Bate, 1881)

This was the most robust species caught in the benthic hauls. It has a widespread distribution, being found in the Atlantic, Pacific and Indian oceans and is regarded as an abyssal species (Gore, 1985b). The specimens from GME were the deepest yet recorded. This species was taken solely in the OTSBs at both King's Trough and GME. However, P. armatus was tentatively identified as swimming just above the bottom from a series of underwater photographs taken with a survey camera at GME, (Domanski, 1986). The shrimp was about 25cm in total length and seemed to be swimming a metre or so above the bottom at a speed of ca. 0.01m s^{-1}. Gore (1985b) also recorded P. armatus sitting on or just above the sediment surface, and Roe (pers. comm.) found this species in a haul made tens of metres above the bottom off Lisbon during gear trials. Thus P. armatus can and does make excursions off the bottom.

A variety of food items were recovered from the foreguts. Most had varying amounts of foraminiferan-rich sediment, some being packed with this material. Ground-up crustacean parts were also found including the remains of a specimen of Benthesicymus in one gut. Also present were fish scales, sponge spicules, crushed shells of small bivalves, tentatively identified as Nucula (Knudsen, pers. comm.), and unidentifiable debris. Gore (1985a) suggested that this species is a benthic detritivore, but the present data suggests that it may also be an active carnivore.

Hepomadus tener Smith, 1884

This species was caught at King's Trough and at GME in each of the three OTSB catches; none were taken by the RMT. Most specimens of H. tener have been recorded from the western Atlantic, (Gulf of Mexico; Perez Farfante, 1973; Caribbean Sea; Gore, 1985a, Sargasso Sea; Bouvier, 1908) and this is the first time that it has been recorded in the eastern Atlantic. It is known to have a large bathymetric range (745-5400). Most specimens have been taken with bottom trawls but Gore (1985a) reported that it has been taken off the bottom and categorized it as abyssobenthic and abyssonektonic. However, its absence in near-bottom RMTs indicates a predominantly benthic habit.

Two foreguts were examined and the contents indicated that this species has a varied diet. the guts were full and contained a mixture of crustacean parts, membraneous tissues, foraminiferan tests and bivalve shell remains. One gut contained a virtually-intact harpacticoid copepod. This seems to confirm Gore's findings that the species is a benthically-directed omnivore or a facultative predator.

Discussion

The occurrences of abundant mesopelagic and bathypelagic species at GME were consistent with previous records, with many of the species having been taken over a wide area of the north-eastern Atlantic, (Foxton 1970a, 1970b, 1972; Fasham and Foxton, 1979; Hargreaves, 1984, 1985a). Many of the mesopelagic species, e.g. O. spinosus, had day and night ranges above 1000m and did not extend into the bathypelagic zone. Others, e.g. Gennadas valens and Sergia tenuiremis, extended to 1500m with evidence of diel migrations to a minimum of 300m, whereas species such as Bentheogennema intermedia and Sergia japonicus extended to at least 2300m and had a total depth range of approximately 1800-1900m. H. glacialis had a total depth range of >2000m.

The extent of vertical movement by individuals within populations of species is problematical. The limits of vertical distribution indicate the distance over which a given species might travel. However, net sampling cannot provide information on the range of individuals, and it is doubtful whether a species such as H. glacialis systematically moves throughout its known depth range. H. glacialis may have an ontogenetic migration - the average size of individuals increases with depth (Hargreaves, 1985a; Domanski, 1986). However, immature individuals also occur throughout the vertical range and the importance of any ontogenetic migration cannot yet be fully assessed. Furthermore the depth range of a given species may depend partly on its geographic distribution. For example Parapasiphaea sulcatifrons occurred below 900m at GME but was found at a minimum depth of 700m by day at 42°N 17°W (Hargreaves, 1985a).

The present data confirm that a near-bottom increase in numbers of decapods occurs at abyssal depths. At GME (depth 5440m) natant decapods were more abundant near-bottom than at 500m higher up in the water column and they were most abundant closest to the sediment surface. Thus abundances at 10-25m above the bottom were often several times larger than at 40-90m above, (see Fig. 17.1). A similar effect occurs at King's Trough (Fig. 17.IV, Domanski, 1986). Hargreaves (1984) also found an increase in numbers of natant decapods in some hauls close to the sea-floor in the Porcupine Seabight, and Omori and Ohta (1981) photographed large numbers of sergestids which accumulated 6-7m above the bottom.

The present data also suggest that some species occur close to the bottom but not on the bottom. For example, some *Hymenodora* species and *B. brasiliensis* occurred in near-bottom RMTs but not in OTSBs. This is unlikely to have been due to net avoidance since *A. microphthalma*, a decapod of similar size, occurred in both RMTs and benthic hauls. It seems doubtful whether a specialised benthopelagic decapod fauna, which lives and feeds just above the bottom, actually exists. Only two species occurring at GME or at King's Trough are possible candidates for a specialised benthopelagic habit. *H. acanthitelsonis* occurred only in near-bottom RMTs, thereby agreeing with previous data (Wasmer, 1972 and Kikuchi and Omori, 1985). *B. brasiliensis* occurred in small numbers in near-bottom nets and, in one instance, well above the bottom. It seems most likely that in the benthopelagic region members of both benthic and pelagic faunas overlap, both exploiting the comparatively rich near-bottom environment.

It is not clear why some of the deeper-living pelagic species at GME did not extend their depth range into the benthopelagic zone. Depth effects may be important. For example the absence of *H. glacialis* from near-bottom hauls at GME may be bathymetric as it has rarely been recorded deeper than 4500m. (Kikuchi and Omori (1985) found this species at >5600m but stated that it could have been a contaminant).

Differences in the size frequencies of *H. glacialis* and *B. iridescens* indicate that there are interspecific differences in the population dynamics of abyssal species. Populations of *H. glacialis* had a relatively high proportion of immature individuals, whereas most *B. iridescens* were adult. There may be an important difference between carid and penaeid reproduction. *H. glacialis* exhibits lecithotropic larval development which may permit its early larval stages to cohabit with older forms. In contrast, if B. iridescens is a typical penaeid, it may be expected to have planktotrophic larval development. This may necessitate trophic and spatial separation of larval and early juvenile stages from the adults. The absence of B. iridescens <20mm cl in benthopelagic samples may indicate that younger forms occur in the overlying water column rather than on the sea floor. Alternatively the absence of young stages may be a seasonal effect or it may indicate that the species is long-lived with low recruitment and low mortality. Further studies on abyssal shrimps are needed in order to understand the mechanisms of their reproduction and dispersal and the extent of their vertical migrations.

RMT 1 Decapoda A.L. Rice

The decapods in these catches were dominated numerically by larvae, the only post-larvae or adult forms occurring in significant numbers being the small segestid Lucifer typus H. Milne Edwards. In all cases the decapods were concentrated in the upper 100 to 200m of the water column, with only occasional individuals being taken in the deeper samples where they were generally present at densities of less than 10 individuals per $1000m^3$ (Table 6.64-66).

There was clear evidence for a small diurnal vertical migration by the Lucifer adults which were concentrated in the 25-50m horizon during the day and in the 0-25m layer at night (Table 17.7). There was no evidence for a similar sub-surface maximum among the larvae. However, in the two most abundant categories, the larvae of the sergestids and of the penaeid genus Gennadas, the daytime maximum concentration in the near surface 25m band was enhanced by an upward movement at night resulting in a corresponding depletion of the deeper populations (Tables 17.8 and 17.9).

The catches provide no indication of a direct connection between the benthic decapod fauna at GME and the overlying surface waters. With only 4 exceptions, the larvae collected were all attributable to holopelagic species, mostly inhabiting the upper 1500m of the water column as adults.

The 4 exceptions consisted of a brachyuran crab megalopa taken in a 50-100m haul, a stomatopod alima taken at 0-100m, a post-larva of the galatheid genus Munida taken at 1200-1300m and a specimen of the larval species Cerataspis monstrosa Gray. Although the first three are definitely benthic as adults, they were not derived from GME species. No members of the taxa to which they belong are known to live significantly deeper than about 1500m and most species live very much shallower. Accordingly, these larvae must have been carried to the area from a neighbouring shallow region such as the nearby Great Meteor Seamount or, more probably, the Moroccan or Iberian coasts to the east or the intervening seamounts and islands.

Cerataspis monstrosa has been reported from a number of oceanic localities in the Atlantic, Indian and western Pacific Oceans, including several records from the Azores-Madeira region (Heegaard, 1966). The identity of the adult form of this large and aberrant larva is unknown. However, Bouvier (1908) suggested that it belonged to the abysso-bentho-pelagic penaeid genus *Aristeomorpha*, a conclusion supported by Burkenroad (1936) who furthermore suggested, with no substantiating evidence, that a related aberrant penaeid larval genus, *Cerataspides*, belonged to a second deep-living bentho-pelagic genus, *Plesiopenaeus*. The larvae of *Aristeomorpha foliacea* were found to be the normal penaeid type by Heldt (1956), thus arguing against the identity of *Cerataspides* with this genus. The larvae of *Plesiopenaeus*, represented by *P. armatus* in the deep GME catches (see previous section), are still unknown, but there is no clear evidence to link this species with *Cerataspis*, *Cerataspides* or with any other shallow-caught larvae.

18. AMPHIONIDACEA A.L. Rice

Seven specimens of the curious decapod-like malacostracan Amphionides reynaudi (H. Milne Edwards) were taken in the RMT1 catches (Table 6.69). With one exception, a stage I specimen from 1300-1400m, these were all taken in the upper 100m, tending to support previous conclusions that the larvae hatch well below 1000m, and rise to the surface where the subsequent stages remain (see Rice and Williamson, 1977).

19. ECHINODERMATA

D.S.M. Billett and Q.J. Huggett

Introduction

Almost all echinoderms live on the seabed. Some species are able to make short pelagic excursions but generally they spend the majority of their lives crawling over the seafloor. A few holothurian species, however, live in the plankton just above the seabed, descending to the bottom to feed on the superficial sediment. These benthopelagic holothurians are restricted to the open ocean and until about a decade ago were known only from a few tens of specimens. With the advent of acoustically-telemetered pelagic trawls (Billett, Hansen and Huggett, 1985; Billett, 1986) and submersibles (Barnes, Quetin, Childress and Pawson, 1976; Pawson, 1976, 1982), many more specimens have been found living within 100m or so of the seabed at abyssal depths.

Apart from the pelagic holothurians the larvae of all the echinoderm classes may be found in the plankton. These may be feeding (planktotrophic) or non-feeding (lecithotrophic) larvae, some of which may have a prolonged larval life. Larvae of abyssal echinoderms have not been found in surface waters, but it is inferred from the small egg size found in a few species that their larvae may migrate to surface waters to feed (Tyler, Grant, Pain, and Gage, 1982). In some cases the juveniles of abyssal benthic echinoderms have been captured in the plankton (Billett *et al.*, 1985).

The RMT samples from the GME area contain the larvae of asteroids, the post-larval stages of ophiuroids and asteroids, the juveniles of benthic and pelagic holothurians, and adult pelagic holothurians.

Asteroidea

Bipinnaria larvae were taken in nine of the ten RMT 1 samples trawled at depths shallower than 200m (Table 19.1). The larvae were found principally between 25 and 100m and their abundance was very low.

Although asteroids are a major component of the benthic invertebrate megafauna in the GME area (Section 28) it is unlikely that the bipinnaria larvae were produced by asteroids living at abyssal depths at this site. The mode of development in asteroids is related to the maximum egg size produced by the adult. Eggs about 100µm in diameter are believed to produce planktonic, feeding larvae, while those about 1000µm in diameter lead to direct development without a larval stage (Tyler *et al.*, 1982). Eggs intermediate in size may produce a planktonic, non-feeding larva. The dominant asteroids in the GME area, *Hyphalaster inermis* Sladen 1883, *Styracaster horridus* Sladen 1883, and *Styracaster elongatus* Koehler 1907, all have a maximum egg diameter of 600µm. From this egg size Tyler and Muirhead (Section 28), consider that a larva with very limited dispersal would be formed. Therefore, it is unlikely that the bipinnaria larvae found in the surface waters are derived from these species.

The egg size of the only other asteroid taken in benthic samples at GME, *Freyastera tuberculata* (Sladen 1889), is unknown. *F. tuberculata* belongs to the order Brisingida, an abyssal group of starfish which has a few Antarctic species living in shallow water (Downey, 1986). Three species of this order from the northeast Atlantic, *Brisinga endecacnemos* Asbjornsen 1856, *Brisingella coronata* (G.O. Sars 1871) and *Freyella elegans* (Verrill 1884), all have large eggs up to 1250µm in diameter indicating direct development (Tyler, Pain, Gage and Billett, 1984). *F. tuberculata* is likely to have direct development as well.

The present bipinnaria larvae are probably derived from shallow-water species living around oceanic islands, such as the Azores, or they may have been carried across the Atlantic from species living on the continental shelf or slope. Bipinnaria larvae may remain in the plankton for more than a year if they are unable to find a suitable substrate at a suitable depth, permitting dispersal over a wide area (Domanski, 1984).

At Station 11261#40 (100-200m) a juvenile was found still attached to its bipinnaria larva. This type of development, in which a brachiolaria stage is absent and which may occur whilst the larva is still in the plankton, is known to occur in some species of the families Luidiidae and Astropectinidae (Tattersall and Sheppard, 1934; Oguro, Komatsu and Kano, 1976; Wilson, 1978; Komatsu, Oguro and Kano, 1982; Domanski, 1984).

Ophiuroidea

A total of 6 post-larval ophiuroids were found in four RMT 1 samples trawled between 100 and 900m (Table 19.2). One further post-larva occurred in a sample at a depth of 5132 to 5233m (200 to 300m above the seabed). Ophiuroid post-larvae are notoriously difficult to identify to species since the usual taxonomic features found in adult specimens have not been developed. There are no descriptions of deep-sea ophiuroid post-larvae smaller than 500µm in disc diameter and the post-larvae of only a few deep-sea species are known (Schoener, 1967, 1969). All the post-larvae caught here were only about 300µm in diameter and had probably just metamorphosed. Based on the morphology of the skeletal plates it is likely that all the specimens from between 100 and 900m were the post-larvae of the same ophiuroid species. However, the different structure of the dorsal plates of the specimen taken at abyssal depths indicates that it was the juvenile of a separate species. No ophiuroids occurred in the benthic samples suggesting that the post-larvae were probably carried into the GME area.

Holothurioidea

Three species of holothurian (sea-cucumber), were found in the RMT 1+8 samples; Scotothuria herringi Hansen, 1978, Enypniastes diaphana (Gilchrist, 1920) and juveniles of a Benthodytes species (Table 19.3). Most of the specimens occurred close to the seabed but some were found several thousands of metres above the seafloor.

1. Benthodytes : Three juvenile specimens were taken; one at 910 to 1000m (5.5mm long), one at 1200 to 1300m (4.9mm long) and the third at 2310 to 2700m (13mm long). The adults live on the seafloor and grow to a length of ca 50cm. The juveniles belong to one of three species known from the Atlantic Ocean; B. lingua R. Perrier 1896, B. valdiviae Hansen 1975, and B. typica Theel 1882.

B. valdiviae is known only from a few specimens taken at a depth of 2480m south of the Canary Islands (Hansen, 1975). B. valdiviae is likely to be a developmental form of B. lingua since the taxonomic characteristics of Benthodytes species appear to be dependent on the size and the method of preservation of the specimens.

B. lingua is widely distributed in the north and south Atlantic between 860 and 3192m (Hansen, 1975; Gage, Billett, Jensen and Tyler, 1985). B. lingua may be synonymous with B. sordida Theel 1882, a species found by the Challenger

Expedition off New Zealand (Theel, 1882), since specimens collected by *Discovery* in the northeast Atlantic at depths between 3310 and 4795m have characteristics of both species (Billett, unpublished data). *B. lingua*, therefore, may occur at depths greater than 3,200m.

B. typica is a cosmopolitan species found in the Atlantic, Pacific and Indian Oceans between depths of 1873 and 4700m (Hansen, 1975). In addition, Deichmann (1954) and Miller and Pawson (1984) record this species as shallow as 315m in the northwest Atlantic.

Adult *Benthodytes* were not taken in benthic samples at GME. The species of *Benthodytes* appear to be more common on the continental rise than on the abyssal plains (Hansen, 1975; Billett, unpublished data). However, some specimens of *B. lingua* are known from around the Azores and from the Mid-Atlantic Ridge but no deeper than 2870m (Marenzeller, 1893; Herouard, 1902). The pelagic juvenile specimens caught here were probably carried into the area from a population of *Benthodytes* on the Mid-Atlantic Ridge, or around the Azores or from the continental rise to the east.

Only 3 juvenile *Benthodytes* have been taken in pelagic nets before. The "Michael Sars" North Atlantic Deep Sea Expedition sampled a juvenile *B. typica*, 13mm long, at a depth of 1400m, some 1600m above the seabed (48°29'N, 13°55'W: (Grieg, 1921 as *B. glutinosa*, syn. Hansen, 1975). A further specimen, 7mm long, was sampled by *Discovery* off the coast of Ghana at a depth of 1205 to 1300m, about 3400m above the seafloor (Billett *et al*., 1985). The third juvenile was a small *B. lingua*, 12mm long, sampled in the northeast Atlantic at a depth of 3485 to 3515m and between 575 and 605m above the seafloor (Billett *et al*., 1985). This specimen had calcareous deposits in the body wall of the dorsal surface that were characteristic of adult specimens of this species. These particular deposits, cross-shaped spicules with a bipartite apophysis, were absent from all three *Benthodytes* juveniles captured at GME, although these specimens did possess small rod-shaped deposits around the tentacles. The development of calcareous deposits may be related to specimen size but since cross-shaped deposits are known to occur in a specimen of *B. lingua* only 12mm long, similar deposits would have been expected in the GME specimens, 4.9 to 13mm long, if they had been this species. By a process of elimination, therefore, it is likely that all three juvenile specimens at GME are *B. typica*, a species in which the calcareous deposits are rod-shaped or totally missing.

The significance of the pelagic development of some abyssal benthic holothurians is discussed in the benthic section of this report (Section 28). Although some juveniles of Benthodytes occur in the meso- and bathypelagic zones at GME they do not appear to have been derived from a benthic population in the area and therefore are unlikely to be a pathway for the transport of material away from this site.

2. Enypniastes diaphana: Six specimens were captured in four RMT 8 hauls (Table 19.3). Five of the specimens were taken swimming within 100m of the seabed, but one juvenile, 6.5mm long, was sampled at a depth of 2310 to 2700m, some 2500m above the seafloor.

E. diaphana is a benthopelagic holothurian which occurs throughout the eastern Atlantic at depths between 995 and 4980m although it is most common close to the seabed at abyssal depths (Billett et al., 1985)

Enypniastes swims vertically in the water column with its anterior end orientated upwards (Pawson, 1982; Ohta, 1985; Billett, 1986) but may also "hang" motionless for extended periods (Pawson, 1976). Despite being a pelagic holothurian E. diaphana nevertheless descends to the seabed to feed on the superficial sediment like a conventional benthic holothurian. E. diaphana has been photographed feeding on the seabed (Billett et al., 1985) and microscopic analysis of its gut contents confirms that it feeds on the superficial sediment layer. The related species, E. eximia Theel 1882, has been observed to fill its gut rapidly and is unlikely to remain on the seabed for long (Pawson, 1982). The short residence time of Enypniastes on the seabed is supported by Ohta (1985) who found that feeding tracks made by Enypniastes on the sediment rarely extend beyond one metre. All E. diaphana collected by nets in the northeast Atlantic up to 175m above the seabed have sediment in their guts, but the intestines of specimens at a greater height above the seafloor are empty (Billett et al., 1985).

In general, adult E. diaphana occur within 500m of the seabed in keeping with their dependence on the seabed for nutrition. However, one 40mm long specimen was taken by Discovery in 1978 some 2000m above the seafloor (Billett et al., 1985), and a specimen 35mm long was found swimming at the sea surface in an area lying over the Mid-Atlantic Ridge (Herouard, 1923). *E. diaphana* adults, therefore, are capable of migrating up through the water column but the reasons for these migrations, their extent and their frequency are unknown.

The majority of specimens collected greater than 500m above the seabed are small juveniles 5 to 10mm long. These have been found up to 3000m above the seabed (Billett *et al*., 1985). The juvenile specimen from GME was captured between 2740 and 3130m above the seafloor. *E. diaphana* produces eggs with a maximum diameter of 3.5mm (Billett *et al*., 1985), similar in size to the eggs produced by the benthic holothurians *Benthodytes* (see this section) and *Psychropotes* (Section 28). These large eggs are thought to lead to the direct development of a juvenile holothurian without a larval stage but still within the pelagic environment. This form of development leads to the wide dispersal of the species. It is not known how many eggs are produced annually from each individual, but the large amount of energy required to form an egg of 3.5mm diameter means that the fecundity of *E. diaphana* will be low.

The migration of adult *E. diaphana* and the production of eggs with pelagic development are two pathways by which this sediment-feeding holothurian may transport material from the bottom, up through the water column, and away from the GME area.

3. *Scotothuria herringi*: Twenty specimens of this benthopelagic holothurian were taken in twelve RMT 1+8 hauls (Table 19.3). Eighteen occurred within 100m of the seabed but two specimens were captured at a considerable height above the seafloor. One, a juvenile 11mm long, occurred at a depth of 2310 to 2700m, some 2500m above the seabed, while fragments of another fairly large specimen were found at a depth of 1400 to 1500m (St. 11261#68 RMT 1), 4000m above the seafloor. There is some doubt whether this bathypelagic specimen is a genuine record since it was noted that the RMT 1 nets during the previous haul (St. 11261#65), fished within 100m of the seabed, were twisted round each other when they were brought inboard. This may have caused some contamination of near-bottom fauna, including *S. herringi*, at St. 11261#68. One specimen of the deep-living ostracod *Bathyconcoechia* was also found in this haul (Section 10).

However, although the specimen from St. 11261#68 was in fragments, this fragile specimen is seldom retrieved intact and the good condition of the fragments indicated that the specimen had been caught only recently. More importantly, three *S. herringi* have been sampled at depths of 1250 to 1500m before, including the holotype specimen from the GME area (Hansen, 1978; Billett *et al.*, 1985). One of the other two specimens, at least 160mm long, was sampled just north of the GME area using a closing codend system which retained the holothurian in its *in situ* water. On board ship the specimen was kept alive for about an hour during which weak swimming movements were observed. It is clear, therefore, that *S. herringi* is capable of migrating up into the bathypelagic zone, and that the specimen at St. 11261#68 is a true record.

Only 17 specimens of *S. herringi* were known before sampling began at the GME site in 1985; 14 from the northeast Atlantic, 1 from off the coast of Ghana and the remaining two from off the coast of Kenya in the Indian Ocean. In addition, it is possible that *Scotothuria* is synonymous with the genus *Dendrothuria* from the Bay of Bengal (Koehler and Vaney, 1905; Billett *et al.*, 1985). A few specimens have been taken in benthic trawls but the majority have been collected by pelagic nets at depths between 1250 and 5440m. There is no relationship between size and the depth of occurrence as in *Enypniastes*. The majority of specimens at GME were found close to the seabed in keeping with the proposal that *S. herringi*, like *E. diaphana*, feeds preferentially on superficial sediment (Billett *et al.*, 1985).

The gut of *S. herringi* is very well developed bearing a great resemblance to the gut generally found in benthic holothurians. The intestines of specimens sampled within 100m of the seabed are packed full of sediment. Recent work on the fine structure of the feeding tentacles of *S. herringi* suggests that they may be able to comb the water for suspended particulate material but the guts of specimens sampled greater than 100m above the seabed have always been completely empty. It is doubtful whether *S. herringi* could maintain itself for long in the pelagic environment and as a result it is thought that it lives for the most part close to the seabed. Therefore, as with *Enypniastes*, *S. herringi* appears to be capable of extensive migrations through the water column but their duration, extent and frequency are unknown.

S. herringi produces large eggs of about 1.8mm maximum diameter probably leading to the direct development of a juvenile holothurian within the deep-sea plankton. Billett et al., (1985) noted a bimodal egg size distribution which may indicate periodic breeding in this species.

As for E. diaphana, the migration of adult S. herringi and the production of eggs with pelagic development are two pathways by which this sediment-feeding holothurian may transport material up through the water column and away from the GME area. The parasitism of S. herringi by nematodes (Billett et al., 1985) is another potential dispersal pathway.

4. Abundance of pelagic holothurians: The abundance of pelagic holothurians close to the seabed was estimated from the RMT 1+8 catch data and from wide-area survey photography (WASP), the latter undertaken by the Geophysics Department at IOS as part of the DOE contract at GME (Huggett, in press). In both cases the abundance of holothurians was expressed as the number of individuals per unit volume ($10^5 m^3$). The number of specimens caught in the RMT 8 net was low and therefore a mean abundance has been calculated for each species by combining the data from all 10 samples taken close to the seabed (11261#46, #54-56, #63-65, 11261#25-27). The wide-area survey camera takes photographs of the seafloor covering approximately $80m^2$ from a height of about 10m (Huggett, in press). This gives a pyramid-shaped volume of water of about $267m^3$ in each photograph with about a 15% overlap between adjacent photographs. However, the volume that is of use in a photograph will be less than $267m^3$ since not all organisms in that volume of water will be in focus. Hence the abundance of pelagic holothurians will be slightly underestimated by the WASP photographs.

Both methods of estimating holothurian abundance have their drawbacks. Although the number of E. diaphana and S. herringi can be determined accurately from the RMT catches, the nets do not sample adequately the five metres nearest to the seabed. Pawson (1976) noted that Enypniastes generally occurs between 1 and 3 metres off the seabed, while Ohta (1985) photographed Enypniastes only "on, or within about 5 metres of, the bottom". RMT net systems, therefore, will miss the bulk of the pelagic holothurian population, and possibly other elements of the benthopelagic plankton (see also Section 11).

The problem may be overcome by using photography (WASP) but in this case it is not always possible to distinguish E. diaphana from S. herringi, and indeed to distinguish pelagic holothurians from other planktonic organisms. E. diaphana may be identified with certainty only when the anterior brim of fused tube-feet is extended. This gives a characteristic "bat-like" appearance to the holothurian (Fig. 19, I). However, there are many postures that may be adopted by Enypniastes when it is not possible to identify the species with any confidence. Pelagic holothurians often appear as dark "blobs" in the WASP photographs (Fig. 19, II) and it is a matter of intuition whether they are recorded as a swimming sea-cucumber.

In the analysis of the WASP photographs (Table 19.4) three categories of pelagic holothurian are noted; first, those specimens that are clearly E. diaphana, second, those specimens that are definitely pelagic holothurians (including all E. diaphana), and third, all possible records of pelagic holothurians. The latter includes pelagic organisms that are the correct size and the same tone on black and white photographs as verifiable pelagic holothurians. The catches from the near-bottom RMT hauls contain no planktonic organisms that could be confused with pelagic holothurians. The best estimate of abundance, therefore, is likely to be the greatest abundance calculated for each station.

One other drawback of photography is the poor resolution of small specimens. Half of the individuals caught by the RMT 8 were only about 10mm long (length estimated from fragments) and specimens of this size are unlikely to have been recorded from the WASP photographs.

The mean abundance of E. diaphana and S. herringi in the RMT samples was 1 and 2 individuals per $10^5 m^3$ respectively. This compares with abundances of E. diaphana ranging from 4 to 11 individuals per $10^5 m^3$, estimated from RMT nets fished close to the seabed on the Cape Verde Abyssal Plain and on the Azores-Biscay Rise (Billett et al., 1985). S. herringi has never been caught before in sufficient number for its abundance to be estimated. WASP photographs from the Azores-Biscay Rise give an abundance of 2 to 7 individuals per $10^5 m^3$ (Billett et al., 1985), similar to the RMT 8 net estimates, but at GME pelagic holothurians are far more common in WASP photographs with a mean abundance of 28.6 pelagic holothurians per $10^5 m^3$ as compared with just 3 specimens per $10^5 m^3$ in the RMT 8 net. There is considerable variability in the WASP estimates of abundance which may indicate a patchy distribution for pelagic holothurians at GME.

E. diaphana is more abundant on the continental slope off northwest Africa than at GME. A dense population was photographed during an epibenthic sledge tow (Billett et al., 1985) but the distribution of E. diaphana was patchy. Patchiness is known to occur in other pelagic holothurians such as Peniagone diaphana (Barnes et al., 1976; Billett et al., 1985), but the causes of aggregation and the persistence of a patch are unknown. Aggregation in benthic holothurians may occur in response to the localized accumulation of organic matter brought about by the combined action of bottom currents and irregular topography (Billett and Hansen, 1982; Billett, Lampitt, Rice and Mantoura, 1983). Emplacement of objects on the seabed may lead to "island effects" in providing sites for the accumulation of organic matter and hence areas for the aggregation of pelagic holothurians.

Taking a working abundance of 30 pelagic holothurians per $10^5 m^3$ and making certain assumptions it is possible to calculate the length of time it would take the pelagic holothurians to feed on a hectare of sediment. First, assuming that pelagic holothurians generally occur within 10m of the seabed, then 30 individuals will be swimming over an area of $10,000 m^2$ (a hectare). Second, assuming that a pelagic holothurian, when feeding, sweeps an area 1m long and 3cm wide (Ohta 1985), then the top 1mm of sediment of $0.03 m^3$ will be fed upon (NB. the area swept by a Scotothuria while feeding is unknown). Third, assuming that a holothurian feeds once per day then 30 holothurians will feed upon about $325 m^2$ per year. The pelagic holothurian population therefore would rework the superficial sediment layer in one hectare in a period of about 30 years.

20. **MIDWATER FISHES** Julian Badcock and R.A. Russell

INTRODUCTION

At the broadest level of understanding, the vertical structure and organisation of the oceanic midwater fish community is reasonably well known (e.g. Marshall, 1979). However, site-orientated investigations examining these aspects in detail have been relatively few and for the North Atlantic subtropics published accounts are available for only 3 sites: 30°N, 23°W (Harrisson, 1967; Badcock and Merrett, 1976); 28°N, 14°W (Badcock, 1970); 32°N, 64°W (introduced by Gibbs and Roper, 1970). The location of a midwater fish in the water column is species dependent but can vary according to individual animal size and maturity or developmental state, as well as to diel and seasonal period. Consequently this report summarizes data on size-range and developmental states of all species sampled at GME (with greater detail provided for the more abundant ones), in addition to that of abundance and vertical distribution. Whilst summary information for most species can be found in CLOFNAM (1973), its Supplement (Tortonese and Hureau, 1979) and in FNAM Vol. 1-3 (1984-86), detailed studies of the ichthyofauna in the vicinity of GME are few. General surveys have been conducted around the Grand Meteor Bank (e.g. Kotthaus, 1972; Maul, 1976; Belyanina, 1984a) but observations on the fine detail of vertical structure and community interrelationships are restricted to accounts for 30°N, 23°W by Merrett and Roe (1974) and Badcock and Merrett (1976).

MATERIALS AND METHODS

Collections made by RMT 8 only were examined (Tables 6.85-86, Fig. 6.XI). Fish collected by the RMT 1 were counted (Tables 6.82-84, Fig. 6.X). RMT 8 catches incorporated 3415 animals each of which was, where possible, identified to species and measured (standard length, SL) to the nearest mm. Neither sex nor maturity stage was recorded. The usefulness of this was undermined either by low catch numbers or, as in the case of abundant Cyclothone, excessive capture-damage to specimens. Catch numbers are expressed as No. animals/$10^4 m^3$ water filtered/stratum/diel period.

No one kind of net samples the midwater fish fauna adequately (e.g. Harrisson, 1967) and a survey such as that conducted at GME is subject to a number of severe limitations, as discussed previously (Badcock and Merrett, 1976, 1977). Consequently, within the more detailed systematic sections following, some literature concerned with aspects of systematics, geographic and vertical distributions, reproduction, development, feeding etc. relevant to GME species is listed in addition to text references. The lists are not intended to be exhaustive.

For ease of reference, the systematic classification above generic level follows that used in FNAM Vol 1-3 (1984-86).

RESULTS

A total of 3415 fishes were caught, representing 41 families, 76 genera, and a minimum of 111 species of which 99 could be positively confirmed. On the whole catch number/species was small. About 2/3 of the total catch comprised just two species, *C. braueri* and *C. microdon*, and the general paucity of material is emphasized by the fact that only 22 species were represented by more than 20 specimens.

The results are considered in two sections, one concerned with the day-night sampling pairs of the upper 1500m series, the other with the stepped oblique and near-bottom samples. Obviously there is some vertical overlap between these two sets in the distribution of some species and this is noted for the appropriate species.

Upper 1500m series.

The upper 1500 series incorporated 3255 specimens (1416 day, 1839, night), excluding obvious contaminants, representing 39 families with 73 genera and 97 identified species (minimum 108). A summary of the number of specimens, their density and the minimum number of species present per depth stratum, day and night, is given in Table 20.1

Stomiatoidei

The stomiatoids were represented by 8 families with 17 genera and 30 species identified (Table 20.2a). They were the most abundantly sampled fish group, mainly by virtue of the *Cyclothone* catches made. The stomiatoids range in size from *ca*. 30-400+ mm SL and most species are poorly sampled by 8m² nets. As here, however, the Gonostomatidae, Sternoptychidae and, to a lesser extent, Photichthyidae are prominent in midwater collections. They are considered in greater detail below. The data for the remaining species are tabulated (Table 20.2b) and further summary information is available in CLOFNAM (1973), its Supplement (Tortonese and Hureau, 1979) and FNAM Vol. 1 (1984).

Family Gonostomatidae

The gonostomatids are a group of small to medium-sized fishes (ca. 30-370mm SL) and comprise the most abundant element of the oceanic ichthyofauna in most areas of the world ocean. Indeed, some claim Cyclothone to be the most abundant fish in the sea. At present, however, gonostomatids are not regarded as a potential fishery resource (but see Gjøsaeter and Kawaguchi, p. 48, 1980). The family contains both migratory (vertical) and non-migratory species with a maximum depth of occurrence at about 3000m (Badcock, 1984a; Schaefer et al., 1986a). Early larval life is spent in the near-surface waters (usually at depths less than 100m) and further development may be protracted and accompanied by a gradual sinking to juvenile-adult diurnal depths of occurrence or else entail a rapid metamorphosis accompanied by a quick sinking (species dependant). Sexual dimorphism is common within the group, usually expressed as differences in maximum size attainable (males smaller). In Cyclothone spp. and Gonostoma bathyphilum additional sex-linked differences in olfactory structure are developed. Reproduction is usually dioecious, species being single or multiple spawners, but some species of Cyclothone and Gonostoma have adopted a strategy incorporating protandrous hermaphroditism (the only deep-sea fish to do so).

Sixteen species in 5 genera have been recorded from the eastern North Atlantic subtropical area (Badcock, 1984a). In the GME collections 12 species of 4 genera were identified (Table 20.2). Those "missing", Cyclothone obscura, Diplophos maderensis, D. taenia, Gonostoma atlanticum, are naturally rare to the GME area (see Badcock, 1984a). The gonostomatids comprised about 75% (76.9%, day; 73.6%, night) of the sampled fish population of the upper 1500m water column but even so, catch numbers/species were generally low. The GME area is near the southern limit of G. bathyphilum, outside the usual tropical environment of C. acclinidens and C. alba, and beyond the normal pseudoceanic limits of C. livida and G. denudatum. In these cases, low catch numbers are unsurprising. On the other hand, Bonapartia pedaliota, G. elongatum and

Margrethia obtusirostra are common throughout the subtropical North Atlantic; they are, however, better sampled by nets larger than the RMT 8. Summaries of vertical distributions indicated by the GME results are presented for all sampled gonostomatids in Table 20.2.

Further details of gonostomatids may be found in Ahlstrom et al., 1984; Badcock, 1986; Fisher, 1983; Grey, 1964; Go and Badcock, 1986; Gorelova, 1980; Gorelova and Tseitlin, 1979; Miya and Nemoto, 1985; Mukhacheva, 1972, 1974, 1976, 1978; Roe and Badcock, 1984.

Cyclothone species.

Cyclothone, the most speciose and abundant of the gonostomatid genera, shares with Gonostoma the greatest vertical range of adult diurnal depth distribution so far demonstrated among midwater fishes. Morphologically species are very similar and show a depth progression that with change of species involves a darkening and enlargement of the body, accompanied by a reduction in bioluminescent and visual capacities (Badcock, 1970; DeWitt 1972; Kobiyashi, 1973; Bond, 1974; Badcock and Merrett, 1976, 1977). The two abundant species sampled at GME, C. braueri and C. microdon, are temperate-subtropical forms whereas the two less abundant ones, C. pallida and C. pseudopallida, have their centres of abundance in the tropics (Badcock and Merrett, 1977; Badcock, 1982, 1984a). The vertical succession of species and general relationships of vertical population structure at intra- and inter-specific levels at GME were the same as those observed previously elsewhere (Badcock, 1970; Bond, 1974; Badcock and Merrett, 1976, 1977).

In the upper 1500m C. braueri ranked first in abundance of all fish species at the GME site (41.9%, day, and 45.3%, night, of the total population). The juvenile-adult population occurred in 300-800m depth day and night, with a centre of abundance in 500-700m at all times (Fig. 20.I). As would be expected, post-larvae were concentrated in the upper 100m but were sampled down to adult depths of distribution. The population size-frequency structure shows a major mode over 23-26mm SL, equatable with females, and lesser ones at 16-18mm and 20mm SL, equatable with juveniles, males and immature females. In essence the structure is the same as that found for the population at 30°N, 23°W (Badcock and Merrett, 1976), as are the changes in length-frequency structure with changing depth - which show the smallest animals dwelling shallowest and females predominating the deepest stratum occupied, day and night (Fig. 20.IIa,b, Table 20.3).

The juvenile-adult population of *C. microdon*, the species ranking second in abundance (29.5%, day, and 24.6%, night, of the total fish population of the upper 1500m), had an upper distributional limit of 600m depth and peak abundance in 900-1000m, day and night. Even so, the bulk of the population occurred deeper than 1000m (Fig. 20.I), and the species was abundant to at least 1900m, with its lower distributional limit occurring around 2300m. In other areas the *C. microdon* population extends to about 2700m depth (Badcock, 1984a). Post-larvae were captured in the upper 50m. There are marked similarities between the results obtained at GME and those collected earlier at 30°N, 23°W (*cf*. Badcock and Merrett, 1976). Thus the population at GME was non-migratory, predominated by adolescents and showed a marked stratification of size with depth, larger animals living deeper (Fig. 20.IIIa,b, Table 20.3).

Cyclothone pallida was centred in 800-1100m day and night, though some specimens were caught both shallower and deeper (Fig 20.I, Table 20.3). Stratification of animal size with changing depth is most usual in this species [though exceptions to this do occur (Badcock, 1982)] and was apparent in the data from GME.

Cyclothone pseudopallida had an upper distributional limit at 600m depth (one specimen taken shallower) and was sampled to 900m and 800m by day and night, respectively. The data indicate an increase in animal size with increasing depth that in this case precludes any migrational implications being placed upon the apparent shoaling of the lower depth limit at night (Fig. 20.I, Table 20.3).

Family Photichthyidae

The photichthyids are small to medium-sized fishes (*ca*. 40-330mm SL) with a maximum depth of occurrence around 1100m, though most species occur in depths less than 800m (Badcock, 1984b; Schaefer *et al*., 1986b). Adults are rather poorly sampled by nets of RMT 8 size but larval studies indicate that some species, at least, are extremely abundant and considerably more important than would be predicted by extrapolation of density data based on net captures of adults (Ahlstrom, 1974). None, however, are regarded at present as a potential fishery resource. The family contains migratory (vertical) and non-migratory species. In all species, early larval life is spent in the upper 100m and the onset of metamorphosis is accompanied by a rapid sinking to adult diurnal depths of occurrence. Reproduction is dioecious.

Five species in 3 genera have been reported from the eastern North Alantic subtropics (Badcock, 1984b) but tropical species such as *Pollichthys mauli* may occasionally enter the area. At GME 3 species of *Vinciguerria* only were sampled. The absence of the benthopelagic *Polymetme corythaeola* is to be expected but *Ichthyococcus ovatus* is resident in the area and normally one would anticipate its capture there.

See also Ahlstrom and Counts, 1958; Ahlstrom *et al*., 1984; Badcock, 1970; Badcock and Merrett, 1976; Grey, 1964; Gorbunova, 1972; Mukhacheva, 1980.

Vinciguerria species

The populations sampled were mainly post-larval, largely metamorphic forms (Table 20.2). Juveniles of *V. attenuata* and *V. nimbaria* were caught by night only, in the upper 100m and 200m, respectively. The patterns of vertical distribution (Fig. 20.IV) conform with those summarized by Badcock (1984b).

Family Sternoptychidae

The sternoptychids are an important group of small (*ca*. 30-120mm SL), relatively abundant fishes with a maximum depth of occurrence around 1500m. In terms of abundance they make a significant contribution to the oceanic ichthyofauna in any given area, temperate to tropical, and at least one species (*Maurolicus muelleri*) has some potential as a fishery resource (e.g. Gjøsaeter and Kawaguchi, 1980). The family includes migratory (vertical) and non-migratory species. Eggs are spawned at depth and early larval life is spent in the near surface waters, sometimes shallower than 100m depth, more often deeper. Reproduction is dioecious.

The eastern North Atlantic subtropical area has 8 resident species in 5 genera, though additionally the waifs of *Argyropelecus affinis* (tropical), *A. olfersi* (temperate) and *Polyipnus polli* occasionally enter the area (Badcock, 1984c). Of the residents, two, *Argyripnus atlanticus* and *Maurolicus muelleri*, were not sampled at GME, the former being benthopelagic (Badcock and Merrett, 1972; Struhsaker, 1973; Badcock, 1984c) and the latter a slope-dweller in the subtropics (Mukhacheva, 1981; Badcock, 1984c). Within the GME collections, 6 species (all subtropical residents) of 3 genera were represented (Table 20.2), comprising about 6% (5.8%, day; 6.2%, night) of the sampled fish population in the upper 1500m. *Argyropelecus aculeatus*, *A. hemigymnus*, *Sternoptyx diaphana*, *S. pseudobscura* and *Valenciennellus tripunctulatus* are permanently present in the GME area. The other species represented, *A. gigas* (Table 20.2), has a pseudoceanic distribution in the eastern North Atlantic (Baird, 1971; Borodulina, 1978; Badcock, 1984c) and the single specimen caught was presumably an expatriate.

Catch numbers at GME were low (larger species are better sampled by larger nets - see Harrisson, 1967) but in each of the species considered below post-larval (metamorphic) to adult stages were represented. The adults sampled were, on the whole, small and in only two species, *A. aculeatus* and *V. tripunctulatus*, were specimens approaching the maximum adult size caught.

See also Ahlstrom *et al.*, 1984; Baird and Hopkins, 1981a,b; Belyanina, 1983, 1984b; Grey, 1964; Hopkins and Baird, 1977; Merrett and Roe, 1974.

Argyropelecus species.

Morphologically *Argyropelecus* spp. are rather similar. *Argyropelecus aculeatus* attains a greater maximum size than *A. hemigymnus* (*ca.* 70 *v.* 40mm SL) and in areas of sympatry, while these species have overlapping vertical distributions, populations of *A. hemigymnus* extend deeper diurnally and do not migrate as shallow nocturnally as *A. aculeatus* (Badcock, 1970; Badcock and Merrett, 1976).

At GME, *A. aculeatus* occurred in 400-600m depth by day and as a split population in 200-300m and 400-500m at night (Fig. 20.V, Table 20.4). During the day, post-larvae (8-13mm SL) were restricted to the shallower parts of the distribution, 400-500m, whereas more advanced stages (42-68mm SL) occurred throughout. The maximum size of the non-migrant element was 12mm SL and the minimum size of migrants, 14mm SL. In this species the adult complement of photophores is attained at about 15mm SL (Badcock, 1984c) and thus a previous conclusion, "that detectable migrations are not made by animals until a certain degree of development has been attained" (Badcock and Merrett, 1976) is maintained by the present observations.

The daytime juvenile-adult population of A. hemigymnus was centred slightly deeper than that of A. aculeatus, in 500-700m depth. A single post-larva was caught in 300-400m (Fig. 20.V, Table 20.4). [In this species the onset of photophore development may be accompanied by a migration to greater depths (Jespersen and Tåning, 1926; Badcock and Merrett, 1976)]. As found elsewhere (Badcock, 1970; Badcock and Merrett, 1976) animals > 18mm SL extended deeper than smaller ones. Nocturnally the juvenile-adult population(10-32mm SL) occurred in 400-700m depth with peak abundance, as by day, in 500-600m (Fig. 20.V). Whether the apparent nocturnal incursion into the 400-500m stratum by juveniles-adults represents migration remains uncertain because the low catch numbers preclude a thorough assessment of population size-frequency structure at different depths. Elsewhere, populations have been reported as being extensively migrant, as containing migratory and non-migratory elements and as being vertically static (Badcock, 1970, 1984c; Gibbs and Roper, 1970; Badcock and Merrett,1976, 1977; Roe and Badcock, 1984).

Sternoptyx species

In both larval and adult stages S. diaphana and S. pseudobscura are extremely alike, though the former attains smaller maximum size (max. ca. 46 v 55mm SL). These species have circum-global, subtropical-tropical distributions and, consequently, broad areas of sympatry. They are non-migratory but their centres of abundance are vertically segregated, S. pseudobscura being the deeper-dwelling form (Baird, 1971; Borodulina, 1978; Badcock and Baird, 1980). In the North Atlantic subtropics, where the genus is represented only by these two species, S. diaphana extends deeper than it does in the tropics and the abundance of S. pseudobscura correspondingly appears to be lower (Badcock and Baird, 1980).

Sternoptyx diaphana was sampled in 600-1000m and 600-900m depth by day and night, respectively, and showed no evidence of undergoing migrations (Fig. 20.V, Table 20.4). As expected, S. pseudobscura occurred slightly deeper, in 800-1000m (day) and 800-1100m (night) and likewise provided no evidence of migrations. The sampled populations of both species were essentially post-larval-juvenile and the maximum adult sizes encountered were much lower than those known for the respective species.

Valenciennellus

Valenciennellus tripunctulatus, a shallow mesopelagic form (100-550m depth), is often non-migratory but in some locations short diel migrations have been reported for the species (Badcock, 1977, 1984c). At the GME site greatest abundance occurred in 400-500m depth throughout the diel period (Fig. 20.V, Table 20.4) and the population showed a stratification of animal size with depth at all times, larger animals lying deeper. Although the relative abundance and mean size of animals showed a nocturnal increase in the 400-500m stratum, the evidence regarding any diel migration is inconclusive. This species is more prone to capture at night and, as argued elsewhere on the basis of far more extensive data, apparent increased nocturnal abundance and mean animal size within a given stratum need not imply migration into that layer (Badcock and Merrett, 1976).

Myctophoidei

The adults of only two myctophoid families, Myctophidae and Notosudidae, occur in midwater; the remaining families are demersal, although their larvae are epipelagic-mesopelagic. Only one species of notosudid, *Ahliesaurus berryi*, occurs within the GME area (Bertelsen, Krefft and Marshall, 1976; Krefft, 1984), but, as with all notosudids, it is best sampled by large nets and its absence in the GME collections is not unexpected. Thus the myctophoid collections included only one family, the Myctophidae (Table 20.5a).

Family Myctophidae

The myctophids comprise a group of small to medium-sized fishes (*ca.* 25-280mm SL), most species of which are relatively abundant. Some species (e.g. *Lampanytodes hectoris*, *Gymnoscopelus* spp., *Diaphus* spp.) are already subject to fishery exploitation or exploration and many have potential as a fishery resource for fish oils and meal (e.g. Nafpaktitis *et al.*, 1977; Kawaguchi and Shimizu, 1978; Hulley, 1981, 1986; Gjøsaeter and Kawaguchi, 1980). Most lanternfishes are diurnally centred shallower than *ca*. 1000m but their maximum depth of occurrence approaches 2000m. On the whole they are active diel vertical migrants and the migrations of some (e.g. *Ceratoscopelus townsendi*, *Notoscopelus resplendens*) are the most extensive reported among midwater animals. Early larval stages occur in the upper 120m of the water column and at metamorphosis larvae sink rapidly to adult diurnal depths of occurrence. Sexual dimorphism can be manifested as differences in size at maturity, eye size, snout shape and luminous organ development. Reproduction is dioecious.

Within the subtropical eastern North Atlantic about 50 species of 19 genera have been recorded but of these some are pseudoceanic and others are expatriates and thus would not necessarily be expected in the GME area (c.f. Nafpaktitis *et al*., 1977; Hulley, 1981, 1984). The myctophid catch from the GME area included 30 species in 16 genera and represented about 10.5% (9.9%, day; 10.9%, night) of the sampled fish population in the upper 1500m of the water column. Catch numbers/species were low but most species are better sampled by nets larger than the RMT 8 and almost certainly their abundance is greatly underestimated. A summary of vertical distributions for species at the GME site is given in Table 20.5b.

Ceratoscopelus species.

Of the two species represented at the GME site *C. maderensis* is a temperate-semisubtropical one and the collection of only a single specimen merely reflects this. On the other hand, *C. townsendi* (syn.*warmingii*) is a resident of the area. However, two Forms, A and B (subspecies) occur in the eastern North Atlantic, and the GME site is located near the easternmost extension of Form B (Badcock and Araujo, in press). Again the single capture of this Form reflects the natural situation.

The distribution characteristics of Form A at GME conform with those described from a much larger data base than available here, taken from the Azores Front area during early summer (Badcock and Araújo, in press). Thus the juvenile-adult population at GME was centred below 1000m by day, without showing any size-stratification with depth, and migrated to the near-surface layers (50-200m depth) at night (Fig. 20.VIa, Table 20.6a). Larvae were centred in the upper 100m, day and night, smallest sizes shallowest. The two specimens captured deeper (6mm SL, 1200-1300m, night) are contaminants from shallower depths.

Lampadena spp.

Lampadena is a genus of relatively large-sized lanternfish (to ca. 230mm SL) and its members are particularly poorly sampled by medium-sized nets such as the RMT 8. Lampadena anomala, represented by a single specimen in the present collections (Table 20.5) is rather uncommon and has only recently been shown to occur in the eastern North Atlantic (Hulley, 1981). The GME site is close to the southern limit of the northern population of the other species sampled, L. chavesi, a schooling form (Krefft, 1970) which has a biantitropical distribution (Nafpaktitis et al., 1977; Hulley, 1981, 1984). The population sampled was primarily larval (larvae have not previously been described though are known in the area, see Belyanina, 1984a). Juveniles showed extensive diel migrations (as do adults, Nafpaktitis et al., 1977; Hulley, 1984) and were caught in 800 - 900m (day) and 50-100m (night). Larvae did not migrate and, distributionally, demonstrated the usual ontogenetic pattern of lanternfishes, premetamorphic larvae occupying the upper 100m, transforming larvae (700-800m) occurring in the adult environment, with some specimens sampled at intermediate depths (Fig. 20. VIa, Table 20.6a).

Lampanyctus species.

Of the 6 Lampanyctus spp. sampled, only two, L. ater and L. cuprarius, were caught in numbers >20 (Table 20.5b). Morphologically these two species are rather alike (L. ater attains a greater maximum length). To a large extent they share diurnal depth ranges but although both are biantitropical, geographically they tend to be mutually exclusive (Nafpaktitis et al., 1977; Hulley, 1981, 1984). The GME site is located in an area of geographic overlap. Diurnally, the two species shared 800-1000m depths (one specimen of L. cuprarius came from shallower and one from deeper; Table 20.5) but whilst overall animal sizes sampled were similar in the two species, centres of abundance were separated (800-900m, L. ater; 900-1000m, L. cuprarius). These centres of abundance were maintained at night but parts of the population of each species migrated to shallower waters (Fig. 20.VIa, Table 20.6a). No distinction, on the basis of size, could be made between those animals that migrated and those that remained at depth.

The night data in each case showed a depth extension (L. ater to 1400m; L. cuprarius to 1300m) not apparent from the day captures (Table 20.5, Fig. 20.VIa).

Lepidophanes species

Lepidophanes gaussi, a bipolar subtropical species, is resident in the GME area whereas its tropical congener, L. guentheri, only occasionally makes incursions there (Nafpaktitis et al., 1977; Hulley, 1981, 1984). As a situation reported previously (e.g. Badcock and Merrett, 1976; Karnella, 1983), the data for L. gaussi indicate adults as residing moderately deep by day, in 800-900m (the night data indicate an extension to 1000m depth, Fig. 20.VIb, Table 20.6b), and for the most part migrating into the upper 100m at night (Fig. 20.VIb). Non-migratory larvae lay in the upper 100m.

Lobianchia species.

Despite the broad, overlapping geographic ranges of L. dofleini and L. gemellarii, these two species exhibit a tendency towards mutual geographic exclusion (Nafpaktitis et al., 1977). The GME site is located in the vicinity of the southern periphery of the centre of abundance of L. dofleini and well to the north of that of L. gemellarii. In this area L. gemellarii specimens are probably sterile expatriates (Nafpaktitis, 1968) and this factor may contribute significantly to its apparent lesser abundance compared with that of L. dofleini (Table 20.5b), though larger animal size may contribute to this as well. Juvenile-adult L. dofleini were sampled in 500-700m depth by day and in 50-200m at night. Nocturnally juveniles penetrated shallower than adults (Fig. 20.VIb, Table 20.6b).

Notoscopelus species

Though one other species of Notoscopelus occurs in the GME area only N. resplendens was caught in more than one sample (Table 20.5b). Juveniles were sampled between 800-1200m depth by day and in 50-200m by night (one was taken in 700-800m). Larvae occurred in the upper 300m and transforming animals were captured to 900m depth (Fig. 20.VIb, Table 20.6b). Adults were not captured.

Remaining species

Species other than those of stomiatoid or myctophid families were represented in the upper 1500m collections by only 146 specimens. Even so, a minimum of 40 species in 34 genera of 26 families were sampled (Table 20.7a). A summary of their capture depths is presented in Table 20.7b, the information of which can be augmented by that from 30°N, 23°W (Badcock and Merrett, 1976). On the whole, the species involved are not particularly uncommon and whilst some may have natural low abundance, others are better sampled by much larger nets. Depth information regarding these species is, for the most part, rather vague (see summaries CLOFNAM 1973; CLOFNAM Supplement, 1979; FNAM Vol. 1-3, 1984-86; Smiths' Sea Fishes, 1986) but most are non-migrants. The adults of *Bathylagus longirostris* (syn. *compsus*), *Benthalbella infans*, *Evermannella indica*, *Melamphaes simus* and *Serrivomer beani* have been reported as showing some shoaling at night (Badcock, 1970; Merrett *et al*., 1973; Badcock and Merrett, 1976; Johnson, 1984).

Some of the species sampled are rare, at least to the GME area. The Cetomimidae and Rondeletiidae are rare anywhere (Paxton, 1986a,b) and *Ditropichthys* has been reported from the eastern North Atlantic only once before (Badcock, 1970). The captures of *Photostylus* and *Hymenocephalus* are unusual in that both are slopedwellers, the former in midwater, the latter benthopelagically (Markle and Quero, 1984; Geistdoerfer, 1986). *Melamphaes pumilus*, a western Atlantic species, is only very rarely captured in the area (Ebeling, 1962).

Stepped oblique and near-bottom series

These two series caught 153 specimens with the largest catch (57 specimens) coming from 1500-1900m depth. The 1500-1900m stratum was dominated by *C. microdon* (*ca.* 77% of catch). Two specimens of *C. braueri* may well have been contaminants from shallower but all other species sampled (*Cyema atrum*, *Gonostoma bathyphilum*, *Haplophryne mollis*, *Melanocetus* sp., lynophrinids) would be expected to occur in this layer.

The vast majority of specimens (conservatively, 83 of 96 animals) apparently caught deeper were contaminants from shallower depths. In effect, the results indicate a highly depauperate ichthyofauna inhabiting depths deeper than 2300m. Indeed, below 2700m depth only Monognathus, Neocyema, and, very questionably, a linophrynid male, could be considered as coming from their indicated capture depths. Monognathus is a little known saccopharyngiform genus currently under investigation (Bertelsen, Nielsen : Copenhagen) and the capture of even 5 specimens (3310-3500; 3330-3910; 5233-5355; 5385-5470; 5410-5430m depth) is remarkable. The specimen of N. erythrosoma is only the third specimen recorded and the first from the North Atlantic, the other two being caught in the South Atlantic, 37°N, 5°E (Castle, 1986).

PERSPECTIVES

Midwater fishes comprise, on the whole, a rather active element of the micronekton fauna that is difficult to sample adequately with nets. Their behaviours vary considerably (e.g. Barham, 1970), as do their sizes, morphologies (e.g. Marshall, 1971) and energetic requirements (e.g. Childress, 1975). Much of our knowledge of geographic and vertical distributions, abundance and migratory behaviour is drawn from data based upon collections made by smallish nets (<10m² mouth area) and the need for complementary investigative techniques (e.g. large nets; larval, acoustic and submersible surveys) in conducting oceanic faunal studies has been well recognised (e.g. Pearcy 1975). Nevertheless, small nets have remained the principal investigative tools and it should be stressed that collections made by such devices continue to provide valuable, if limited, assessments of the interrelationships within the oceanic micronekton community.

The North Atlantic subtropical region is faunally complex (for example, Backus et al., 1977, recognize it as containing 4 provinces) and within it dominant species show a variety of geographic patterns. In other words, the centres of abundance of different species are not necessarily coincidental and thus different areas may have somewhat different faunas (i.e. differences in species composition, inter-specific rank abundance and infra-specific abundance can exist between areas, e.g. Backus, et al., 1969). In the light of this often subtle complexity, an evaluation of the GME results has to be restricted to comparisons with the detailed report on midwater fishes at 30°N, 23°W presented earlier by Badcock and Merrett (1976).

At the GME site, the RMT 8 collections included 41 families in 76 genera and a minimum of 111 species, compared with 37 families in 66 genera and a minimum of 110 species at 30°N, 23°W. Confirmation of only 99(GME) and 98 (30°N,23°W) species was possible due to either damage or developmental state. Sixty-three species were common to both sites. Of the 68 caught solely at one or other site, only Macrorhamphosus scolopax, a species usually associated with slope areas, was caught in great abundance (30°N, 23°W). The remainder were mostly poorly sampled and clearly included some expatriates, but on the basis of their known geographic ranges, all would be expected to occur at both sites.

The dominant species by far at both sites were Cyclothone braueri and C. microdon but juvenile-adult catch rates were lower at GME, more so for C. braueri. To some extent this catch reduction can be rationalized in the context of breeding cycles. The spawning season of C. braueri occurs mainly over April-October in the eastern North Atlantic (Badcock, 1984a), individuals usually spawning once, with spawned-out animals dying soon afterwards (Bond, 1974; Badcock and Merrett, 1976; Badcock, 1984a). At 30°N, 23°W (April) spawning had only recently begun (Badcock and Merrett, 1976) whereas at the GME site the spawning season was considerably more advanced, as indicated by the higher incidence of larvae. Bond (1974) found the abundance of post-spawning populations to be drastically reduced off Bermuda, from where he reported catch-rates over June - September to be half those over January - March. Despite these attritional effects, C. braueri remained the most abundant species at both sites, and seasonal influences are more dramatically indicated by rank changes in the order of abundance among the myctophids. At 30°N, 23°W in early April Benthosema suborbitale, Hygophum hygomii and Diogenichthys atlanticus were indicated as being highly abundant. In addition their larvae were present in abundance and the data indicated that recruitment had begun (Badcock and Merrett, 1976). Yet at GME (June-July) these species were hardly represented [though transforming forms (recruitment) were taken] and their ranks in myctophid abundance were superceded by Lampanyctus ater, L. cuprarius and Lobianchia dofleini (Table 20.5). The former group of species are annuals (Karnella, 1983) and their drastically reduced adult abundance at GME most probably reflects a post-spawning demise. Similar seasonal fluctuations in abundance, and hence a seasonal succession of adult groups of species, has been shown to occur off Bermuda (Karnella, 1983). Very little is known of seasonal fluctuations of midwater fishes and even less of annual ones that may occur.

The GME and 30°N, 23°W sites were sampled 13 years apart and whether or not annual fluctuation is also a contributing factor to the differences in abundance observed at these two sites is unknown.

Despite differences in abundance and some differences in rank order of abundance the general synopses of species interrelationships (e.g. vertical distributions, diel migrations etc.) at the two sites are very similar. However, diurnal depths of occurrence at the GME site were a *maximum* of 100m deeper than those found at 30°N, 23°W (c.f. Badcock and Merrett, 1976). Even so, the migratory fraction of the total population was still largely contained within the upper 1000m and only four migrant or partially migrant species, *Lampanyctus cuprarius* (to 1300m), *Notoscopelus resplendens* (to 1200m), *L. ater* (to 1400m) and *C. townsendi* (to 1500m) were sampled deeper. The maximum diurnal depth of occurrence of *C. townsendi* is about 1800m depth (Badcock and Araújo, in press) and since the 1500-1900m stratum was fished only by night, the possibility of *C. townsendi* occurring within this stratum diurnally cannot be denied.

The slight deepening of the mesopelagic fish population at the GME site is unlikely, on the basis of the *Cyclothone* data, to be a consequence of ontogenetic migrations. Equally, seasonal vertical displacements are unlikely to occur in the subtropics, although there is evidence that mesopelagic fish populations undergo such displacements, in addition to ontogenetic migrations, in the temperate North atlantic (Badcock 1981). However, distributions are greatly influenced by temperature structure but may be modified locally by prevailing light conditions (Foxton, 1972). A deepening of populations would not be anticipated from the temperature structure at GME; greater water transparency may contribute to this but no light data are available.

Midwater depths >2000m have been little sampled in the past and few discrete depth data are available. Nevertheless, the GME results are consistent with those obtained at two other Discovery Stations (9541, 20°N, 21° 30'W; 9801, 42°N, 17°W), fished to at least 4000m depth, where the fauna below 2700-3000m was also extremely depauperate (IOS unpublished data).

21. MIDWATER MISCELLANEA

Tunicata

Tunicates were represented at GME by the three thaliacean orders Salpida, Doliolida and Pyrosomatida, and by appendicularians (Tables 6.70-81). None were identified to species but the large Pyrosoma colonies were presumably P. atlanticum (Van Soest, 1981).

The small salps, doliolids and appendicularians were relatively numerous in the upper part of the water column. However, their fragility, coupled with their tendancy to stick to other animals and thereby become damaged during sample processing, make accurate counting impossible. Buckmann and Kapp (1973) found that appendicularians were common in the upper 100m in the GME area.

All these animals are gelatinous, and their importance in the present context is their relatively high volume and wet weight. They therefore contribute significantly to the biomass profiles (Section 6). This is particularly true for the large Pyrosoma colonies (Table 6.72-73) which dominated the midwater biomass although the numbers of colonies were not particularly high. The small Pyrosoma (Table 6.70-71) may be juvenile colonies of P. atlanticum or they may be a different species.

22. BENTHIC BIOMASS AND TOTAL NUMBERS M.H. Thurston

Extensive collecting in the deep sea began over one hundred years ago (Thomson, 1873), but it is less than forty years since the first attempts at quantitative sampling were made (Zenkevitch, 1961,1969; Spärck, 1951, 1956). Currently rates of processes are perceived as being central to many problems in deep-sea biology. However, the elucidation of such rates must be preceded by determination of biomass, an understanding of the role played by the various size components of that biomass together with the factors which control them.

Rowe(1983b) and Thiel(1983b) have summarized the various interpretations in terms of size of the megafauna, macrofauna, meiofauna and nanobiota. Usually, megafauna is defined as comprising those organisms visible on the seafloor in deep-sea photographs (Barham et al., 1967) or retained in trawls (Haedrich and Rowe, 1977). Both definitions are open to considerable latitude. The upper size limit of the macrobenthos corresponds with the lower limit of the megabenthos. In some macrofaunal studies based on box core samples, larger animals, which occur at densities so low that they would be sampled inadequately, have been regarded as megafauna. The mesh size used as the lower limit for the macrofauna has varied from 1.75mm (not stated by Spärck (1956), but presumed by Jumars and Hessler (1976)) down to 120μm (Paul and Menzies, 1974). Most workers have used 500μm, 420μm, 297μm or 250μm, with the size chosen tending to decrease with time due to a growing appreciation of how small traditionally macrofaunal taxa can be in the deep sea. Thiel(1983b) fixed the meiofaunal size limits as 42-1000μm which corresponded well with a maximum nanofaunal size of 40μm (Burnett, 1977). Although the smallest species in traditionally macrofaunal phyla may be orders of magnitude smaller than the largest species of 'meiofaunal' phyla, macrofauna and meiofauna do have a factual basis (Schwinghamer, 1981, 1985; Warwick, 1984). It is possible, though as yet untested, that the megafauna may also be a distinct unit within the benthos (IOS observations).

Studies of the megafauna in the deep sea have been undertaken using trawls and, more recently, by photographic or visual surveys using towed gear or submersibles (Grassle et al., 1975; Dahl et al., 1976; Haedrich and Rowe, 1977; Haedrich et al., 1980; Rowe et al., 1982; Rice et al., 1982; Ohta, 1983; Smith and Hamilton, 1983; Sibuet _et al_., 1984; Sibuet and Segonzac, 1985; Lampitt _et al_., 1986). Comparisons are difficult due to differences in methodology (Haedrich _et al_., 1975) and geographical area (Lampitt _et al_., 1986). General tendencies observed include a more or less rapid decrease in biomass with increasing depth (Ohta, 1983; Lampitt _et al_., 1986) and a diversity maximum at 1500-2000m (Haedrich _et al_., 1980).

The larger macrobenthic organisms are relatively rare, and can be sampled adequately only by towed gear, but the smaller macrobenthos is sampled best with coring devices. Coring devices can be regarded as quantitative in nature, whereas towed gear is at best only semiquantitative. Rowe (1983b) analysed data from over 700 quantitative samples collected worldwide to provide data on the relationship between macrobenthic biomass and depth. An exponential decrease in biomass relative to depth was found to extend from the continental shelf to abyssal depths, but that trenches were richer than would be expected from such a relationship. Higher biomass in trenches has been attributed to increased food availability due to accumulation of sediment from adjacent continental margins (Belyaev, 1966; Rowe, 1983b). Higher biomass in higher latitudes results from relatively poor coupling between primary productivity and pelagic consumption in high latitudes (Vinogradov and Tseitlin, 1983). Although some of the wide scatter of biomass values plotted by Rowe (1983b, Fig. 7) can be explained by regional and latitudinal differences, some must be due to varying sampling techniques and precise size limits used by various authors.

Outside circumstances prevented sampling of benthic communities with gear other than otter trawl and epibenthic sledge. As a consequence densities and biomass of megafaunal and larger macrofaunal organisms have been obtained, but no information is available for smaller elements of the fauna. Descriptions of trawl and sledge, and of sample treatment have been given in Section 5. Six trawl hauls were made, but the results given here are based on four hauls only. Haul 43 has been discounted as there was some doubt as to what portion of the total time at depth was occupied by full bottom contact, and thus efficient sampling of the benthos. During haul 60 the net came fast on the bottom, and on recovery was found to be damaged. The extent of loss of catch could not be quantified.

There is some evidence to suggest that the fine mesh net of the sledge fished less efficiently than did the coarse nets, at least for some taxa. As a consequence, densities and biomass derived from the 1-4mm size fraction should be regarded as minimum values.

This discussion deals in general terms with invertebrates and fish. For more detail on some taxa, see Sections 25-30.

Megafaunal abundances based on trawl hauls were very low, but reasonably consistent (Table 22.1). Total abundances for all invertebrate taxa on the four hauls varied from 1.68 to 3.07 individuals/1000m^2 with a mean of 2.21. If fish are included the corresponding figures are 1.83-3.35, mean 2.47.

Asteroids formed the most abundant taxon in three of the four hauls, and overall achieved an abundance of 1.36/1000m^3, 62% of all organisms. Natantian decapods ranked second in abundance with values in the range 0.30-1.33/1000m^2 (mean 0.66/1000m^2, 30%). Of the remaining taxa represented, only holothurians, bivalves and gastropods contributed more than 1% of the total numbers.

Megafaunal abundances as determined by the >4mm catches of the sledge were higher than those derived from trawl catches (Table 22.2). This difference in abundances was due largely to the difference in mesh size of the two gears. The mean abundances (individuals/1000m^3) for all taxa was 17.84, with bivalves (5.53, 31%), natantian decapods (5.04, 28%) and asteroids (3.60, 20%) together accounting for 79% of the total. Each other taxon contributed less than 10% of the total.

In the 1-4mm fraction (Table 22.3), abundances were an order of magnitude higher than in the >4mm fraction (187.67 individuals/1000m^3). Major contributions to this total were made by bivalves (111.61, 59%) and asteroids (46.22, 25%) with a subsidiary contribution of 15.70 (8%) by gastropods.

Biomass determinations have been based on preserved wet weight, and therefore take no account of calcareous inclusions such as shells and skeletal elements. Total biomass estimates of invertebrates from the four trawl hauls (Table 22.4) ranged from 8.44 - 18.64g/1000m^2 with a mean of 12.58g/1000m^2. Asteroids

(6.27g/1000m², 50%) and natantian decapods (4.76g/1000m², 38%) dominated catches with cephalopods (0.65g/1000m², 5%) and holothurians (0.58g/1000m², 5%) of lesser importance. All other taxa were insignificant, individually not exceeding 0.1g/1000m², and collectively representing only 2% of the total biomass. Because of their large individual size, fish have a much greater effect on overall biomass figures than they do on densities. If fish are included then total biomass estimates from the four trawls fell within the range 16.39 - 70.64g/1000m² with a mean of 38.08g/1000m². The mean fish biomass was 25.5g/1000m², and proportions of the total catch were fish, 67%; asteroids, 16%; decapods, 12%; cephalopods, 2%; and holothurians, 2%.

Biomass in the >4mm catches from the sledge (Table 22.5) varied from 11.51 to 21.96g/1000m² (average 16.12g/1000m²). The major contribution to this total came from asteroids (9.65g/1000m², 60%) with smaller but significant amounts attributable to bivalves (2.13g/1000m², 13%), natantian decapods (1.98g/1000m², 12%), galatheid decapods belonging to Munidopsis (0.89g/1000m², 6%) and holothurians (0.83g/1000m², 5%).

Biomass in the 1-4mm fraction (Table 22.6) varied from 0.53 to 2.57g/1000m² and averaged 1.62g/1000m². This average is just one-tenth of that for the >4mm fraction. The numerous small bivalves found in the fine fraction resulted in this group dominating the biomass figures (1.18g/1000m², 73%). Gastropods (0.11g/1000m², 7%), asteroids (0.10g/1000m², 6%) and annelids (0.07g/1000m², 4%) made minor contributions, with all other groups totalling 0.16g/1000m² (10%).

Previous attempts at semiquantitative sampling of the megabenthos on the Madeira Abyssal Plain, the location of the GME area, are limited to the investigations of Monniot and Segonzac (1985) who worked two stations northeast of the GME area during Campagne Abyplaine. Although they used a beam trawl and a modified Sanders-Hessler epibenthic sledge and sieved catches down to 1mm and 0.5mm respectively, their results are comparable, to some extent, with those presented here. Beam trawl samples gave animal abundances of 19.0 and 11.0 individuals/1000m² at the northerly station and 3.5 and 2.3 individuals/1000m² at the southerly station. These figures are in good agreement with the GME data (1.68-3.07 individuals/1000m²) when differences in gear characteristics and sieving regime are taken into account. The two Abyplaine stations differed not only in animal abundances, but also in the proportions of the various taxonomic groups constituting the fauna. At the northern station, bivalves were the most important group (40%) with brachiopods (12%) and fish (9%) in significant proportions. In contrast, at the southern station natantian decapods (30%) were most abundant, followed by fish (17%), actiniarians and zoanthideans (15%) and ophiuroids (10%). Fish, asteroids and natantian decapods dominated at GME. The two Abyplaine sledge samples gave abundances of 241 and 351 individuals/1000m^2. Comparable figures for the IOS sledge samples at GME were 470, 185, 130 and 37 individuals/1000m^2. Again, agreement is good when gear and sieving differences have been taken into acocunt. The Abyplaine samples were dominated by bivalves (72%), with crustaceans, mainly peracarids forming 10% and polychaetes 8%. GME sledge samples contained mainly bivalves (57%). The differences between the two sets of samples is attributable to the differing sieving regime and an undersampling of the small mobile fauna by the IOS sledge.

Megafaunal abundance estimates at abyssal depths in the Atlantic Ocean are sparse. Sibuet et al., (1984) worked two stations on the Demerara Abyssal Plain at depths of 4420m and 4850m. At the deeper station a density of 10.6 individuals/1000m^2 was found, whereas at the shallower station, nearer to the Amazon Cone and therefore with a greater nutrient input, the figure was 24.6 individuals/1000m^2. These figures are higher than those from GME. The difference is partly real and due to shallower depths and higher nutrient input, and partly an artefact of sample treatment. Megafaunal abundances at 4700m and 4500m in the Bay of Biscay (Laubier and Sibuet, 1979) were 30 and 43 individuals/1000m^2. The gear and sample treatment used were the same as those of Sibuet et al., (1984) so the same constraints apply in any comparison with the GME results. More comparable with the GME data are the figures obtained by Rutgers van der Loeff and Lavaleye (1986) from collections made at the NEA Dumpsite (46°N, 17°W). They found a mean abundance of 4.25 individuals/1000m^2, not very different from the GME figure. Haedrich et al., (1980) studied megafaunal numbers from the shelf to the abyss in the northwest Atlantic. Faunal zones were identified, and in the deepest zone, the lower continental rise and abyss (3900-5000m), the abundance of decapods and echinoderms was about 7 individuals/1000m^2. Megabenthic abundances at GME, based on decapods and echinoderms alone was 2.12 individuals/1000m^2. The disparity between these figures is likely to be related to the proximity or otherwise of sampling site to continental slope.

Megafaunal biomass values for the deep ocean are even more sparse than figures for density. On the Demerara Abyssal Plain, Sibuet et al., (1984) found biomass values of 160.6 and 45.7g/1000m². The constraints which governed the intercomparison of density figures applies equally to biomass data. At the first station, the biomass was dominated by holothurians (87.0g/1000m², 54% of total biomass), asteroids (35.3g/1000m², 22%) and echinoids (18.0g/1000m², 11%) with fish (5.0g/1000m²) forming just 3%. At the deeper, more offshore station holothurians (12.9g/1000m², 28%), cephalopods (10.0g/1000m², 22%) and fish (9.5g/1000m², 21%) were the most abundant organisms. In neither case is the faunal composition similar to that at GME. Megafaunal biomass at the NEA Dumpsite was 92.9g/1000m² (Rutgers van der Loeff and Lavaleye, 1986) and was dominated by holothurians (51.34g/1000m², 55%), cnidarians, probably largely zoanthideans (19.12g/1000m², 21%) and fish (11.55g/1000m², 12%). Haedrich et al., (1980) found a megafaunal biomass of 59.1g/1000m², comprising mainly fish (34.0g/1000m², 57%), decapods (15.1g/1000m², 26%) and echinoderms (6.9g/1000m², 12%). The dominance of fish in the study of Haedrich et al., (1980) parallels the situation found at GME. It is probable that some, at least, of the disparity between these two data sets and those of Sibuet et al., (1984) and Rutgers van der Loeff and Lavaleye (1986) is not real. The first two sets of results were derived from otter trawl catches, whereas the others came from samples taken with a beam trawl. Otter trawls have a greater effective catching width (c. 8m) and height (c. 2m) and are towed faster (0.75-1.25m/sec) than are beam trawls (0.5-1.0m/sec) which have mouth dimensions approximating to 3.5-6m by 0.8m. Thus otter trawls will be more efficient catchers of fish, but perhaps less effective in sampling the invertebrates.

From the samples available it is not possible to provide an accurate estimate of macrofaunal biomass at GME which would be strictly comparable with estimates from elsewhere. A figure which is thought to be as nearly representative as possible can be obtained by subtracting the value of invertebrate megafaunal biomass obtained from the trawl (12.58g/1000m²) from the sum of the biomass values for both size fractions of sledge catches (17.74g/1000m²). The resultant figure, 5.16g/1000m², will be an underestimate as macrofaunal organisms passing through a 1mm mesh have not been taken into account. However, this figure agrees with the value of 5g/1000m^2 derived from grab samples from the southern part of the Madeira Abyssal Plain (Kuznetsov, 1960).

Because grabs and corers cover a small area but penetrate deeply, and sledges cover a large area but skim the surface only, both types of gear will underestimate the true biomass. Grabs and corers will miss the larger and rarer organisms, whereas sledges will miss those which burrow more than a few centimetres into the sediment. Large echiuran worms produce characteristic star-shaped feeding traces on the sediment surface around the mouths of their burrows (Ohta, 1984; Huggett, in press, unpublished observations). Photographic records have indicated that echiurans are an important element of the macrofauna/megafauna at GME (Section 23), but net catches suggest a low density and biomass. Clearly corer catches and sledge catches are not likely to show close agreement in terms of taxonomic constitution of sampled communities. However, the disparity between these types of gear may be less pronounced in terms of overall biomass. The analysis by Rowe (1983) of most published data on macrofaunal biomass gives a picture against which to set the GME data, despite the latter being derived from sledge samples. At a depth of 5440m, macrofaunal biomass would be about 10-20g/1000m^2. As the GME estimate is a minimum, macrofaunal biomass there would appear to be somewhat below the average value for the depth. This result is to be expected, as the GME site is far from continental influences, whereas many of the data utilized by Rowe have come from transects down the slope and across the continental rise.

In general, feeding strategies of abyssal organisms have been determined by analogy with shallow-water organisms rather than direct observation. Within the context of the GME collections, it is possible to assign those taxa identified in Tables 22.1-6 into broad categories such as sestonivores, detritivores and carnivores. The proportion of each feeding type, in terms of abundance and biomass, for trawl and sledge samples is shown in Table 22.7. Detritivores, those animals feeding on the organic material on the sediment surface or incorporated into subsurface layers, dominated catches whether measured by abundance or by biomass. Carnivores were important in the larger size fractions, particularly in trawl catches where they accounted for 81% of the biomass. This reflects the selectivity of the trawl and the large individual mean size of fish relative to most invertebrates. Sestonivores were unimportant in all size fractions. Sokolova (1968, 1976, 1981) has shown that the ratio of detritivores to sestonivores in the deep sea is related to organic input to the near bottom layers and thus to surface production. Detritivore dominance is associated with eutrophic conditions in peripheral, equatorial and high latitude areas of the deep sea, while sestonivores form the major part of the macro- and megafaunal biomass in subtropical central area. The correlation between primary productivity and the detritivore/sestonivore ratio is not exact throughout all oceans. The amount of material reaching the seafloor is affected by seasonality or otherwise of surface production, and may be enhanced by terriginous inputs. However, in the GME area, the correlation does exist. Koblentz-Mishke et al (1970) show the GME area to be in an area where surface production was of the order of 100-150mgC/m^2/day. This value is likely to be an underestimate as measurements made during Discovery Cruise 156 to GME gave a mean value of 227 mgC/m^2/day (Roe et al., 1986). For sledge catches as a whole, detritivores formed 89% of the biomass whereas sestonivores formed only 1%.

In common with other ocean areas far from the continental slope and the nutrient inputs associated with the slope, the GME area has a very low biomass. Although potential biological transport mechanisms have been identified among isopods (Section 26), amphipods (Section 27), holothurians (Section 29) and gastropods (Section 30.2), their overall significance must be neglible relative to physically moderated mechanisms.

23. BENTHIC TRANSECT PHOTOGRAPHY A.L. Rice

Transect photography using the IOS underwater camera system (Rice, Aldred, Darlington and Wild, 1982; Lampitt, Rice and Thurston, 1984) was attempted on the four epibenthic sledge hauls obtained in the GME area. However, a switching fault resulted in no benthic photographs being obtained from one haul while a focussing problem produced poor resolution photographs on a second haul. Consequently, a total of 544 usable frames were obtained from the turbidites of the abyssal plain in association with epibenthic sledge catches. In addition, a photosledge transect, without an associated benthic sample, was undertaken on the abyssal hill to the north of the main sampling area (11262#20). This transect was primarily undertaken to examine the distribution of manganese nodules located during Discovery Cruise 134 in 1983 (Huggett and Somers, in press), but nodules were apparent only in the first few frames of the transect (Fig. 23.I) and the remaining photographs were from the pelagic sediment above the nodule field. A total of 274 usable frames were obtained during this transect (Table 23.1).

Results

Each usable frame was examined for evidence of megabenthic organisms, including some tracks, trails and burrows (lebensspuren), and the results are summarised in Tables 23.2 and 3.

Epibenthic animals

Recognisable epibenthic animals were rare in the photographs, so rare in fact that density estimates based on them must be treated with considerable caution. Nevertheless, in general the phototransects confirm the low abundances indicated by the trawl and sledge catches. Thus, the mean density of organisms calculated from the photographs taken during the two abyssal plain epibenthic hauls was $18.3/10^3m^2$ (20 animals - Table 23.2 in $1088m^2$ Table 23.3.) compared with a mean of $2.2/10^3m^2$ (range 0.18-3.06) from the OTSB hauls and $17.8/10^3m^2$ (range 6.3-47.4) from the >4mm fractions of the epibenthic sledge catches (Tables 22.1-2). The two data sets are not strictly comparable since while the photographs record only those animals living on the surface of the sediment (the epifauna), both the sledge and trawl also sample animals living buried or burrowed within the sediments (the infauna). On the other hand, towed gears, and particularly trawls, are notoriously inefficient at obtaining quantitative samples of both the sessile and mobile fauna (see Rice, Aldred, Billett and Thurston, 1979; Rice et al, 1982) and the discrepancy between the photographs and OTSB estimated densities could easily be explained by this. Moreover, since the trawl hauls and photographs were taken at different localities, the two sets of results could also reflect the horizontal variations in the benthic fauna.

However, the apparent close agreement between the photograph and epibenthic sledge estimates is also questionable. First, the epibenthic sledge mean density is strongly influenced by data from haul 11262#15 during which no photographs were taken but from which the catches indicated a rather high numerical abundance ($47.4/10^3m^2$, Table 22.2). When the mean photograph density is compared only with the catch densities from the two hauls during which the photographs were taken a much less close agreement is found ($18.4/10^3m^2$ compared with only $6.3/10^3m^2$ for 11262#16 and $6.8/10^3m^2$ for 11262#19). Moreover, the sledge estimates include several groups of organisms which were not seen in any of the photographs, presumably either because they were so small or because they were generally buried. If these taxa are omitted, essentially leaving only the coelenterates and echinoderms, the sledge estimates are reduced to $2.8/10^3m^2$ for #16 and $3.4/10^3m^2$ for #19, thus showing even less agreement with the photograph densities. As for the OTSB catches, the discrepancies between these density estimates could reflect the catching inefficiency of the sledge. This is certainly possible in the case of the pennatulids which are known to be poorly collected by trawls and dredges (Rice, Patterson and Taylor, in prep.). On the other hand, it is less easy to explain the higher densities of asteroids estimated from the photographs than from the catches since the dominant star-fish in the GME region, Hyphalaster inermis, is presumed to spend much of its time beneath the sediment surface and should therefore be collected more consistently than it is photographed (see Section 28). However, the number asteroids, like the other megabenthic groups, recorded on the photographs is so small that little reliance can be placed on the resulting density estimates.

In the absence of a simultaneously obtained sample, the results of the photosledge transect on the abyssal hill (11262#20) can be compared only with the photographic results from the abyssal plain transects. The total density of megabenthic organisms calculated from #20 ($18/10^3m^2$) was very similar to that obtained from the other transects, though the organisms recorded were quite different. Thus, the pelagic sediment photographs were dominated by the echinoid Plesiodiadema microtuberculatum (Fig. 23.IV) which was rare in the abyssal plain photographs, whereas no asteroids were seen on the abyssal hill transect.

Animal traces (Lebensspuren)

As is typical of abyssal benthic photographs (see Heezen and Hollister, 1971; Young et al, 1985), traces of animal activity were far more common in the GME photographs than were epibenthic animals. These traces include a wide variety of well or poorly defined mounds and depressions, circular, meandering or relatively straight grooves and ridges, and pits or holes in the sediment surface occurring either in association with these other features or independent of them (Figs 23.II-V). A very similar range of features has been encountered in other bathyal and abyssal situations (see, for instance, Mauviel and Sibuet, 1985; Young et al, 1985).

In the GME sledge transect photographs three types of "sedentary" traces were particularly abundant and are considered here.

1. Conical mounds up to about 10-15cm in diameter and 3-5cm high with a single apical opening (Figs 23.III, 28.II) tentatively attributed to the holothurian Molpadia blakei. These mounds were encountered at roughly equal abundances on the turbidites and pelagic sediment, occurring at about one mound per $100m^2$ (see also Section 28).

2. Spoke burrows consisting of a series of linear marks radiating from a single central burrow opening, the whole system covering a roughly circular area up to about 80cm in diameter (Figs 23.II, III). Such traces have in the past been identified as the feeding traces of echiuran worms (Ohta, 1984; Lampitt et al, 1984), or possibly also of pelecypods, sipunculans and polychaetes (Young et al, 1985). These traces were fairly common in the two turbidite phototransects, occurring at a density of $40\text{-}50/10^3m^2$, but were three to four times as abundant on the pelagic sediment transect (Table 23.3.).

3. Circular grooves, up to about 8cm in diameter, each surrounding a low mound with a central hole through which a straight or curved tube projects in many cases (Figs 23.III, IV). Similar features have been reported from other abyssal localities (Heezen and Hollister, 1971; Ewing and Davis, 1967) and have recently been tentatively attributed to the activity of oweniid polychaete worms of the genus *Myriochele* (Young *et al*, 1985). In the GME transects they occurred in densities of about $30/10^3m^2$ on the turbidites and about $70/10^3m^2$ on the pelagic sediment.

Huggett (in press) reported on a major photographic survey in the GME area using the WASP (Wide Angle Survey Photography) system and obtained rather different results from those presented here.

In addition to the trails of mobile organisms, Huggett recorded three types of spoke burrow distinguished on the basis of size. His largest category, more than 200cm in diameter, were not encountered at all on the pelagic sediments and were very rare on the turbidites, occurring at a density of only $0.033/10^3m^2$. Since the two turbidite photosledge transects together covered an area of only about $1100m^2$ it is not surprising that no traces of this size were recorded and, in any case, they would probably be difficult to recognise on photographs with an individual areal coverage of only $2m^2$ (the WASP photographs each covered an average of $80m^2$).

Huggett's middle-sized category, 40-200cm in diameter, were recorded more or less equally frequently on the pelagic and turbidite sediments, but again at densities of $<1/10^3m^2$. The smallest category (<40cm in diameter), however, were much more abundant on the turbidites ($c30/10^3m^2$), but were virtually absent from the pelagic sediments.

The WASP results are clearly at variance with those obtained from the sledge photographs, even allowing for size discrepancies between the two techniques and for the possibility that Huggett included ?*Molpadia* mounds and ?*Myriochele* burrows in his small spoke burrow category. Thus, traces of sedentary animals were consistently recorded more frequently on the pelagic sediments in the sledge photographs and on the turbidites in the WASP survey.

Huggett's results tend to agree with those of Young et al (1985) from the Venezuela Basin since these authors also reported relatively fewer "sedentary" traces and more "mobile" traces on pelagic sediments than on turbidites. Young et al attributed these differences to differences in food availability on the two types of sediment, reporting a lower mean organic carbon content (0.33%) for the surface layers of the pelagic sediments than for the turbidites (0.80%). A similar, but less dramatic, difference in organic carbon content was encountered in the two sediment types at the GME (0.15% for the pelagic sediments and 0.25% for the turbidites (Huggett, in press)). A more detailed examination of the lebensspuren in the transect photographs is currently in progress in order to investigate the above discrepancies further.

24. TIME LAPSE PHOTOGRAPHY R.S. Lampitt

Introduction

Bathysnap is a time lapse camera and current meter instrument. It is deployed free fall and after a period of up to a year it is recovered on acoustic command from the ship. Photographs are taken of a $2m^2$ patch of seabed at a preset time interval (4-512 mins) up to a maximum of 800 exposures.

Information is obtained on rates of change to the sediment topography both on a small scale (1-5cm) and on a large scale such as deposition of detritus which may cover up most of the small scale features. Information is also obtained about the behaviour of any epibenthic organisms which may enter the field of view and all these observations are related to the ambient hydrographic conditions.

The object of the work reported here was to examine temporal changes in the benthic environment while the other benthic sampling or photographic techniques assess spatial variability and absolute levels of abundance and biomass. It is important to determine if GME differs substantially from other deep-sea sites and if so, to evaluate the significance of such differences.

Method

A bathysnap module (Lampitt and Burnham, 1983) was deployed on 19.7.85 (Day 200) at the centre of the 10km box at GME. Photographs were taken of $2m^2$ of seabed every 512 minutes for 123 days after which the instrument was recovered. The current meter (Aanderaa RCM5) recorded current speed, direction and temperature every 60 minutes. A second Bathysnap was deployed on 21.7.85 but unfortunately was not recovered, and a third deployed on 20.11.85 and recovered on 5.11.86 was unsuccessful due to a camera fault.

Results and Discussion

The area of seabed photographed was of similar appearance to the majority of the benthic photos taken by the epibenthic sledge (Section 23) and so may be considered typical of the area. The camera was pointing due south. Figure 24.I

shows the first and last frames taken during the deployment (Nos 7 and 343) and these have been compared to estimate the extent to which the surface topography has been modified during the 4 month deployment. There were three disturbances in the size range 5-10cm, eleven in the range 1-5cm and many more of smaller size. This reflects the expected size distribution of the benthic community with increasing numbers of specimens in smaller size categories. Disturbances >1cm occurred therefore at a rate of $21/m^2/yr$ and these are identified on Figure 24.I.

There is a very great difference between this site and those on the continental slope southwest of Ireland, the Porcupine Seabight an area which has been examined in some detail. In this shallower environment the kinds of changes occurring at GME in 4 months take only about 10 days but the scale of the perturbations also tends to be greater such that small changes are rapidly modified by larger ones. The simple explanation for this is that there are very many more megafauna on the continental slope than on the abyssal plain (Section 22) and they tend to be larger (Lampitt et al, 1986). It is difficult to compare results from GME with ones at the base of the slope off Ireland (ca. 4000m) because at these sites phytodetritus deposition occurred early in the deployment. At one station (51720#7) there were 6 weeks prior to deposition during which there were 8 disturbances >1cm giving a rate of $35/m^2/yr$, a value close to that at GME. There is also a close similarity between results at GME and those reported for the central north Pacific (Thorndike et al, 1982) where several deployments showed seabed changes (>1cm) occurring at a rate of about $26/m^2/yr$.

Although this similarity between GME and other areas is gratifying, the changes noted at GME may, however, be higher than normal because of an unusual carrion deposition. On day 246, a decaying specimen tentatively identified as a tunicate arrived in the field of view. The body was 17cm long and 3-4cm wide and it seems most likely to be of the genus Pyrosoma considering the dominance of such specimens in the surface plankton. It stayed in the field of view drifting with the nearbed currents (Fig. 24.II) for 16 days during which it was fed upon at least twice by the squat lobster Munidopsis sp (2 cm carapace width) and at least once by the asteroid Hyphalaster inermis (3cm radius) (Fig. 24.III). Both of these specimens fed on the carcass and then buried themselves in the sediment, the squat lobster for only a short period but the asteroid for

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present in one photograph was clearly responsible for a large number of 5mm depressions in the seabed presumably in its search for food. It was considerably larger at 8cm body length than the other specimen of the genus which ate the *Pyrosoma* sp. The specimens cannot be identified to species level. The second arrival was the echinoid *Plesiodiadema microtuberculatum* of test diameter 2.5cm which was present in only one frame on day 252. This species has very long spines (5cm) and left no impressions on the sediment surface. The third arrival was on day 263 when one photograph showed a 13cm long unidentified organism. It left no mark on the seabed and seemed to be devoid of body structure.

Conclusion

From a single bathysnap deployment over only 4 months of the year, it is possible to make a few general observations.

1. Changes to the seabed topography >1cm occur at a very similar rate to that reported in the Central North Pacific and noted at the base of the continental slope off SW Ireland.

2. Water current did not appear to alter the seabed topography in any way.

3. When dead the planktonic tunicate *Pyrosoma* may be a significant source of organic material to the deep sea floor and on arrival it attracts megafauna.

4. It is not possible to determine if there is a seasonal supply of phytodetritus to the seafloor as has been found off SW Ireland (Billett *et al*, 1983; Lampitt, 1985) as there was insufficient temporal coverage. Seasonal trends in primary production in the Sargasso (Menzel and Ryther, 1961) and sediment trap data from GME (Lampitt, in prep.) suggest that deposition of detritus would be most apparent in the first half of the year.

25. RHIZOPODA

A.J. Gooday

Introduction

The rhizopods dealt with in this section comprise two groups, the foraminiferans and the xenophyophores. These testate (shelled) protozoans may attain a considerable size (several cm) in deep-sea environments. Their study involves several difficulties, notably fragmentation of the often delicate tests (a particular problem in epibenthic sledge samples), the need to distinguish live from dead specimens, and the presence of numerous undescribed taxa (Gooday, 1983a). However, despite these problems, the abundance and diversity of rhizopods in many deep-sea environments (Tendal and Hessler, 1977; Bernstein et al., 1978; Snider et al., 1984; Gooday, 1986c) makes their evaluation necessary and rewarding.

Methods

All complete and fragmentary rhizopod tests were extracted from the epibenthic and suprabenthic residues and sorted into putative species. In order to determine which were alive when captured, the tests were inspected for protoplasmic contents, Rose Bengal being used to stain the protoplasm where appropriate. Species with opaque walls (miliolinids, multichambered agglutinated forms, some spherical astrorhizaceans) had to be broken open in order to view the interior clearly. However, the taxonomic value of the specimens precluded their wholesale destruction and hence the live : dead ratios for these opaque species were estimated from subsamples.

Komokiacean foraminiferans pose special problems because the sparcity of their protoplasm makes routine discrimination between live and dead specimens difficult. Following the experience of Tendal and Hessler (1977) and Gooday (1986c) all komokiaceans were regarded as living, although this may lead to a slight overestimate of their actual numerical importance.

Results

A total of 78 morphologically distinct entities, hereafter referred to as species, have been recognised in the benthic and suprabenthic catches taken at station 11262 (Tables 25.1-2). The two nets sampled somewhat different elements of the fauna and hence are considered separately.

(I) Epibenthic net The total number of complete specimens extracted from the samples is 1666, 58.9% of which were alive; the corresponding figure for fragmentary specimens is 351, 71.5% of them living (Table 25.3). Sixty species occur alive and a further ten are represented only by dead tests (Table 25.4). The living rhizopods are dominated by komokiaceans which include 75% of specimens and 21 out of the 60 species (Table 25.5). Two other fairly important groups are the sphaerical ammodiscaceans (mainly *Crithionina*-like forms) and the miliolinids. The dead assemblage is dominated by miliolinids (Table 25.6). Some 28% of specimens of one komokiacean species, *Lana* sp 3, are intergrown with colonies of the ctenostome bryozoan *Nolella*. The bryozoans are suspension feeders and their presence indicates an epifaunal mode of life for the komokiaceans associated with them.

(II) Suprabenthic net The sample obtained during haul 17 consisted mainly of crustacean fragments and fish scales. The remaining three catches were more productive, yielding large numbers of smaller benthic foraminiferans and dead planktonic foraminiferan shells. This material must have originated from sediment resuspended by the sledge. Although the suprabenthic net clearly did not sample benthic foraminiferans quantitatively, it is still of interest to establish the relative proportions of the species and higher taxa present in the catch. All live and dead specimens therefore were sorted completely from subsamples of the residues. In addition, soft-walled species (komokiaceans, "tectinous chains", allogromiids) were extracted more or less completely from the light fractions in which they tend to accumulate. However, it was not possible to remove some *Lana* species since these occur mainly as tangled fragments.

The relative abundances of the higher taxa are summarized in Table 25.5. Again, komokiaceans are important although less so than in the benthic catch. However, what is particularly striking is the abundance of multichambered agglutinated species (mainly lituolaceans) which make up about a third of the live assemblage. "Tectinous chains", rotaliids and lageniids are also more common than in the benthic samples and the latter two groups, both of which are calcareous, are important elements in the dead assemblage (Table 25.6). It is clear from these results that the suprabenthic net may provide a useful sample of the smaller species rarely retained by the coarser meshes of the benthic net.

Discussion

The larger foraminiferans occurring at GME are typical of abyssal, open ocean environments in the northeast Atlantic. Astrorhizacean genera such as Bathysiphon, Hyperammina, Pelosina, Rhabdammina and Saccorhiza, which are often abundant on the continental slope and rise (Gooday 1983a, 1983b, 1986a), are unrepresented, while the recently described komokiaceans (Tendal and Hessler, 1977) are a dominant element. The latter taxon, is represented by some 23 species at GME, compared with the total of 32 species recognised in IOS samples from other parts of the northeast Atlantic (Gooday, 1983a). The high komokiacean diversity is consistent with previous observations that this group is most abundant and diverse on abyssal plains (Tendal and Hessler, 1977; Schröder, 1986). The genera occurring at GME include Baculella, Ipoa, Komokia, Normanina and Septuma, all of which are typical abyssal komokiaceans. They are also found at IOS Stations 9128 (5726-6059m) and 9129 (5590m).

The association between the komokiacean Lana and the bryozoan Nolella is widespread in the northeast Atlantic (Gooday and Cook, 1984). The GME record allows a downward extension of its bathymetric range from 4850m to 5440m. Two other soft-walled groups, the allogromiids and "tectinous chains", are also fairly abundant and diverse. Like the komokiaceans, these foraminiferans have been largely overlooked in the deep-sea (Gooday, 1983a, 1986b, 1986c), although the "tectinous chains", in particular, are sometimes common in IOS epibenthic sledge samples (Gooday, 1983a).

Notable elements among the smaller, hard-walled foraminiferans retained by the suprabenthic net are multichambered agglutinated forms, mainly lituolaceans, and calcareous species belonging to the suborders Rotaliida and Lageniida. All three groups are virtually unrepresented in the epibenthic catches. These are familiar taxa which, unlike some soft-walled forms, are instantly recognisable as foraminiferans and have been widely reported in the deep-sea literature. All the species identified at station 11262 have been recorded previously from comparable depths in the North Atlantic (Brady, 1884; Cushman, 1918-1931; Schott, 1935; Marie, 1946; Phleger *et al.*, 1953, Stackelberg *et al.*, 1976;

Lutze, 1980; Haake, 1980, Levy et al., 1982; Larsen, 1982; Lutze and Coulbourne, 1984; Schröder, 1986).

Xenophyophores are scarce in the GME samples, being restricted to occasional fragments of Aschemonella, a genus who xenophyophore affinities were recognised only recently (Gooday and Nott, 1982). These giant rhizopods seem to be more common along the continental margin of northwest Africa than in more oceanic environments (Tendal and Gooday, 1981; Gooday and Tendal, in press). However, in other abyssal parts of the northeast Atlantic xenophyophores have been seen in bottom photographs (e.g. Stations 9128, 9129, 5590-6059m) or box cores (BIOTRANS, 4500m) but are not represented in epibenthic sledge catches, probably because this is too brutal a gear for such fragile organisms. Hence it is possible that delicate species, such as the widely distributed Reticulammina labyrinthica Tendal, 1972, occur at the GME site but have not yet been recovered in a recognisable form.

26. **ISOPODA** M.H. Thurston

This section should be read in conjunction with that on pelagic isopods (Section 14) as many of the remarks made there are pertinent to the present note.

Surprisingly, isopods were not found in the main nets of the sledge but were present in the suprabenthic net. In all, 143 individuals belonging to 17 species were obtained. Of this total, 66 specimens and six species were parasellotes and 77 specimens in eleven species were cryptoniscin larvae of the parasitic group Epicaridea (Table 26.1).

The parasellotes were dominated numerically by *Acanthecope* cf. *galatheae*, a species found also in a near-bottom haul. Comments on the identity, distribution, bathymetry and food of this species have been included in Section 14. *A.* cf. *galatheae* belongs to the family Eurycopidae, one of the four families within the Parasellota in which the distal articles of paraeopods 5-7 are flattened, strongly setose, and modified for swimming. Two other eurycopid specimens were present, both belonging to the poorly known subfamily Bathyopsurinae. One specimen could be assigned to *Paropsurus*, but the other was too damaged for generic placement. The swimming ability, and the delicate, parchment-like nature of the integument which is characteristic of bathyopsurins is indicative of a demersal existnece (Wolff 1962). The four species in the subfamily are based on a total of about eleven specimens, all of which have been taken in benthic samples. Feeding habits - *Sargassum* in Bathyopsurus and omnivory in *Paropsurus* - also indicate an association with the bottom. It is probable therefore, that the bathyopsurins, in common with many other eurycopids, belong to the community of crustaceans observed by Wolff (1971) to be abundant within 1-2m of the deep-sea floor.

As in midwater catches, epicarid larvae were numerically dominant. All were members of the Cryptoniscina. As has been mentioned above (Section 14), the taxonomy of this group is chaotic, and no identifications have been possible. Points worthy of notice were the high diversity (eleven species), the distinct nature of the suprabenthic community (only two species common to near-bottom midwater and suprabenthic catches) and the dominance by Cryptoniscin C (74% of all epicarids). Cryptoniscin C was one of the two suprabenthic species found also in midwater samples. It has been speculated above, that this entity might parasitize one of the abyssopelagic decapods proven to have a wide bathymetric range.

Stomach contents from 23 of the fish taken in the trawl and sledge have been analysed. Isopods formed a major element in the diet of two of the fish species (*Echinomacrurus mollis* Roule, 1916 and *Abyssobrotula galatheae* Nielsen, 1977) and a minor component of a third (*Coryphaenoides (Chalinura) profundicola* (Nybelin, 1957)). *E. mollis* was an important component of the fish fauna at GME, and of the 14 specimens examined only one had an empty stomach. The remaining fish had fed mainly on isopods (Table 26.2) together with smaller numbers of copepods, amphipods, tanaids,mysids and polychaetes. All of the isopods taken were parasellotes and at least 13 species were present. The swimming families Eurycopidae and Munnopsidae accounted for 83% and 5% respectively of the total number of individuals. It is probable that the species in these families were a major component of the suprabenthic community (Wolff, 1971). The most abundant species, as in the suprabenthic catches, was *A*. cf. *galatheae*. The second-ranking species, *Betamorpha indentifrons*, was not found in any net sample. It has been recorded from depths of 2031-4980m throughout the Atlantic Ocean and in the Weddell Sea (Thistle and Hessler, 1977). *Syneurycope parallela*, the third most abundant species has been recorded only from 3474m in the northwest Atlantic (Menzies, 1962). *A*. cf. *galatheae* and *B. indentifrons* were the major prey species of the single *Abyssobrotula galatheae* examined. A single *B. indentifrons* was found in one of the five *C. (C.) profundicola* whose stomach contents were studied. This fish is a larger species than the others examined and individuals had been feeding mainly on near-bottom decapods.

Evidence for feeding habits in those species with swimming peraeopods, which are presumed to belong to the suprabenthic community, is fragmentary. Some appear to be detritivore/omnivores dependent on the water/sediment interface as a food source (Wolff, 1962). Even less is known about the food of species which lack paddle-like posterior peraeopods and therefore are confined more rigidly to the bottom. Some of these species utilize plant remains of various sorts for shelter and/or food (Wolff, 1976, 1979, 1980). Genera recorded in association with plant remains by Wolff and which were present in the GME collections included *Heteromesus* and *Macrostylis*.

There is a potential for horizontal transport of material by the isopods of the suprabenthic community. This potential may be modified by isopods serving as the main prey for some of the common demersal fish species. Isopods brood eggs until hatching and have no larval stage, so there is no additional transport potential such as is found in some other groups (see, for example, gastropods, Section 30.2).

27. AMPHIPODA M.H. Thurston

In common with the Isopoda, the Amphipoda are thought to be under-represented in catches taken with the fine mesh net of the epibenthic sledge. Amphipods were present, however, in the suprabenthic net (Table 27.1).

The suprabenthic net catches were dominated by lysianassoids (25%) and eusirids (59%). Six lysianassoid entities were taken. Cyclocaris sp. nov., Orchomene gerulicorbis Shulenberger and Barnard, 1976 and two species of Paralicella were caught also in deep midwater and near bottom hauls with the RMT multiple net system. All four species belong to the necrophage guild which is concentrated very close to the seafloor (Wolff, 1971; Thurston, 1979; Ingram and Hessler, 1983) but which extends a considerable distance up into the water column (Section 15). The two remaining lysianassoids were damaged, which precluded identification.

Leptophoxoides molaris Barnard, 1962 has been reported only from the type locality, the Cape Basin in the southeast Atlantic, at 4961m. The Phoxocephalidae are fossorial organisms, and L. molaris is, with the possible exception of the unidentified lysianassoids, the only infaunal amphipod taken. Some shallow water phoxocephalids are predators of meiofaunal taxa, others are detritivores, filter feeders or micrograzers (Bousfield, 1982), but L. molaris is an apomorphic species with highly modified mouthparts, so may rely on a different food source.

The Eusiridae is one of the dominant families in the deep sea, where, as here, it provides more species and individuals than any other. Typically, Cleonardo is a deep-sea genus, with species known from the benthos at abyssal or continental rise depths or from the bathy- and abyssopelagic realms. All four species in the present collections are undescribed. However, their presence has been noted in earlier IOS samples taken on and close to the bottom in depths of 3900-4500m on either side of the Cape Verde Rise, to the south of the GME area. Rhachotropis is a speciose genus with many representatives in the deep sea (Thurston, 1980), where it is more confined to benthic catches than Cleonardo. The genus has a wider distribution than Cleonardo in that species occur at shelf depths in cold temperate and polar waters in both hemispheres. Rhachotropis proxima Chevreux, 1911 was described from abyssal depths in the Bay of Biscay.

Due to an error in the original description recognized by Thurston (1980) this species has remained obscure. Extensive collections throughout much of the eastern North Atlantic have revealed entities close to Chevreux's concept. However, minor differences in morphology abound, and it is not clear whether a single rather variable species is represented, or a series of sibling species. The present material, although not in very good condition, appears to represent yet another variant on the theme. Single specimens of *Rhachotropis* cf. *proxima* and *Rhachotropis* sp. nov. B were found in two catches taken with the fine mesh nets of the epibenthic sledge, and were the only amphipods taken by these nets. Numbers of *Cleonardo* and *Rhachotropis* are long-legged, often relatively large species, many of which are members of the epibenthic fauna. They must contribute substantially to the concentrations of peracarids observed close above the sea bed by Wolff (1971). Such evidence as exists suggests that *Cleonardo* and *Rhachotropis* are predators on smaller epibenthic organisms (Bousfield, 1982). Individuals of two species of *Cleonardo* have been taken in baited traps on rare occasions (Chevreux, 1935) and so may be facultative necrophages. *Cleonardo* does not have a mandible structure of a type associated with necrophagy, however, so it is perhaps more likely that individuals were attracted to feed on small fragments of bait detached and dropped during feeding by fish and lysianassoid amphipods.

The stegocephalid *Evandania gigantea* (Stebbing, 1888) is a cosmopolitan abyssal pelagic species found between 1200 and 3500m (Barnard 1962). The species is not common, but is not confined to the pelagic realm, having been taken immediately above the bottom at GME and in epibenthic sledge hauls elsewhere (Thurston, unpublished observations). This species has been taken also in baited traps (Desbruyeres *et al*., 1985; unpublished observations) and may be a facultative necrophage. This mode of feeding would not be a feasible one in midwater. It is possible that medusae are preyed upon as appears to be the case in the shallower dwelling deep meso- and bathypelagic *Parandania boecki* (personal observations).

The pardaliscid species found in two samples were damaged, and therefore not identifiable.

Paragissa belongs to the small, poorly known family Hyperiopsidae, whose members are cosmopelagic, abyssal (Barnard, 1969). *Parargissa curticornis* Birstein and

Vinogradov, 1960 has been reported twice only, from the tropical West Pacific and Indian Oceans (Birstein and Vinogradov, 1960, 1964). It is not clear whether the minor differences between published material and that from the Atlantic Ocean are real or merely an artefact of illustrative procedures, and if real whether significant at the species level.

Organisms of the epibenthic fauna are vulnerable to predation by demersal fishes (see Sections 26, 29), and amphipods are no exception. Most of the demersal fish species taken at GME had been feeding to a greater or lesser extent on amphipods. Amphipods were less important than isopods in the food of *Echinomacrurus mollis* Roule, 1916, and were outnumbered 10 to 1 in stomach contents of this fish (Tables 26.2, 27.2). The amphipod species eaten by *E. mollis* agreed rather closely with the composition of suprabenthic net and near-bottom underwater catches (Tables 15.2.2, 15.2.4, 15.2.5), the only entity not found there being *Monoculodes* sp. This genus is an oedicerotid, and members of the family are epibenthic mainly, although fossorial tendencies are shown by most species (Bousfield, 1982; Sainte-Marie and Brunel, 1983, 1985). Specific identifications of amphipod material from three other fish species were made. Single specimens of *R.* cf. *proxima* were found in one specimen of *Abyssobrotula galatheae* Nielsen, 1977, and in one of six specimens of *Coryphaenoides (Chalinura) profundicola* (Nybelin, 1957). Most interestingly, the one specimen of *Barathrites iris* Zugmayer, 1911 examined contained single specimens of *Eurythenes gryllus*, *Paralicella tenuipes* and *Cyclocaris* sp. nov. All of these amphipod species are necrophages, and it is tempting to believe that the fish had been feeding at a food fall in the way that *Paraliparis bathybius* (Collett, 1879) has been shown to do (Lampitt *et al*., 1983).

As has been pointed out above (Section 15), gammarid amphipods, although not hugely abundant, are a potential source of horizontal and, more important, vertical transport of material from the seafloor up into the water column.

28. ECHINODERMATA

Ecology D.S.M. Billett

Introduction

The echinoderms include the sea-lilies (Crinoidea), sea-urchins (Echinoidea), sea-cucumbers (Holothurioidea), sea-stars (Asteroidea) and brittle stars (Ophiuroidea). All of these groups apart from the brittle stars were found in the benthic samples from GME. Echinoderms often dominate the benthic invertebrate megafauna at abyssal depths both in abundance and biomass (Zenkevitch, 1963; Haedrich, Rowe and Polloni, 1980; Sibuet, Monniot, Desbruyeres, Dinet, Khripounoff, Rowe and Segonzac, 1984; Sibuet, 1985; Lampitt, Billett and Rice, 1986; Rutgers van der Loeff and Lavaleye, 1986). At GME echinoderms, principally asteroids and holothurians, account for over half of the biomass in both the otter trawl and epibenthic sledge samples (see Section 22). Echinoderms are well adapted to life at abyssal depths and most of the species at GME belong to families that are found exclusively in the deep sea. They are consumers of superficial sediment and smaller organisms, and will have an important effect on the mixing and stability of sediments through their feeding, burrowing and ploughing activities.

Asteroidea

Four species of asteroid were collected from the GME site (Table 28.1); three porcellanasterids, *Styracaster horridus* Sladen 1883 (159 specimens), *S. elongatus* Koehler 1907 (19 specimens) and *Hyphalaster inermis* Sladen 1883 (629 specimens), and a single freyellid *Freyastera tuberculata* (Sladen, 1889).

1. Porcellanasteridae: This group of seastars is confined to the deep sea. None of the species have been found living at depths shallower than 1000m and the majority of specimens have been sampled at depths in excess of 3000m (Madsen, 1961). Many species have wide bathymetric and geographic distributions and they are important components of the benthic fauna in several Atlantic basins (Sibuet, 1977, 1979).

Hyphalaster inermis (Fig. 28.I) is widely distributed in the Atlantic, Indian and Pacific Oceans at depths between 2278 and 5440m (Sladen, 1883; Madsen, 1961; Cherbonnier and Sibuet, 1972; Sibuet 1977, 1979; Gage, Pearson, Clark, Paterson and Tyler, 1983). Sibuet(1975) recorded Hyphalaster from a depth of 1444m in the South Atlantic (no mention is made of the size of the specimen) but generally this species occurs deeper than 3000m (Sibuet, 1977, 1979; Khripounoff, 1979; Billett, unpublished data).

Styracaster horridus has a similar distribution to Hyphalaster, and occurs in the Atlantic, Indian and southwest Pacific Oceans at depths between 3410 and 5610m (Sladen, 1883; Koehler, 1909; Madsen, 1961;Sibuet, 1975, 1979; Briggs, 1985).

S. elongatus is not as common as the other two porcellanasterid species, but like them S. elongatus has a wide geographic distribution in the Indian Ocean and eastern part of the Atlantic Ocean at depths between 3310 and 5440m (Koehler, 1909; Madsen, 1961; Sibuet 1975, 1979).

Four other porcellanasterid species occur at similar depths at localities near to GME, namely Thoracaster cylindratus Sladen 1883, Styracaster armatus Sladen 1883, S. chuni Ludwig 1907 and Porcellanaster ceruleus Wyville Thomson 1877 (Madsen, 1961). Many porcellanasterids have wide geographic distributions so it is possible that these species could also occur at GME.

All species are thought to lead a similar lifestyle, living buried within the sediment, at least for most of the time, and feeding by swallowing copious amounts of mud (see Jangoux, 1982 for references). However, there are very few direct observations on porcellanasterids (Heezen and Hollister, 1971; Briggs, 1985; Young, Jahn, Richardson, and Lohanick, 1985) and a great deal of their habits have been inferred by comparison with a shallow-water goniopectinid asteroid, Ctenodiscus crispatus (Retzius), (Shick, Edwards and Dearborn, 1981) which was formerly classified with the Porcellanasteridae.

C. crispatus is a non-selective deposit feeder and is often known as the mud star (Shick et al., 1981). It burrows into the mud maintaining contact with the water column by its epiproctal cone, a protruberance in the centre of its dorsal surface (Hymen, 1955). The burrow is irrigated by ciliary currents drawn in at the epiproctal cone and expelled from channels passing from the tips of the arms to the sediment surface (Shick et al., 1981). The respiratory current is driven by specialized channels at the side of the body, the cribriform organs (Hymen, 1955). These are situated in the interradii between the marginal plates and vary in number from 5 to 9 in each interradius in the three species found at GME. Apart from driving the respiratory current, the cribriform organs also act as sites for the uptake of dissolved amino acids (Shick et al. 1981). However, the importance of dissolved organics in the nutrition of the starfish, in relation to the particulate food taken into the stomach, is unknown.

Like Ctenodiscus, porcellanasterids are believed to spend most of their time in temporary burrows. This is corroborated by observations made using time-lapse photography (Bathysnap) at GME (Section 24), which indicates that a new burrow may be formed every three days or so. The burrows are probably seldom deeper than 4cm.

Burrowing appears to be related to the ingestion and elimination of sediment from the stomach. Porcellanasterids do not possess an intestine, rectum or anus and so must extrude the stomach contents back through the mouth. It is assumed that after digestion has taken place the asteroid ascends to the sediment surface, voiding its stomach at the same time, and moves a short distance before filling its stomach with new sediment as it burrows back into the seabed. Digestion occurs while the seastar resides in its burrow. Madsen (1961) believed that porcellanasterids did not leave their burrows to feed, but the data of Sokolova (1958), Carey (1972), Shick et al. (1981), Briggs (1985) and the Bathysnap results from GME, indicate that a "po-go stick" feeding strategy is more likely. This would allow the seastar to utilize a wide area of superficial sediment, higher in organic matter than the rest of the sediment (Briggs, 1985).

The stomachs of porcellanasterids can be expanded greatly and often a porcellanasterid can take in its own weight in mud. The stomach contents of H. inermis, S. horridus and S. elongatus from GME were analysed and were found to consist mainly of unsorted bottom sediment in accordance with previous studies (Jangoux, 1982). The samples were sieved over 150μm and 63μm meshes and roughly sorted for metazoan and foraminiferan meiofauna. The foraminifera are abundant and diverse and dominate the sample. They include allogromiids (2 species of Nodellum + 5 other species), Komokiaceans (Baculella, Lana + 2 to 3 other species), tubular ammodiscaceans (*Bathysiphon*, *Hyperammina*, *Rhizammina* spp.), spherical ammodiscaceans (*Lagenammina* + 5 other species), multichambered agglutinated species (*Ammobaculites*, *Ammoscalaria*, *Hormosina aff. aduncus*, *Leptohalysis* sp., *Reophax aff. scorpiurus*, *R. aff. subfusiformis*, *Rheophax* sp., *Trochammina* sp.), rotaliids (*Cibicides robertsonianus*, *Epistominella exigua*), lagenids (*Lagena* spp., *Fissurina sp.*) and miliolids (*Spiroloculina* sp.). Large branched foraminiferans were also found. The total diversity amounts to at least 36 species (A.J. Gooday personal communication). The following metazoans were also found; nematodes, desmoscolecids, harpacticoids and kinorhynchs. The foraminiferans are the most abundant meiofaunal group in many deep-sea areas (Gooday, 1986b,c) and will probably act as an important food source for deposit feeding asteroids.

The skeletal parts around the mouth of a porcellanasterid may be widened to a considerable extent and the oral membrane around the mouth can be greatly dilated to form a wide funnel leading into the stomach (Madsen, 1961). Fisher (1928) concluded that fairly large objects could be ingested but little or no evidence has been found previously. The stomach contents of large *Hyphalaster* and *Styracaster* at GME, however, include pebbles up to 14mm long, in some cases bearing epifauna such as brachiopods. Also several specimens had ingested the dead tests of the large pelagic pteropod *Cavolinia gibbosa* (see Section 9). The asteroid may feed on meiofauna living inside the shell or on the fungal hyphae which ramify within the test (Thiel, 1983a).

Porcellanasterids appear to feed primarily on sediment detritus, bacteria and meiofauna (see Jangoux 1982, Briggs 1985). However, both the present stomach contents and the Bathysnap photographs - showing possible feeding behaviour on a decomposing *Pyrosoma* (Section 24) - show that they also scavenge and predate larger animals. In addition, some nutrition may be derived from dissolved organic matter. This omniverous feeding is in keeping with the general trend that asteroids become less specialized in their feeding with increasing depth (Carey 1972, Khripounoff, 1979).

The mean abundance of porcellanasterid asteroids at GME, estimated from the epibenthic sledge data is 3.6 individuals per 10^3m^2, about three times the abundance calculated from the otter trawl data (Table 22.1). The abundance of porcellanasterids in the otter trawls at GME was similar to values calculated by

Monniot and Segonzac (1985) in this area but was generally higher than the *total* asteroid abundance calculated for other Atlantic abyssal plains using similar trawls (Sibuet, 1985; Feldt, Kanisch, Kanisch, and Vobach, 1985; Rutgers van der Loeff and Lavaleye, 1986). In these cases it is not known what proportion of the asteroid fauna was accounted for by porcellanasterids. The abundance and biomass of asteroids at GME will be underestimated by the sledge and trawl since the majority of the porcellanasterids will be buried within the sediment and therefore will not be sampled adequately. Only one specimen of *Hyphalaster* was photographed on the sediment surface (Fig. 28.I) during benthic transect photography at GME (Section 23) and no porcellanasterids were seen in wide-area survey photography (WASP, see Section 19) undertaken at GME.

The arm radius (R, the distance from the centre of the body to the tip of the longest arm) of all the *Hyphalaster* and some of the *Styracaster* specimens was measured to the nearest millimetre. Many *Styracaster* were in poor condition and only a few measurements could be made. Therefore only the arm radius data for *Hyphalaster* has been analysed in detail. Fig. 28.III shows the size frequency analyses of both the OTSB and epibenthic sledge samples (samples combined). The epibenthic sledge samples were dominated by very small specimens, 38% and 64% of the population with an arm radius <2 and <10mm respectively. There will be a bias towards the smaller size classes in the sledge samples since larger specimens will be buried deeper and hence will not be sampled as well. In contrast small specimens were not taken in the larger mesh (44mm) otter trawl. The OTSB samples were dominated by a large adult population with a mean arm radius of 30.8mm. Presumably these result from the deeper "bites" taken by the OTSB and the much greater area sampled. The largest specimen at GME was only about half the maximum size known for the species.

From the combined data from the two types of trawl it appears that many juveniles are recruited to the population but that only a few survive to reach adult size. Gametogenesis in *H. inermis* and *S. horridus* is continuous (see subsequent section by Tyler and Muirhead). Both species produce eggs with a maximum diameter of about 600µm indicating a non-feeding larval stage with limited dispersal. In view of this a slow and steady input of juveniles to the population would be expected to occur.

Porcellanasterids are an important group of sediment-feeding benthic invertebrates at GME. They play an important role in mixing and irrigating the sediments through their burrowing and feeding activities. Nothing is known about the distribution of these asteroids on the seabed but they may aggregate in areas where organic matter accumulates - in a similar fashion to deposit-feeding holothurians (Pawson, 1982; Billett and Hansen, 1982). The emplacement of objects on the seabed could therefore produce "island effects" and hence lead to the aggregation of porcellanasterids around them.

2. Freyellidae: One specimen of Freyastera tuberculata with a disc radius of 6mm was taken at GME (Table 28.1). These species usually have 11 to 13 long arms which are extended into the water column to capture detrital material and possibly zooplankton (see Jangoux 1982, for references). F. tuberculata, however, has only 6 to 7 arms. On the few occasions these brisingids have been observed their arms have never been raised off the seabed indicating that they feed on material lying on the sediment surface. The gut of F. tuberculata is small and delicate suggesting that it is not a deposit feeder. A few suspension-feeding animals, including the stalked crinoid Bathycrinus gracilis (see below), occur at GME indicating that the area is favourable to suspension feeders, at least for part of the time. It is possible that F. tuberculata is omniverous and only raises its arms for suspension feeding when it is opportune to do so.

F. tuberculata appears to have a cosmopolitan distribution at abyssal depths (Downey, 1986). Three brisingids from the northeast Atlantic studied by Tyler et al. (1984) all had large eggs with a maximum diameter of 1250μm. This size of egg may occur in Freyastera and will lead to the direct development of a juvenile seastar without passing through a larval stage. However, since it is a cosmopolitan species it is possible, as with holothurians (see below), that the development of the juvenile occurs in the abyssopelagic plankton.

Crinoidea

Fragments of four stalked crinoids were taken in four samples from GME (Stas. 11261#50, 52, 58 and 11262#15). The arm fragments from St. 11262#15 probably belonged to Bathycrinus gracilis Wyv. Thomson 1872 since all the other fragments from the other three stations were of this species (A.M. Clark, personal communication). The fragment from St. 11261#58 was only a small piece of the stalk but two crowns were sampled at the remaining two stations. One was 45mm high making it the largest record of *B. gracilis* (A. M. Clark, pers. comm.).

B. gracilis is distributed throughout the northeast Atlantic at abyssal depths (4330 [4430] - 5440m) ranging from GME (the deepest record) to Madeira, North Spain, Bay of Biscay and southwest of Ireland (A.M. Clark, 1977, 1980; Roux, 1985). Two other species are recognized in the northeast Atlantic; *B. carpenteri* (Danielssen and Koren 1877) from the Norwegian Sea (A.M. Clark, 1980) and *B. aldrichianus* Wyv. Thomson 1876 from the equatorial and South Atlantic (Macurda and Meyer 1976; A.M. Clark, 1980) and from off the USA (A.H. Clark, 1908). A.M. Clark (1977) indicated that *B. aldrichianus* and *B. gracilis* could be synonymous in which case this species is distributed throughout the Atlantic Ocean at abyssal depths (3300 to 5600).

Crinoids are filter feeders capturing organic detritus and microscopic organisms such as foraminiferans, small crustaceans and radiolarians (Meyer, 1982). They are more common in shallow water than in the deep sea where their distribution is patchy (Fell, 1966; Heezen and Hollister, 1971; Lemche, Hansen, Madsen, Tendal and Wolff, 1976). Of the stalked crinoids only the small forms with dendritic roots occur on soft sediments at abyssal depths and are apparently confined to areas where there are moderate currents and unconsolidated sediments (Macurda and Meyer, 1983). The postures adopted by deep-sea crinoids, as seen in photographs, are similar to those of shallow-water species suggesting that they feed in similar ways and are dependent on a current carrying food to them. Current-meter data from GME (Saunders, 1985) show a surprising variation in current direction over small horizontal distances near an abyssal hill. Currents 10m above the seabed exceed 10cm/s least frequently on the plain and most frequently at the foot of the hill. This type of difference may influence the patchy distributions of deep-sea crinoids.

Echinoidea

Fourteen sea urchins were sampled in the benthic trawls. Abundances are given in Table 22.1. All were specimens of the echinoid *Plesiodiadema microtuberculatum* (A. Agassiz 1979). Knowledge of this species is very poor and it is possible that it is synonymous with two other species, *P. molle* (Doderlein 1901) from the Indian Ocean and *P. antillarum* (A. Agassiz 1880) from shallower water in the Atlantic (Mortensen, 1940). Mironov (1975) gives a bathymetric range of 651 to 3109m for P. antillarum and it seems likely that in the Atlantic there are two species, on inhabiting bathyal depths and one abyssal depths. P. microtuberculatum was first sampled at a depth of 3640m in the South Atlantic by the Challenger Expedition (Agassiz, 1881). This species is likely to occur in mid oceanic areas throughout the Atlantic and possibly also in the Indian Ocean.

Plesiodiadema is a regular sea urchin with very long, slender, downwardly-curved primary spines whose tips touch the ground (Hymen, 1955). The spines are some 3 to 4 times as long as the horizontal diameter of the test (Mortensen, 1940). These may act as sensory structures, the tips of the oral spines are widened at the end, and/or protect the sea urchin from predation.

Analysis of gut contents shows that P. microtuberculatum feeds on sediment, forming little boluses that are passed through the gut. This is in keeping with other species in the family Aspidodiadematidae (de Ridder and Lawrence, 1982). The balls include foraminiferans and other meiofauna. Many regular echinoids form food pellets or mud balls bounded by a mucoid coat which remain intact throughout their passage through the gut (de Ridder and Jangoux, 1982). Bacteria are associated with these food pellets and probably assist in digestion. P. microtuberculatum is likely to be omnivorous picking up anything that can be manipulated by its Aristotle's lantern.

P. indicum, which occurs at depths of 300 to 520m around the Malay Archipelago (Mortensen, 1940), has a maximum egg size of about 100µm suggesting that it probably has a pelagic feeding larva (Mortensen, 1940). This is not surprising for an upper slope species. However, the maximum egg size found in P. microtuberculatum at GME also appears to be about 100µm. The data are very limited and more work is necessary before it is certain whether this is the maximum egg size developed by the species. Pelagic feeding larvae of two deep-sea gastropods have been identified in near-surface plankton samples (Bouchet, 1976a, b; Bouchet and Waren, 1979, see also Section 9) and it is possible that P. microtuberculatum produces a similar pelagic larva.

Holothurioidea

Six benthic holothurian species (40 specimens) were sampled in the ten benthic trawls and sledges taken at GME (Table 28.2). In addition, one pelagic holothurian, *Enypniastes diaphana* (see section 19), was captured in the suprabenthic net on the epibenthic sledge during the photo-sledge transect (St. 11262#20). Five of the species, *Psychropotes semperiana* Théel 1882, *Peniagone lugubris* Théel 1882, *Pseudostichopus atlanticus* R. Perrier 1902, *Synallactes crucifera* R. Perrier 1898 and *Mesothuria candelabri* Hérouard 1923, are epifaunal and crawl over the seabed feeding on superficial sediment, while the sixth species, *Molpadia blakei* (Théel 1886), lives within the sediment and forms cone-shaped mounds (Fig. 28.II). The epifaunal holothurians are discussed subsequently as a group. Little is known about *P. lugubris*, *S. crucifera*, and *M. candelabri* but their biology will be similar to that of the well known *P. semperiana* and *P. atlanticus*. The feeding biology of epibenthic holothurians and their affect on the sediment is therefore discussed in general terms. *M. blakei* is treated separately.

1. Epifaunal holothurians

Psychropotes semperiana (Fig. 28.IV) is distributed in tropical and sub-tropical areas of the North and South Atlantic and the western part of the Indian Ocean at depths between 3465 and 5600m. It was the most common species in trawl samples at GME (Table 28.2). Specimens varied between 8 and 105mm long but most individuals measured between 45 and 85mm in length (Fig. 28.VI). The large characteristic dorsal appendage was broken off in all cases, presumably while the holothurian was in the net. Its function is unknown.

Peniagone lugubris is a rare holothurian previously known only from a single specimen collected by the Challenger Expedition at a depth of 4572m in the Mid Atlantic (St. 104, 2°25'N, 20°1'W Théel, 1882). The calcareous deposits are distinctive and those in the present material agree with the descriptions given by Théel (1882) and Hansen (1975). The measurements of the deposits given by Hansen(1975) are in error and are one tenth of the stated values (Hansen, personal communication). The present specimens measure between 22 and 40mm long and are about the same size as the type specimen. The species has a well developed velum on its dorsal surface formed from two pairs of fused papillae. This may help the holothurian to swim, as in the related species *P. diaphana* (Hansen, 1975; Barnes *et al.*, 1976; Billett *et al.*, 1985) and *P. leander* (Pawson and Foell, 1986), but *P. lugubris* did not occur in any of the pelagic samples from GME (Section 19). *P. lugubris* probably walks on the tips of its tubefeet, like *P. azorica*, lifting its body clear of the seabed and leaving the sediment surface almost untouched (Lemche *et al.*, 1976).

Synallactes crucifera (Fig. 28.V) is another rare species known previously from a single specimen taken off the coast of Morocco (2212m, 30°3'N, 14°2'W, Perrier, 1902). The genus *Synallactes* is well represented in the Indo-Pacific Ocean (Deichmann, 1930) but only 4 species are known in the Atlantic, two from off South Africa (Cherbonnier, 1952),*S. crucifera* off Morocco and *S. longipapillata* Sibuet 1978 from the Bay of Biscay (2 specimens).

Mesothuria candelabri is an abyssal holothurian known principally from the northeast Atlantic ranging from GME to the Bay of Biscay (Hérouard, 1923) and the Porcupine Abyssal Plain (Billett, unpublished data) at depths of 4540 to 5440m (Madsen, 1953; present data). Data from the Porcupine Abyssal Plain show that *M. candelabri* may occur as shallow as 4000m but it is more common in samples deeper than 4500m (Billett, unpublished). Sibuet (1977) found the species at depths 2200 to 3100m but these records need to be confirmed. Apart from the northeast Atlantic Hansen (1975) records *M. candelabri* at abyssal depths in the Kermadec Trench in the Pacific.

The geographic and bathymetric distribution of *Pseudostichopus atlanticus* is rather uncertain. The species of this genus are difficult to distinguish and it is likely that *P.atlanticus* and *P. villosus* have been confused in several cases. The bathymetric range for *P. villosus* is 896 to 7000m (Gage *et al.*, 1985). This wide bathymetric range seems unlikely and *P. villosus* has undoubtedly been used as a catch-all species for a variety of forms. The present specimen at GME is identical to *P. atlanticus* taken at depths 4017 to 4795m on the Porcupine Abyssal Plain (Billett, unpublished). It is clear that this species is the same as *P. atlanticus* referred to by Deichmann (1930) at a depth of 2920m in the West Indies. It is likely that this species occurs at abyssal depths throughout the north Atlantic (2920 to 5440m).

P. semperiana, *P. lugubris* and *S. crucifera* are probably not important in terms of bioturbation. They have well developed tubefeet that carry the body above the sediment surface and as a result only a trail of pin-point impressions is left on the seabed (Heezen and Hollister, 1971; Mauviel and Sibuet, 1985). *P.*

atlanticus and M. candelabri, on the other hand, have very small tubefeet and move by ploughing through the sediment, leaving characteristic trails behind them (Heezen and Hollister, 1971; Lemche et al., 1976; Young et al., 1985). These furrows are 5 to 8cm across (Young et al., 1985) and are probably about 1cm deep. The speed at which these holothurians travel is unknown but taking a rate of about 90cm h^{-1}, (as calculated for the bathyal holothurian Benthogone rosea (Lampitt and Billett, 1985)), each holothurian would bioturbate about $1m^2$ of sediment per day, assuming that is constantly active and that bathyal and abyssal holothurians move at a simlar rate.

It was not possible to calculate the abundance of P. atlanticus and M. candelabri from the epibenthic sledge or photographic data, but the combined abundance of these holothurians can be calculated from wide-area survey photography (WASP see Section 19) since they can be recognized at the end of their distinctive furrow trails. Abundance data for these two species combined is given in Table 28.3. Using the mean value of 2.28 Pseudostichopus/Mesothuria per hectare and assuming that they bioturbate $1m^2$ of sediment per day on average, these holothurians would bioturbate the top 1cm of sediment over 1 hectare in about 12 years.

Another feature of the Pseudostichopus/Mesothuria trails in the WASP photographs was the apparent rapidity with which the furrow marks were erased. Rarely was a furrow photographed without the holothurian that was making it, and even within a photograph the breakdown of the furrow was evident. This may indicate the rapidity of physical or biological reworking of the sediment surface or indicate that Pseudostichopus and Mesothuria move much more slowly than the projected rate of 90cm h^{-1}.

Stomach-content analysis of all 5 epibenthic holothurian species shows that they are deposit feeders, deriving their nutrition mainly from organo-mineral aggregates (usually 20 to 65μm in diameter), faecal matter, and organic encrustations of mineral grains (Khripounoff, 1979; Khripounoff and Sibuet, 1980). The organic matter contained in the sediment in the oesophagus of deep-sea holothurians is generally higher than that in the sediment sampled in the same area (Bordovskiy, Sokolova, Smirnov, Akhmet'yeva and Zezina, 1974; Khripounoff and Sibuet, 1980; Sibuet et al., 1982). This may result from selectivity by the holothurian for particles with a higher energetic content

(Khripounoff and Sibuet, 1980), the deftness with which holothurians sweep the superficial layer of the sediment (Briggs, 1985) or it may reflect the heterogeneous distribution of organic matter on the seabed (Billett and Hansen, 1982; Billet et al., 1983). Most of the organic matter assimilated is of detrital origin. Sibuet et al. (1982) and Deming and Colwell (1982) calculated that only about 3% of the organic matter absorbed by a holothurian during digestion was of bacterial origin.

Epibenthic holothurians, therefore, appear to feed primarily on detrital material that has settled only recently on the seabed. This is corroborated by radioecological studies which show that holothurians were high in radionuclides which had been scavenged from the water column by particulate material and deposited on the seafloor (Feldt et al., 1985). Some of the radionuclides had short half-lives. Osterberg, Carey and Curl (1963) found similar gamma-ray sectra for fall-out radionuclides with short half-lives in deep-sea and shallow-water holothurians. This is an indication not only that particles sink rapidly in the ocean but also that holothurians are particularly adept at feeding on these particles, which are, in all probability, mainly zooplankton faecal pellets.

Digestion in holothurians is aided by the presence of an enteric, barophilic microbial population in the posterior intestine. The bacteria are directly associated with the intestinal lining in the hindgut and are thought to act as a commensal gut flora that transforms ingested sediment (Deming and Colwell, 1982; Sibuet et al., 1982; Tabor, Deming, Ohwada and Colwell, 1982).

Microbial activity in holothurian guts is more rapid than in the surrounding deep-sea sediments. P. longicauda has a potential turnover time for sediment in its gut of 16 hours and, if feeding continuously, would process about 105g wet weight of sediment per day (Deming and Colwell, 1982). This is similar to a rate of 100g wet weight of sediment per day processed by a deep-sea holothurian, calculated from photographic observations by Rowe (1974). It is clear that holothurians play an important role in the recycling of material at the sediment surface.

Little is known about reproduction in the epibenthic holothurian species at GME. However, some information may be gleaned from the maximum egg size since, like asteroids (see Section 19), the mode of development in holothurians is related to the size of egg produced by the adult. The maximum egg size found in deep-sea Synallactidae varies widely (Tyler and Muirhead, 1986b) but direct, or some form of abbreviated development, would be expected for *S. crucifera*, *M. candelabri* and *P. atlanticus*. *P. lugubris* may produce eggs with a maximum size of about 300μ like *P. diaphana* (Théel, 1882) and *P. azorica* von Marenzeller 1893 (Tyler, Gage and Billett, 1985) indicating abbreviated larval development.

Species of *Psychropotes* produce the largest eggs known in holothurians, up to 4.4mm in diameter (Hansen, 1975; Billett *et al*., 1985; Tyler and Muirhead 1986c). Hansen (1975) noted a maximum egg diameter of only 0.8mm for *P. semperiana* but it is evident from the GME material that eggs reach a diameter of at least 3.5mm in this species. *P. semperiana*, therefore, produces an egg that is comparable in size to that of other members of the genus and other members of the family Psychropotidae (see *Benthodytes*, Section 19). It is assumed that the large egg, with its ample yolk reserves, will develop directly into a juvenile without passing through a larval stage. Species with this type of development often have a restricted geographic distribution since the dispersal role of the larval phase is dispensed with. However, the deep-sea holothurians that produce large eggs have wide, usually cosmopolitan, distributions. Juveniles of these species have been sampled by pelagic nets thousands of metres above the seabed (Billet *et al*., 1985; Section 19 this report), and it is evident that development from the egg to juvenile holothurian takes place in the bathypelagic and abyssopelagic zones allowing wide dispersal.

It is not known how long the juveniles stay in the plankton and hence how far they are carried. However, it is clear that juvenile benthic holothurians can rise up through the water column to a depth of at least 900m and as a result will act as a link between abyssal depths and the mesopelagic zone. The production of eggs by *P. semperiana* is therefore a means by which material can be dispersed from GME. The abundance of juvenile benthic holothurians in midwater is low and no juvenile specimens of *P.semperiana* have yet been caught by a pelagic net. The fecundity of *P. semperiana* is unknown but it is probably low and similar to that found in *Benthodytes sordida* Théel 1882, *P. longicauda* and *P. depressa*, each with an "actual fecundity" (the number of eggs ready for spawning) of 260, 8, and 250 eggs per individual respectively (Tyler and Muirhead, 1986c). All species have a higher "potential fecundity" (the total number of oocytes) of 4000, 250 and 5000 respectively (Tyler and Muirhead, 1986c) but in terms of egg production even these abundances are low. Fecundity is inversely proportional to the size of egg formed and therefore the number of eggs produced annually by P. semperiana will be low.

Although P. semperiana is the most abundant holothurian in the trawl samples (Table 28.2), P. atlanticus and M. candelabri were more evident in the wide-area survey photography (Table 28.3). This discrepancy may be related to size since many P. semperiana were less than 55mm long (Fig. 28.VI) and therefore would not have been particularly obvious in the WASP photographs. The abundance of holothurians at GME was low (Table 22.1) in comparison with abundances for other abyssal plains calculated from trawl samples (Sibuet, 1985; Feldt et al., 1985; Rutgers van der Loeff and Lavaleye, 1986). The abundance of holothurians at GME was too low to be adequately resolved from epibenthic sledge transect photography (Section 23).

2. Infaunal holothurians

Molpadia blakei is distributed throughout the North Atlantic at depths between 1747 and 5270m (Gage et al., 1985). In the Rockall Trough it occurs between 1991 and 2916m but generally it seems to be more common at depths greater than 3000m in the northeast Atlantic (Sibuet, 1977; Tyler, Billett and Gage, in press).

Little is known of the biology of M. blakei but its lifestyle is assumed to be similar to M. oolitica (Pourtales 1851) which occurs in soft muds at depths greater than 22m in Cape Cod Bay, Massachusetts, USA (Rhoads and Young, 1971). This species was observed in aquaria to burrow vertically keeping the anus above the sediment-water interface. Divers confirmed the aquaria observations and found that M. oolitica made cone-shaped mounds produced by the accumulation of faeces. The mounds are typically 10 to 30cm in diameter and about 2 to 3cm high. M. oolitica appears to feed at depth causing voids underneath the sediment surface leading to a high sediment water content.

Similar cones were noted by Young et al., (1985) at abyssal depths in the Venezuela Basin where M. blakei occurs. In one case they photographed the apparent ejection of faecal material from the apical opening of the cone. The cones ranged in diameter from 10 to 25cm and were about 5cm high. They occurred in three different types of sediment, turbiditic, hemipelagic and pelagic, but were most common on hemipelagic sediments. Their abundance in the three sedimentary provinces was 0.069, 0.887 and 0.104 per m^2 respectively, but it is not certain how many of the cones were active.

4 specimens of M. blakei were sampled at GME (Table 28.2) and cone-shaped mounds made by this species were evident in the epibenthic sledge transect photography (Fig. 28.II). The largest mounds were about 10 to 15cm in diameter and about 5cm high, similar to those photographed by Young et al., (1985). The mounds often occurred in a series of 3 or 4 cones ranging from fresh structures to those being degraded. It appears that M. blakei moves progressively across the seabed forming a series of mounds but its residence time in each mound is unknown. The abundance of cones at GME was estimated from three epibenthic sledge hauls and varied between 74 and 114 cones per $1000m^2$ (Table 23.1). Only those cones with an apical opening were counted since cones without an aperture are probably not active. It is likely that cones made by small specimens were overlooked and therefore the abundance of M. blakei calculated from the photographs is a minimum. The abundance of cones at GME is similar to their abundance in the Venezuela Basin turbiditic and pelagic sediments (Young et al., 1985), and it is clear that M. blakei will play an important role inmixing the top 10cm or so of sediment.

Khripounoff and Sibuet (1980) analysed the stomach contents of M. blakei from abyssal depths in the Bay of Biscay. Ingested particles closely reflected the granulometry of the sediment, in contrast to the gut contents of epibenthic holothurians which appear to select for finer surface particles (see previously).

Thomson, Coley and Weaver (in prep.) have found that although the turbidite at GME is only 200-300 years old, there has been considerable bioturbation down to 10cm and in an isolated case down to 20cm. In one core there was a subsurface maximum of ^{210}Pb which may be due to mixing by large infaunal organisms like M. blakei. In the Venezuela Basin similar subsurface maxima in radionuclides were found, indicating greater subsurface than surface working rates by large megabenthos, including holothurians (Li, Guinasso, Cole, Richardson, Johnson and Schink, 1985).

It is not possible to calculate the feeding rate of *M. blakei* but a related shallow water species, *Paracaudina chilensis* (Müller 1850) passes about 160g wet weight of sediment through its gut per day. This is similar to the rate of sediment processing by an epibenthic holothurian described previously.

The four specimens of *M. blakei* range between 22 and 64mm long (excluding the tail section). These specimens are comparable in size with those sampled on the Porcupine Abyssal Plain, southwest of Ireland (Tyler *et al*., in press). *M. blakei* grows to a length of at least 125mm.

M. blakei produces an egg with a maximum diameter of about 200µm (Tyler *et al*., in press). This is similar in size to the egg produced by many other molpadiid species including *M. intermedia* (Ludwig 1894), found between 7 and 2925m, studied in detail by McEuen and Chia (1985). *M. intermedia* has a maximum egg size of about 270µm. The egg develops into a doliolaria larva which remains in the plankton for several days. A similar planktonic larva is expected for *M. blakei* although its residence time in the plankton may be much longer. Development of the gonad in *M. blakei* starts when the holothurian is about 18mm long and breeding appears to be continuous for the population as a whole, although spawning may be periodic in each individual (Tyler *et al*., in press).

Reproduction of Porcellanasteridae

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This section reproduces parts of Tyler and Muirhead (1986a) work on the reproductive biology of three species of Porcellanasteridae. Two of these - *Hyphalaster inermis* and *Styracaster horridus* were taken at GME on Discovery Cruise 156 and Tyler and Muirheads' study of these two species is included here for completeness (see Section 1). The original should be consulted for figures and general background.

Material was taken in the otter trawl (Section 5, Table 1.1). All samples were fixed in buffered 5% seawater formalin and later transferred to 70% alcohol for storage. Before dissection, each species was measured from the centre of the mouth to the tip of the longest arm (R) (Mortensen, 1927). The gonads were dissected out, processed through graded alcohols, cleared in histoclear and embedded in paraffin wax. Sections were cut at 7µm and routinely stained with

Mayers haemalum and eosin, whilst selected sections were stained with PAS, alcoholic toluidine blue and Massons Trichrome.

Hyphalaster inermis has an arm radius (R) of up to ca. 42mm at GME. The gonads do not lie in the arm, as this appears to consist of solid calcareous elements, but in the periphery of the disk at the base of each arm. Each gonad consists of a number of tubules which are laterally flattened as they are compressed between the rigid body wall and the sediment-packed distended stomach. The macroscopic appearance of the gonad is very similar in *Styracaster horridus*. The sex ratio does not differ significantly from 1:1 in either species.

Microscopic observation suggests that the pattern of oogenesis is similar in both species but unlike that yet observed in any other deep-sea asteroid (Tyler, Pain and Gage, 1982; Tyler and Pain, 1982a,b; Pain *et al*., 1982a; Pain *et al*., 1982b; Tyler *et al*., 1984). Young oocytes ca. 20µm lie peripherally in the gonad and consist of a large nucleus and relatively little cytoplasm. They are, however, covered in a dense coat of follicle cells. By 60µm diameter the volume of cytoplasm has increased and stains very pink with Massons. There is a very thin peripheral amorphous layer. Vitellogenesis starts at an oocyte size of 100-150µm. In newly vitellogenic oocytes the periphery becomes granular whilst the perinuclear area retains the appearance of a previtellogenic oocyte. Vitellogenesis proceeds until a maximum oocyte diameter of ca. 600µm is reached. This process appears to occur in two phases. Initially the cytoplasm becomes filled with moderately PAS-positive granular material spreading in from the periphery after which a narrow band develops round the periphery which is PAS-positive but amorphous in fully grown oocytes. The oocyte membrane is strongly PAS-positive and β-metachromatic and histochemically appears to be very similar to the genital haemal sinus in the ovary wall. This granular cytoplasm gives way to a very reticulate cytoplasm in the maximally developed oocytes. Thus at the maximum oocyte size the cytoplasm is reticulate with some PAS-positive material but a number of voids which, we believe, represent neutral fat deposits that have been dissolved out during processing. The periphery of the cytoplasm is still covered with amorphous PAS-positive material which in come cases is also found in the lumen of the gonad. Even at this well developed stage, the oocytes are covered in follicle cells.

Breakdown activity appears to be fairly restricted, especially when compared to other deep-sea seastars, although occasional specimens do show extensive oocyte breakdown in which the oocyte becomes packed with phagocytes which degenerate the cytoplasm until the oocyte wall collapses. In other deep-sea asteroids this material is believed to be redistributed for further oocyte development.

Development of the testis in both species appears to be typical of deep-sea seastars previously examined. In newly developing tubules colonettes form to increase the surface area for spermatogenesis but as the lumen becomes packed with spermatozoa the testis wall is stretched out and the colonettes disappear.

Both H. inermis and S. horridus have a maximum oocyte diameter of 600µm which would suggest direct development omitting the larval stage. From previous experience we would predict direct development with minimal dispersal. However, studies of the related species Ctenodiscus crispatus, which also produces an egg of 600µm diameter, have shown that these eggs and the larvae formed from them are found in the plankton, especially in mid-winter (Falk-Petersen, 1982). Other species of Ctenodiscus viz. C. australis brood (Lieberkund, 1926). We can find no reference in the literature to a description of the larva of C. crispatus.

By analogy, we may suggest that the eggs of the two species studied here develop into larvae and are dispersed. However, most evidence from directly developing species suggests demersal development with very limited dispersal. Thus we believe that there will be very little transport of radionuclides away from the population by these species.

29. DEMERSAL FISH

N.R. Merrett

Introduction

The understanding of deep-sea demersal fish assemblages has been much advanced in recent years from several detailed studies incorporating a variety of sampling gears (see Merrett and Marshall (1980) for a literature review). Most, however, have concentrated upon the ichthyofauna of the continental slope and rise. In both the North Atlantic and Pacific Oceans, the pattern commonly found from trawl samp[illegible] is a lack of clear faunal zonation induced by a fairly uniform addition [illegible] species with increasing soundings over the range investigated. This is coupled with a progressive decline in relative abundance and biomass with depth (e.g. Merrett and Marshall, op. cit. (off N.W. Africa, south of Canary Is); Pearcy, Stein and Carney, 1982 (eastern North Pacific); Sulak, 1982 (Middle Atlantic Bight, U.S.A. and Bahamas); Gordon and Duncan, 1985 (Rockall Trough); Merrett and Domanski, 1985 (off N.W. Africa, Morocco); Snelgrove and Haedrich, 1985 (off Newfoundland); I.O.S. unpubl. data (Porcupine Seabight, S.W. of Ireland)).

While some of these studies have extended into abyssal soundings (here taken to be >4250m), the proportion of fishing effort there has been minimal. For instance, out of seven recent major deep-sea demersal ichthyofaunal studies that have sampled abyssally (Haedrich, Rowe and Polloni, 1980 (south of New England); Merrett and Marshall, 1980; Pearcy, Stein and Carney, 1982; Sulak, 1982; Merrett and Domanski, 1985; Stein, 1985 (eastern North Pacific); I.O.S. unpubl. data), only 3.8% (45 out of 1170 trawl hauls) of the collections have been from >4250m soundings. This figure may be further reduced to 34 (=2.9%) in the light of recent comparisons of catches from large and small nets (e.g. Gordon and Duncan, 1985; Merrett and Domanski, 1985), by invalidating those samples taken with small nets which are now known to be unrepresentative (and see below). This restricts the relevant comparative data to the Bahamas, Middle Atlantic Bight, south of New England and the Porcupine Abyssal Plain (PAP) in the Atlantic and to one area in the eastern North Pacific. Currently, a summary atlas of deep-living demersal fishes in the North Atlantic Ocean, which includes these and other samples collected largely with the same gear (the semi-balloon otter trawl, see below), has drawn these results together on a basin-wide basis (Haedrich and Merrett, in prep).

Bearing in mind this under-representation of abyssal samples in demersal ichthyofaunal studies, the five successful collections made at GME reported here (Merrett and Nielsen, in press), are augmented by a roughly north-south transect of 5 samples together with 4 more from the PAP (overall sounding range (4090) 4250-5440m) (Merrett, in prep.) to contribute substantially to the knowledge of abyssal fish assemblages (Fig. 29.I). Furthermore this is the only such transect reported covering 19° of latitude to link samples from below relatively eutrophic seasonal surface waters to others beneath oligotrophic surface waters largely unaffected by seasonality. Care is exercised in drawing conclusions from this data set which, being comprised of largely single station observations from a range in soundings of 1350m, may be subject to variance. Nevertheless, in the absence of comparable data and despite the reservations, the trends which are apparent are likely to be substantive.

Materials and methods

In addition to the samples collected at GME (Tables 29.1-2), the data set are augmented by 4 samples ('Discovery' Collection Stn nos 50515, 50711, 50811, 50910) from 4292-4787m mid-depth soundings in the area 49°38'-49°51'N, 14°34'-15°47'W, together with a set of 5 samples ('Discovery' Stns 10652, 11116, 11118, 11121#14, 11134#1: 4090-5112m mid-depth soundings) at 2°-4° intervals of latitude across a longitudinal range of some 7° broadly connecting the northerly site with the GME area (Table 29.3, Fig. 29.I: Merrett, in prep.).

Sorting and preliminary identification of the catches were carried out immediately on retrieval of the gear. The specimens were then weighed by species groups. Their length (macrourids head length (HL); others, standard length (SL)), sex and gonad maturity stage (I, immature; II, stage of yolk and chorion formation; III/V growth stage of vitellogenesis) was then recorded before fixation in 10% seawater formalin. Later the samples were transferred to 5% seawater formalin for preservation. Identities were confirmed ashore, when the specimens were eviscerated for dietary analysis.

Relative density was estimated, from the OTSB catches only, on the same basis as employed in earlier studies, i.e. from the area swept per tow (Merrett and Marshall, 1980; Merrett and Domanski, 1985). This was calculated from the estimated wing-end spread and fishing distance, expressed as the number of fish per 1000m² and constrained in its reliability by the limitations of sampling previously discussed (Merrett and Marshall, 1980).

Percentage similarity (PS), a commonly used measure of faunal overlap, was calculated according to the formula of Whittaker and Fairbanks (1958):

$$PS = 100 \sum \min (p_{ia}, p_{ib})$$

where p_{ia} = the proportion assumed by species i in sample a; p_{ib} = the proportion assumed by species i in sample b. This was subsequently examined with nonmetric multidimensional scaling (MDS) (Kruskal 1964a) to provide ordinations. In addition single linkage cluster analysis was used to give a supplementary mechanism for classification of groupings.

Results and discussion

Relative Density and Biomass.

The 5 successful OTSB hauls yielded 153 specimens representing 17 species from 14 genera and 5 families (Table 29.1). Thirty five specimens of 6 species from 5 genera and 3 families were collected from the 4 BN tows (Table 29.2). The OTSB catches ranged in total fish wet weight from 0.15-7.01kg, giving a spread in biomass of 0.006-0.051kg/1000m² (mean; 0.02kg/1000m² and (0.04-0.51 fish/1000m²). The specimen mean wet weight from the samples was 120gm. Comparing this biomass with the region to the north (Table 29.3), it is some 4 times lower than the value for the next shallower station (at 37°N) which, incidentally, was the nearest station occupied to the continental land mass (Tagus Abyssal Plain). On the other hand, the GME value is an order of magnitude lower than the mean biomass at soundings greater than 4250m in the PAP (49°N : Fig. 29.II), Much less discrepancy exists in terms of relative density over the latitudinal range; GME comparing favourably with the abyssal PAP in this regard (Fig. 29.III). Thus mean fish wet weight trends through more than an order of magnitude over the 19° latitudinal range between the latter area and the GME (Table 29.3 and see below).

Species composition

Apart from one aphyonid specimen, as yet unidentified, all the species (6) represented in the BN catches were duplicated in the species composition (17) of the OTSB collections. Since the ipnopid, Bathymicrops regis, dominated both sets of collections, the faunal overlap between the pooled sets of samples (PS = 54%) was somewhat greater than might have been expected from earlier work (Merrett and Domanski, 1985) in which the BN was found to sample a narrower range of size and diversity among fish species. Among OTSB samples the variation in faunal overlap is considerable (PS = 0-66%). This suggests that perhaps fish density at 5440m was so low that some of the towing times were too short to optimise specimen, and therefore species, encounters. Indeed, this conclusion is reflected in Fig. 29.IV, where specimen accumulation relative to the number of species per haul are compared. The tentative curve fitted to these points indicates that only after the capture of some 30-40 specimens is the asymptotic level of maximum species richness approached. By this criterion, hauls #43 and #50 sampled too few specimens to be representative. The variation in PS among the remaining three hauls is reduced to 57-66% by omitting these values from the faunal overlap analysis.

The percentage composition of the two sets of collections indicates that Bathymicrops regis, dominated both and augmented in the case of the OTSB by another ipnopid (sensu Hartel and Stiassny, 1986), Bathypterois longipes and the macrourid, Echinomacrurus mollis (Fig. 29.V). These three species comprised 78% of the OTSB collection and the balance was composed of the remaining 14 species captured. It is clear from Table 29.4 and the MDS plot derived from it (Fig. 29.VI) that this dominant assemblage at GME differs markedly from that encountered in the PAP and several of the intervening stations. It appears that the measure of faunal overlap is moderately high over the latitudinal range 49°-41°N. Species richness there is rather consistent (8-10 spp.), but drops at 37°N (7 spp.) and increases considerably to the south (34°-31°N : 15-17 spp.). Despite this variation a moderate degree of faunal overlap occurs among the southerly stations (37°-31°N), confirmed by a cluster analysis of the same percentage similarity analysis (Fig. 29.VII), to suggest a faunal transition between 37°-41°N. (Inspection of the percentage similarities ordered by soundings indicates that the range of 1300m among the samples has little apparent affect on these results). Assuming that this data set is a reflection of the true situation, the transition occurs around the frontal zone of marked seasonality in primary production demonstrated by the relatively abrupt change in the depth of the winter thermocline (Robinson, Bauer and Schroeder, 1979 their Fig. 42).

There is considerable ecological contrast between the northern dominant assemblage (i.e. the macrourids, *Coryphaenoides (Nematonurus) armatus*, *C. (Chalinura) leptolepis*, *C.(C.) profundicola* and the synaphobranchid, *Histiobranchus bathybius*) and the southern (i.e. the ipnopids, *Bathymicrops regis*, *Bathypterois longipes* and the macrourid, *Echinomacrurus mollis* - Table 29.3). The assemblage in the north is characterised by large (ca 1-9kg wet weight adult size), benthopelagic fishes, facilitated in their mobility by functional swimbladders providing neutral buoyancy to their robust bodies. Fecundity among this group is generally high (of the order of 10^4-10^6 eggs). Dominating in the south are species of much smaller adult size (ca 0.001-0.1kg), the more abundant of which (*B. regis* and *Bathypterois longipes*) are negatively buoyant benthic species. *Echinomacrurus mollis* is a seemingly benthopelagic fish, yet its neutral buoyancy is achieved at the expense of a reduction in density of ossification and musculature rather than from a functional swimbladder. It can therefore be expected to be a less mobile macrourid in comparison with the dominant northern relatives. Fecundity in the species dominating the southerly assemblage is relatively low (ca 10^2-10^3 eggs).

A similar transition between deep-sea demersal fish species with energetically expensive life histories (i.e. active predators, continual swimmers, species with very high relative fecundities) and those with energetically stringent life histories (such as those species dominating at GME) has recently been observed between 2 localities in the western North Atlantic (Middle Atlantic Bight and the Bahamas) by Anderson *et al*. (1985). While they relate this change to the variable food supply available beneath different regimes of surface primary productivity, they are unable to indicate any frontal zone of faunal change on the bottom. In the current context, where critical pathways of potential contamination are being considered (see following section), the discovery that such faunal change at abyssal depths can be associated relatively closely with a recognisable surface phenomenon is clearly of value.

The broader distribution around the North Atlantic basin of 4 of the 7 dominant species (*viz*. *Bathypterois longipes*, *Histiobranchus bathybius*, *C. (Chalinura)* *leptolepis* and *C. (Nematonurus) armatus*) has been treated in a summary atlas of deep-living demersal fishes of the area (Haedrich and Merrett, in prep.). The charts for these species, reproduced here (Figs 29.VIII and 29.IX), are based very largely on comparable OTSB catches and indicate both horizontal distribution and relative abundance in terms of percentage catch composition by 750m strata per area. Evidently these are all widespread species, at least beneath the tropical and temperate parts of the North Atlantic that were sampled.

Potential exposure pathways

The summary atlas charts (Haedrich and Merrett *op. cit.*) indicate that *C. (Nematonurus) armatus* dominates the group of abyssal species figured. It is widespread in the Indo-Pacific as well as in the Atlantic and is of a size (adults up to at least 150mm HL/845mm TL : 2+kg) and density in some regions that conceivably might attract specialist commercial interest. Indeed GESAMP (GESAMP, 1986:25) envisaged this species when considering the hypothetical "bathys restaurant" exposure pathway via the food web to man, which supposes an entrepreneur establishes a restaurant which serves only bottom-living deep-sea fish. The present evidence is consistent with the Haedrich and Merrett chart (in prep. (Fig. 29.IX) which suggests that this species in the North Atlantic dominates in the fauna of the mid-latitudes.

In considering *C.(N.) armatus* and the closely related *C.(N.) yaquinae* in the Pacific, Wilson and Waples (1983) found that *C.(N.) armatus* was a deep slope - upper rise (2000-4300m) species more or less confined to the oceanic rim and was distributed mainly beneath eutrophic waters, while the deeper-living *C.(N.) yaquinae* (3400-5800m) was an oligotrophic specialist. The known North Atlantic distribution of *C.(N.) armatus* tends to corroborate this view, although *C.(N.) yaquinae* is not known in this ocean. Thus at 5400m soundings at GME below oligotrophic surface waters only a single *C.(N.) armatus* was captured. *Coryphaenoides (C.) profundicola* is the only other species captured at GME of comestible size (known up to 225mm HL) 1120mm TL : ca. 9kg) yet it has never been found in remotely exploitable densities and it is noteworthy that only small specimens (<1.3kg) were sampled in the GME collections. Hence, it seems that potential contamination of the demersal ichthyofauna at GME is unlikely to pose a threat to man along a direct exposure pathway.

Reproduction

The BN and OTSB samples were pooled for gonad maturity analysis which, despite the relatively small overall sample size and lack of seasonal coverage, provide some indication of species potentially breeding in the area. Individuals of 5 species from 3 families (Ipnopidae - Bathypterois longipes, the gen et. sp. nov (Merrett and Nielsen, in press) and Bathymicrops regis; Ophidiidae - Bassozetus sp. I; Macrouridae - Echinomacrurus mollis) were found with ovaries, or ovarian portions of their ovotestes, in the chorion and yolk formation or growth stages of oogenesis (Table 29.5). Three of these (B. regis, B. longipes and E. mollis) dominated the rank order of abundance in the area. That the dominant species breed in the area is not an unlikely situation, particularly as two, B. regis and B. longipes are relatively sedentary benthic forms. Much more evidence is required to ascertain whether other species breed there also. (Evidence from the more seasonal Porcupine Seabight region suggests that only about 20% of the slope-abyssal dwelling species reproduce there (IOS unpubl. data) inferring that many are migratory in habit.).

Very little is known generally of the breeding biology of the abyssal ichthyofauna. Considering the five families represented in these catches in systematic order (Table 29.5). Synaphobranchus, a slope-dwelling congener of Histiobranchus, is known from the larval stages to breed in the Sargasso Sea region (Bruun, 1937 and see GESAMP, 1986:85). Nothing is known of the breeding biology of H. bathybius, save that it has a fecundity of up to 1.3×10^6 eggs (IOS unpubl. data).

While some ipnopid larvae have been collected in midwater and thus might habitually undergo their early ontogeny in the relatively near-surface waters (Okiyama, 1986) the only information on the species represented at GME, which are all hermaphroditic, is given below. Length-frequency analysis of both Bathymicrops regis and Bathypterois longipes indicates the distribution of ovarian maturity stages (Figs 29.X and 29.XI). Bathymicrops regis, in common with a variety of other deep-sea fishes, shows a skewed bimodal distribution. The smaller peak, comprising the sexually immature (Stage I) shorter length groups, is linked via the transient yolk and chorion formation stage (II) to the major peak containing fish with the ovarian sections of their ovotestes in the growth phase of oogenesis (Stage III/V). While the sample size of Bathypterois *longipes* is smaller, a similar situation probably prevails. Fecundity in *Bathymicrops regis* was found by Nielsen (1966) to be some 300 eggs of the more advanced generation in one ovary of a 117mm SL specimen. The most advanced generation of eggs in the ripe gonads of 11 *B. regis* from the GME (SL range 82.0-92.5mm) gave considerably lower counts (41-103 eggs, $\bar{x}$=73), perhaps attributable to their smaller size. Only 2 of the *Bathypterois longipes* had ovarian sections sufficiently advance to obtain reliable fecundity estimates. They were in fish of 189 and 195mm SL and gave counts of 2237 and 2152 eggs, respectively.

The single specimen of *Bassozetus* sp. I was a female in the growth phase of oogenesis (Stage III/V - Table 29.5), the only ophidiid approaching breeding condition. While there is no direct evidence on the breeding biology of any of the species represented at GME, all belong to one of the oviparous families of the suborder. The Aphyonidae on the other hand are viviparous ophidiiforms (*sensu* Cohen and Nielsen, 1978) with a relatively low fecundity and presumed benthopelagic early ontogeny.

Nothing is known of the early life-history of abyssal macrourids yet, as they are considered to have evolved from slope-dwelling ancestors (Marshall, 1965), this may be analogous with the pattern followed by species on the slope. Recently, it has been argued (Merrett, in press) that, contrary to previous ideas (e.g. Marshall, 1973; Merrett, 1978 and see GESAMP 1986:78), macrourid early ontogeny may take place close to the sea-bed in the adult living depth, rather than in the near-surface waters. The dearth of eggs and larvae of members of this family in collections is a major factor in the argument. Another factor, especially for abyssal species, are the risks of predation and dispersal involved in undergoing a midwater distributive phase. High fecundity could ameliorate this, yet the species approaching breeding condition at GME, *Echinomacrurus mollis* (Table 29.5), was found to have a low fecundity (7 specimens (50-68mm HL) 360-941 eggs; diameter ca 1.6-2.6mm).

Fish feeding

Where possible the specimens from both the OTSB and the BN samples were examined for stomach and intestinal contents. All the dominant species collected were investigated (Merrett, Roe and Thurston, in prep.); only those unusual specimens whose identification requires further confirmation have been omitted. In general, the level of stomach fullness was so low that stomach and intestinal contents were taken together as indicative of the overall diet, rather than a precise evaluation of the last meal eaten. Species are treated in order of relative abundance.

Bathymicrops regis

Fifteen individuals contained identifiable material which yielded a similar number of food items in total (15 - Table 29.6). Small crustacea (present in all but 1 stomach with identifiable contents) dominated the diet, with isopods being most frequent. The occurrence of sediment in 5 specimens suggests that feeding often takes place in contact with the bottom. This conclusion is consistent with what is known of the prey organisms and the negatively buoyant character of the fish itself. It is enigmatic that the numerically dominant fish species in the area should be found to be so lacking in food items.

Bathypterois longipes

Evidently crustacea (91%) were the dominant prey of B. longipes, judged by the 21 individuals with recognisable food items. Copepods were most frequent in the diet, followed by natant decapods and amphipods (Table 29.6).

No sediment was found, which suggests that this microphagous species does not probe the sediment for food. Indeed, the feeding behaviour of congeners, observed from submersibles, is that they stilt above the bottom on their elongate pelvic and caudal fin rays and, facing up current, leap from their three point stance to catch food within range (Church, 1971; Sulak, 1977). The distribution of the dietary organisms identified from the current samples are generally consistent with such an epibenthic feeding tactic.

Echinomacrurus mollis

Eight specimens of E. mollis were too damaged for inspection. The stomachs of the remainder were all <1/4 full and all but one contained identifiable remains in the digestive tract. Another microphagous feeder, this species was richest in identifiable material with a total of 317(+) items recovered from 13 specimens (Table 29.6). Crustacea again dominated the diet isopods were the most frequent constituent group and were found in all specimens. The dominant isopods were Acanthecope cf. galatheae (in 9 individuals with a frequency of 9.6 organisms/individual) and Betamorpha indentifrons (again in 9 specimens; frequency 7.1/specimen). The known ecology of these and the other dietary isopods indicates that they occupy a broadly suprabenthic habitat (see Section 26). Copepods and amphipods were the next most abundant dietary organisms.

Polychaete annelids were present in 10 stomachs. They were recognisable by their setae and/or chitinous jaws and so could not be accurately counted. Their presence, together with that of copious amounts of sediment in all specimens, tends to confirm that E. mollis feeds from, or very close to, the bottom. Such a feeding pattern seems to be consistent with the salient anatomical features of this species (i.e. regressed swimbladder, reduced musculature and ossification).

Coryphaenoides (Chalinura) profundicola.

Contents were found in 6 of the 7 specimens of C. (Chalinura) profundicola, which were up to 3/4 full, yielding a total of 24(+) food items (Table 29.6). Although of smaller individual size than those sampled farther north (e.g. in the PAP area), this is a robust and mobile, benthopelagic species (see above) which is not a microphagous feeder as an adult. Consequently natant decapods of large individual size were the most important prey. They were present in 5 stomachs with a total of 14(+) items. Two species dominated, Acanthephyra microphthalma (7(+) from 2 stomachs) and Benthesicymus sp (4(+) from 3 stomachs). The former species concentrates at or just above the bottom, but has a wide vertical range between 2700m-bottom, whereas the latter was the commonest decapod collected benthic trawls at GME (see Section 17).

In addition, polychaetes were found in 3 stomachs, a bivalve lamellibranch in 1 and a pair of cephalopod beaks in another. These two entities indicate bottom feeding, as do two fragments of Pyrosoma, which were most likely scavenged as a dead organism (cf. Section 24).

Histiobranchus bathybius

Both specimens were opened but, apart from mucus, were found empty.

Barathrites iris.

Only one specimen contained recognisable contents, but bottom sediment was absent from both fish. Three necrophagous amphipods(Eurythenes gryllus, Paralicella tenuipes and Cyclocaris sp. nov.) were identified, suggesting that the B. iris may have been browsing on a food-fall in a manner similar to that described by Lampitt, Merrett and Thurston (1983) for the liparidid, Paraliparis bathybius.

Abyssobrotula galatheae

Stomachs of both specimens were empty, although identifiable remains were present in one intestine. They consisted of the isopods Acanthocope cf. galatheae (8 specimens) and Betamorpha indentifrons (4). These two species dominated the diet of Echinomacrurus mollis so, perhaps both were common in the area, rather than subjects of feeding selectivity.

Bassozetus sp. II.

Three identifiable food items were found in the digestive tract of the single specimen caught. They were an amphipod, Rhachotropis cf. proxima, a scolecithricid copepod and unidentifiable mysid.

Coryphaenoides (Nematonurus) armatus

The single specimen of this species contained only white amorphous residue.

In summary, the two dominant demersal fish species, Bathymicrops regis and Bathypterois longipes, are microphagous feeders, taking a mixture of benthic and epibenthic organisms (Fig. 29.XII). Most of their food was perhaps derived from a similar fauna to that observed by Wolff (1971), during a dive to 4160m in the French bathyscaphe Archimede, who recounted seeing "..... an incredible number of isopods and amphipods swimming close to the bottom (from 0 to 1-2m above it)". *E. mollis* apparently feeds upon epibenthic prey and also on the bottom, ingesting copious amounts of sediment; whereas *C. profundicola* feeds partially upon large, active benthopelagic animals and partially upon sedentary or dead material on or within the sediment.

30. BENTHIC MISCELLANEA

30.1 Decapoda A.L. Rice

Apart from the natant decapods taken in the OTSB (Section 17) the only other decapod taken in the GME benthic catches was the reptant galatheid *Munidopsis thieli* Türkay, which was represented by occasional specimens in three of the OTSB catches (11261#43, #50, and #51) and in two of the epibenthic sledge catches (11262#16 and #19).

Munidopsis is one of a very small number of reptant decapod genera which penetrate the deep ocean. Worldwide the genus is represented by well over one hundred species and occurs over a very wide depth range, one curious species even being known from a single sub-terranean pool on the island of Lanzarote! The remaining species, however, occur from the upper continental slope to abyssal or even hadal depths. In general, and as with other deep-sea groups, the deeper-living species are more widespread than the shallower ones. Thus those species living on the upper continental slope have a fairly restricted geographical distribution, generally being found in only one sea area such as the north-east Atlantic, whereas those living at abyssal depths are often found throughout an ocean and may even occur in more than one ocean.

Munidopsis thieli belongs to the *crassa* group of species which includes several very widespread abyssal forms. *M. thieli* itself, however, is known outside the GME area only from the Iberian abyssal plain from which it was originally described. It is therefore probably restricted to mid-latitudes in the North Atlantic.

All the deep-living *Munidopsis* species for which reproductive information is available produce relatively small numbers of large eggs which almost certainly hatch as very advanced larvae having a rather short pelagic or benthopelagic existence during which they remain close to the bottom.

30.2 Gastropoda M.H. Thurston

The gastropods have been identified by Dr. A. Waren, Zoologiska Institutionen, Göteborg, Sweden, to whom we tender our thanks.

At least 18 species were present in the whole collection. In common with most other animal groups in the deep sea, many taxonomic problems remain to be resolved. Consequently complete identifications have been possible only for a minority of these species. Of the 134 specimens captured, eight examples of the large turrid Theta vayssierei were taken in three trawls. The remaining 126 specimens were found in epibenthic sledge samples, and have been summarized in Table 30.2.1.

Because of the incomplete identifications and the consequent uncertainty as to how many species were present, it was not possible to quantify precisely the relative proportions of prosobranchs and opisthobranchs in the GME collections. It was clear, however, that this material was weighted more towards the prosobranchs than were the extensive Gay-Head-Bermuda Samples (Rex and Waren, 1982) in which prosobranchs represented 76% of the gastropod species. A similar bias was found at the specimen level. Over 98% of the GME specimens were prosobranchs, whereas in the northwest Atlantic material the total was only 87%.

The relatively high diversity within the Trochacea and Turridae is in keeping with the known taxonomic structure of deep-sea gastropod assemblages (Clarke, 1962a; Bouchet and Waren, 1980). The paucity of eulimids and buccinids in our collection is at first sight surprising, as both families figure prominently in deep-sea faunas (Bouchet and Waren, 1985, 1986). However, an examination of distribution tables in the quoted papers showed both families to be much more speciose at continental slope and rise depths, with rather few species with truly abyssal distributions. This pattern confirmed the study by Rex (1973) who found gastropods to be markedly less diverse at abyssal depths.

All of the seven species which have been identified fully, have been recorded previously from the Atlantic Ocean. The single specimen of "Eulima" chionea represents a northward range extension of this rare, recently recognized species (Bouchet and Waren, 1986), and that of Pleurotomella benedicti an eastward extension across the mid-Atlantic Ridge (Clarke, 1962a). For most of these species, the present records are the deepest known, in the cases of *P. benedicti* and *Benthonia tryoni* by over 1000m (Clarke, 1962a; Bouchet and Waren, 1985). *Benthonella tenella* is the most abundant gastropod species at abyssal depths in the western North Atlantic, and is a common constituent of deep-sea gastropod assemblages throughout the Atlantic to depths exceeding 5000m (Rex, 1977; Rex *et al*, 1979; Bouchet and Waren, 1979). Despite these reports only two specimens have been found in the present collections.

There is little direct evidence for feeding strategies in deep-sea gastropods but feeding morphology tends to be fairly conservative within major taxa. Shallow-water trochids and rissoids are largely detritivores or microparticulate grazers (Fretter and Graham, 1962), and it is probable that deep-sea members of the families feed in the same way. Eulimids are parasites of echinoderms (Waren, 1981, 1984), and possess a long stout proboscis which enables them to maintain attachment to the host without the help of the foot (Fretter and Graham, 1962). Eulimids are thought to parasitize their hosts for limited periods of time, and this combined with the trauma of sample sorting and sieving results in dissociation of snails and echinoderms and thus a limited knowledge of host species. Of the 100 eulimid species listed from the North Atlantic (Bouchet and Waren, 1986) hosts are known from 19 species only. Hosts include ophiuroids, echinoids, holothurians and crinoids, but not asteroids. Eulimid species do parasitize asteroids (see, for example, Waren, 1981) but the relatively low incidence of gastropods on this group may explain why only a single eulimid was found in a collection where asteroids were the dominant echinoderm groups (Sections 22, 28).

Embryonic shell whorls of prosobranchs remain exposed into adult life, and the mode of development, planktotrophic or lecithotrophic, can be related to larval shell characters (Robertson, 1971). Although lecithotrophic development, ie direct development or at most a very short larval existence, has been postulated as the norm for the deep-sea, Rex and Waren (1982) have shown a significant increase in the prevalence of planktotrophic development, ie a long-lived planktonic larval stage, with increasing depth among mesogastropods and neogastropods. This increase applies in terms of both species and individuals. Among the entities found at GME, *Benthonella*, *Belomitra*, *Benthomangelia*, *Pleurotomella* and *Xanthodaphne* are known to have planktotrophic development. Knowledge of dispersal patterns, both horizontal and vertical, of the larvae of planktotrophic deep-sea prosobranchs is rudimentary. However, larvae of some species, including *Benthonella tenella* and *Benthomangelia macra*, are known to occur in near-surface waters (Bouchet, 1976a,b; Bouchet and Waren, 1979; Bouchet and Fontes, 1981). Indeed, *Benthonella* larvae were taken in midwater nets at GME (Section 9). Therefore, there is evidence for a direct transfer of material from abyssal depths to the near-surface layers among gastropods, albeit in very small quantities. *B. tenella* does not show evidence of seasonality of breeding (Rex *et al*, 1979) so any potential transport would not be seasonal.

30.3 Bivalvia M.H. Thurston

The bivalves were submitted to Dr. J. Knudsen, Zoological Museum, Copenhagen, and the results presented here are based on his identifications. We are most grateful for his efforts.

Twelve species of bivalve were identified of which eleven occurred in sledge catches (Table 30.3.1) and four in trawls. Of the latter Lyonsiella smidti Friele, 1886 was not found in sledge catches. The distribution of species among superfamilies resulted in a pattern agreeing closely with that established in a survey of all known abyssal bivalves (Knudsen, 1970), in that about half the entities were nuculanoids.

Because the fine mesh centre net of the epibenthic sledge (Aldred et al, 1976; Rice et al, 1979; Rice et al, 1982) fished less efficiently than did the coarse outer nets, the numbers and weights of individuals in the 1-4mm size fraction have been adjusted in an attempt to render them comparable with data from the >4mm fraction. There was a very considerable variation in mean species size (1-526µg) among the bivalves found in these collections. Catches were dominated numerically by two small species, Ledella ultima (39%) and "Yoldiella" (38%). However, in terms of biomass, these species were of minor importance only, representing 4% and 2% of the total respectively (Table 30.3.1). In contrast, the large species Abra profundorum which accounted for 9% and Nuculana pallida for 6% of all individuals, were very significant in terms of biomass, representing 67% and 20% respectively.

Excluding the incompletely determined entities "Yoldiella" and Tindaria cf callistiformis, all species obtained have been recorded previously from the Atlantic Ocean, with N. pallida, A. profundorum and Poromya tornata known also from the Indian and/or Pacific Oceans. Most of the fully determined species have been taken previously in the abyss, and appear to be confined more or less to those depths. Exceptions are Pristigloma nitens a continental slope species recorded once (dubiously according to Knudsen, 1970) from the continental rise, and Microgloma turnerae known only from mid-continental slope depths (Sanders and Allen, 1973). With the exception of P. nitens, A. profundorum and P. tornata none of the species have been recorded from more than a few localities. This apparent rarity is more likely to be a function of under-funding and therefore low effort in taxonomy, than a true reflection of species rarity.

Clarke (1962b), by analogy with shallow-water species, summarized feeding in abyssal bivalves, recognizing deposit feeders, suspension feeders, and carnivores. Knudsen (1970) in his analysis of abyssal bivalves found that these categories contained 47%, 24% and 25% respectively of the known species, with the remaining 4% having unknown feeding modes. In material from the sledge, three species (27%) could be classified as carnivores, two (18%) as deposit feeders, and six (55%) as deposit feeders which may have a secondary ability as suspension feeders. The absence of any specialist suspension feeders reflects the low surface productivity and negligible resuspension of sediment particles by weak near-bottom currents. In terms of individuals, carnivores represented only 2% by number and 2% by biomass. Comparable figures for deposit feeders, and deposit feeders with a possible suspension feeding mode were 13% and 73%, and 85% and 25% respectively.

Most abyssal bivalves undergo lecithotrophic development, ie the dispersive larval stage is of very short duration (Knudsen, 1967, 1970). Kundsen (1970) listed 23 species for which development type had been determined. Eighteen of these species showed lecithotrophic development including P. tornata and a species related to P. permirum. Only two species were listed as having pelagic development with long-lived planktonic larvae. However, one of these species was A. profundorum which constituted 67% of the bivalve biomass. There is, therefore, a potential among bivalves for appreciable horizontal if not vertical transport relative to the overall biomass.

30.4 Benthic Ostracoda

Benthic ostracods, predominately podocopids, were identified by Dr. R. Whatley (University College, Aberystwyth) - Table 30.4.1.

They were sampled either by the fine mesh net of the BN1.5 (#16), by the suprabenthic net (#50), by a small conical net of mesh 61µm mounted inside the mouth of the OTSB (#43, 50, 58) or by a plastic tube mounted in the mouth of the otter trawl. The data have been combined in Table 30.4.1 and not attempt has been made to standardise the numbers.

31. DISCUSSION AND CONCLUSIONS

The overall biological problems associated with the disposal of radioactive wastes in the deep oceans and the general questions which need to be addressed have been reviewed previously (Rice 1978, Angel, Fasham and Rice 1981, Park, Kester, Duedall and Ketchum 1982, GESAMP 1983, Angel 1983b, 1984b, Holliday 1984, NEA 1984, Booty 1985, Yayanos 1986). Recent reports associated with the disposal of low/intermediate level radioactive wastes in the NE Atlantic are given by NEA (1985), Feldt, Kanisch, Kanisch and Vobach (1985) and Rutgers van der Loeff and Lavaleye (1986). Much of this previous work draws attention to the paucity of knowledge concerning biological systems and processes within the deep ocean (see Rowe 1983a for a recent synthesis) and, prior to Discovery Cruise 156, information on the deep biology of GME was similarly scanty (Roe 1985b).

It would be possible to discuss many aspects of deep-sea biology from the present data set. However, individual authors within this report have set their work in context with previous observations, and it is not the purpose of the present discussion to reiterate all of these individual comments. Rather it will focus on the primary contract objective of the biological work at GME viz the quantification of "the processes by which radionuclides may be transferred through the deep ocean environment by marine biota".

Most mass midwater flux is accounted for by rapidly sinking large particles of biogenic origin (McCave 1975, Fowler and Knauer 1986). It therefore follows that flux through the water column is dependant upon biomass, and that a major requirement for an assessment of biological transport processes is a reliable estimate of biomass.

The midwater biomass profiles at GME (Section 6) are similar to those made elsewhere. Diel changes occurred mainly within the upper 1000m and there was an exponential decrease in biomass with depth (Jaschnov 1961, 1962, Grice and Hulsemann 1965, 1967, Vinogradov 1968, Wishner 1980a, Angel and Baker 1982, Hargreaves 1985a, Kikuchi and Omori 1985). Absolute comparisons with previous studies are impossible to make because of differences in sampling gear - and hence size range of animals caught, and possible differences due to different areas and seasons. The total measured midwater biomass at GME was ca 2g dry weight beneath 1m^2 of sea surface (Section 6). The most comparable data are those taken further to the north and east in the Atlantic by identical RMT 1+8 nets (Angel and Baker 1982, Hargreaves 1985a). The present GME values are lower than these previous records (Fig. 6.IX). However, when compared with data taken with smaller mesh nets (and assuming that small plankton will have a greater biomass than large) the present values seem relatively high (Jashnov 1961, 1962, Grice and Hulsemann 1965, 1967, Vinogradov 1968, Wishner 1980a).

The present values will certainly underestimate the total midwater biomass at GME because they are based upon limited size spectra which do not encompass the entire biological size range. In this respect they are no different from previous results - all of which will be underestimated by an amount dependant upon the size ranges not sampled. The major ommission at GME is probably the smaller plankton, <0.32mm in size. This must have been abundant, at least in the top 1000m, to sustain the populations of Pyrosoma (Section 6). Some idea of the mass of small particles at GME can be obtained from Large Volume Filtration System (LVFS) data obtained at GME between 1982 - 1986 (Simpson et al., in press, in prep). The LVFS samples particles (both biogenic and non-biogenic) within the size ranges 10-170μ and 8-266μ. The mean wet weight of profiles made between 41-474m was 54.5 gm/m^3 (Range 19.1-80.0) and of profiles between 684-5434m was 12.2 mg/m^3 (Range 6.8-19.9). Most of these particles were probably biogenic and these figures are up to an order of magnitude higher than the corresponding derived wet weights of plankton and micronekton given here (Table 6.2-8)

Similarly the benthic bomass was underestimated by virtue of not sampling the smaller size fractions - the meiofauna, nanofauna and bacteria, (see Section 22). The meiofauna at least will probably form a very significant part of total benthic biomass (e.g. Thiel 1975, 1983b).

Despite the underestimates there is little doubt that the biomass at GME is low. This is presumably a function of low primary production (Section 4) and depth, although the relationship between surface productivity and bathypelagic biomass is not clear (see Section 6). However, it seems unlikely that the biomass values at GME (both midwater and benthic) are abnormal. They reflect the general paucity of the biota at abyssal sites throughout the world's oceans.

If the low biomass at GME is typical then so too is the decline in biomass with increasing depth. The similarity in the rate at which midwater biomass decreases with depth over wide geographic areas and size ranges (Wishner 1980a, Angel and Baker 1982, Section 6, Fig. 6.IX) strongly suggests that the processes controlling the distribution of biomass in the deep oceans are similar despite differences in surface productivity.

As far as biomass is concerned therefore, GME is probably a typical deep ocean site. However, it is pertinent to ask whether the situation at GME is likely to be constant or whether it is subject to variability. Data from temperate regions may be expected to show considerable seasonal variability, but the effects of this on deep-sea pelagic and benthic faunas are uncertain. The biomass data recorded by Angel and Baker (1982) and by Hargreaves (1985a) were taken from areas to the north of GME in April/May. Massive depositions of phytodetritus originating from the spring bloom have been observed at depths of up to 4475m off SW Ireland and in the Rockall Trough (Billett, Lampitt, Rice and Mantoura 1983, Lampitt 1985, Barnett pers. comm). A similar seasonal sinking, this time of senescent radiolaria, occurs in late summer in the north Pacific (Vinogradov and Tseitlin 1983). Such variations are not restricted to temperate regions however. Seasonal variations in midwater fluxes have been observed in deep sediment traps in the Sargasso Sea and Panama Basin (Deuser and Ross 1980, Deuser 1984, 1986, Honjo 1982, Ittekot, Deuser and Degens 1984, Ittekot, Degens and Honjo 1984), and seasonal variations in zooplankton abundance occur to depths of at least 2000m in the Sargasso Sea (Deevey and Brooks 1971). Other indirect evidence of seasonality in the deep sea comes from seasonal reproduction in several species of echinoderms and fish (Tyler and Gage 1980, 1984, Tyler, Grant, Pain and Gage 1982, Rannou 1975, Gordon 1979), from the existence of varves in the Gulf of California (Calvert 1966), from supposed annual growth bands on deep-sea molluscs and fish otoliths (Turekian et al., 1975, Savvatimskiy, Kokh and Yernst 1978, Geistdorfer 1982), and from variations in the deep-sea community oxygen consumption (Smith and Baldwin 1984b).

Thus seasonal variability may be expected to occur at GME and there is indeed evidence to suggest that it does. Indirect indications of such variability are provided by the midwater fish data (Section 20), but seasonality has been observed directly from sediment traps deployed at GME between December 1985 and

October 1986. Fluxes were highest between December and May and lowest between May and July (Lampitt in prep.). Measurements from sediment traps, LVFSs and transmissometers all show similar trends in fluxes at GME (Lampitt in prep., Simpson et al., in prep.) and these data need confirming and extending.

The effects of any seasonal variations on biomass are uncertain. A seasonal increase in food may stimulate reproduction in both benthic (e.g. Tyler et al., 1982) and midwater animals (Vinogradov and Tseitlin 1983), but whether the production of small progeny is balanced by the loss of large parents is unknown.

A variety of other variants could influence the present data (see Angel 1984a for a general discussion). Regular variations which are non-seasonal are less likely to influence the bathypelagic and benthic communities at GME. Diel migrations probably do not extend to depths below 2000m (Angel, Hargreaves, Kirkpatrick and Domanski 1982, Roe 1985b, IOS unpublished data), and cyclic ontogenetic migrations have not been found in abyssal depths though they do occur to depths of at least 2000m in polar and temperate regions (e.g. Longhurst 1976, Badcock 1984a).

The present data could also be influenced by sporadic migrations or by patchiness and sampling variability. Sporadic migrations are very difficult to detect with conventional sampling programmes (Roe 1974, Pearre 1979). A very few possible examples were found at GME and are discussed later. Patchiness will probably effect the catches of some groups (and hence the biomass) in the upper 1000m e.g. pteropods, euphausiids (Sections 9, 16), but the influence of patchiness and sampling variability on deep sea communities is not well known. No significant variability was found in the catches of various pelagic groups taken in a series of repeated hauls at a depth of 3500m to the north of GME (Roe in prep) but patchiness does occur in deep sea benthic communities e.g. Jumars and Eckman (1983).

The present data are derived essentially from a single set of observations made at a particular time of year. They are therefore subject to a variety of potential uncertainties, and extrapolations based upon this single sample set may be more or less unsatisfactory. Verification of the data is required by some level of repeated sampling. If we assume that the potential effects of variability on the present biomass data are unimportant, then it is most unlikely that any significant biologically mediated mass flux will occur at GME.

The previous discussion has centred upon downward flux, but from the viewpoint of radioactive waste disposal it is flux back up through the sediment and water column which is most important. Any such fluxes which are biologically active will go against biomass gradients, and any passive fluxes may be diminished by the scavanging activity of sinking particles (see e.g. Angel 1984b). No evidence for mass upward flux has been found at GME and none would be expected, agreeing with GESAMP (1983), NEA (1984), Needler (1986), and Rowe, Merrett, Shepherd, Needler, Hargrave and Marietta (1986) all of whom concluded that mass flux by biological transport was unimportant when compared with physical processes.

Although mass biological transport will almost certainly not occur at GME, there is some evidence of biological pathways whereby radionuclides could be transported between the deep sea floor and the surface. It is also likely that most of those pathways will occur in the large organisms (both plankton and micronekton) sampled here - and consequently the absence of data on midwater biota smaller than 0.32mm will be unimportant in this context. Radionuclides escaping from emplaced containers have to cross the sediment barrier prior to exiting into the water column. The current estimates for emplacement depths are 50±20m using penetrators and several hundreds of metres for drilled emplacement. If faulty disposal occurs so that containers are not buried then radionuclides will eventually escape directly into the surface sediment or into the water column. Biota may take up contaminants by ingestion or absorbtion, and these contaminants could then be biologically transported by isolated movements of individuals within populations, by mass migrations of populations, or by feeding and reproductive processes. Since upward transport is of prime interest here it is logical to begin consideration of the present evidence for potential pathways with the benthos.

Assuming correct disposal, and subsequent to any upward physico-chemical migration through the sediment, the first animals exposed to radionuclides will be the infauna, ranging in size from bacteria to echiurans whose surface feeding trails extend to several metres (Huggett in press, Ohta 1984). No cores were taken on Discovery Cruise 156 so there are few quantitative data on infaunal animals to complement those taken by the sledge and otter trawl.

Bioturbation will mix sediments within the top 10s of cms and has been observed at GME to a depth of 20cm (Thompson et al., in prep., Section 28). This process should therefore only influence the movement of radionuclides after (if?) they have migrated through the sediment from considerably greater depths. However, open burrows exceeding 2m in length have been found at GME (Weaver and Schultheiss 1983). These are presumed to be biogenic and recent in origin and it is conceivable that they are made by the large echiuran worms photographed by Huggett (in press). Bioturbation by the infaunal holothurian Molpadia has been discussed in Section 28; this is believed to extend to a depth of 10cms.

Apart from mixing near surface sediment, bioturbation may also influence the mobility of isotopes by active ejection of suspended material up into the water, and by roughening the bottom texture so that it is more readily eroded by bottom currents (Angel et al., 1981). Again Molpadia provides an example of both mechanisms - by defaecation and by the construction of mounds. Many further examples of animal tracks, trails and surface irregularities have been photographed at GME (see Sections 19, 23, 24, and 28).

The Bathysnap observations at GME (Section 24), indicate that the rate of change in bottom topography >1cm in height, due to biological activity, was comparable to rates observed in the central N. Pacific and at the base of the continental slope off Ireland (Thorndike et al., 1982, Lampitt et al, 1986). However, the changes at GME may have been accentuated by the arrival of a food parcel (Pyrosoma) from the surface layers. Such food falls are rare events in the deep ocean (Stockton and DeLaca 1982), although decaying Pyrosoma have been previously found on the bottom (see Van Soest 1981). Nevertheless the Bathysnap sequence of the activity around the decaying Pyrosoma is of considerable interest. Erosion of bottom topography by currents was not observed by Bathysnap, and is therefore presumably slow. Bottom currents at GME are variable and are most rapid near to an abyssal hill (Saunders 1985). Slow bottom currents may account for the relative scarcity of suspension feeders at the site (see Sections 22, 28, 30).

Not surprisingly direct evidence for bioturbation has been found at GME and this could bring buried material to the sediment/water interface. Once there it could be ingested by sediment feeding organisms living on or close to the sediment surface.

Again there is direct evidence for such feeding here. Stomach/gut contents of decapods, asteroids, echinoids, holothurians and demersal fish have been examined, and sediment and/or infaunal animals have been found in representatives of all these groups (see Sections 17, 19, 28 and 29). Previous work on the feeding of these animals supplement and amplify the present observations (see previous references), and ingestion of sediment occurs in other benthic groups sampled at GME (e.g. bivalves - Knudsen (1970), gastropods (Fretter and Graham (1962), Section 22). Deep-sea holothurians concentrate radionuclides scavenged from the sediment surface, and a variety of other deep sea taxa, caught adjacent to low level radioactive waste dump sites, have been found to contain elevated concentrations of radioisotopes (Feldt et al., 1985). Estimates have been made here of the rates at which some abyssal holothurians may perturb sediment (Sections 19,28). For each 10,000m^2 area of sediment (these rates vary from 12 to 30 years - but it is difficult to assess the reliability of the estimates. However, it is important to note that these estimates exclude the effects of the dominant benthic invertebrates, the porcellanasterids and the infaunal holothurian Molpadia for which there are no reliable abundance data.

If sediment consumers remain close to the bottom then so would any ingested contaminants. However, some of these species have vertical distributions at GME which extend thousands of metres up into the water column, thereby allowing the possibility that they may directly transfer benthic material (plus contaminants) into midwater. Once in midwater they may become subject to vertical transport processes prevailing in the pelagic ecosystem.

Among the decapods (Section 17), Acanthephyra micropthalma was caught between the bottom and a depth of 2700-3100m - i.e. a vertical range extending half way up the water column. The guts of individuals caught near to the bottom contained sediment, but the gut contents of midwater specimens were not examined. Benthesicymus iridescens was almost entirely benthic, feeding partially upon the bottom, but individuals were also caught up to 90m above the sea bed. Adults of the pelagic holothurians *Scotothuria herringi* and *Enypniastes diaphana* were relatively common at depths of up to 90m above the sea bed (Section 19). Large individuals of *S. herringi* have also been caught some 4000m above the bottom at GME and adult *E. diaphana* have been taken thousands of metres above the sea bed in other areas of the Atlantic. The guts of near bottom specimens were usually packed with sediment but those of midwater captures were empty.

Other species and groups were caught at GME which are known to occupy both benthic and pelagic realms, and which have previously been recorded as ingesting sediment or infaunal animals. The chaetognath *Heterokrohnia davidi* ingests sediment and has been found within 20m of the bottom and up to 2700m above it (Section 8, Casanova 1986). Necrophageous amphipods (Section 15) are frequently caught at considerable distances off the bottom, e.g. *Orchomene gerulicorbis* occurred here between the sea bed and a depth of 3110-3500m. Another species, *Eurythenes gryllus*, found here close to the sea bed, is known to make extensive vertical excursions and a specimen has been caught over 4000m above the bottom with sediment in its gut (McGowan 1974). The demersal macrurid *Coryphaenoides armatus*, represented here by a single specimen (Section 29), has been caught well above the bottom with midwater prey in its stomach; it feeds mainly at the sediment surface (Pearcy and Ambler 1974, Haedrich and Henderson 1974, Mauchline and Gordon 1984). *Bathypterois longipes* was relatively abundant at GME, apparently feeding just above the sediment surface; its cogenor *B. dubius* has been caught ca 1000m above the bottom S.W. of the Azores (Booty 1985). Finally, bathypelagic copepods may have vertical ranges of several thousand metres (e.g. Grice and Hulsemann 1965); near bottom copepods are known to ingest particles which may originate from the bottom (Gowing and Wishner 1986).

Vertical transport via feeding requires either that individual animals undertake extensive migrations, or that a ladder effect exists whereby the primary sediment consumer is eaten by an animal which migrates further up the water column before itself being eaten and so on. Vinogradov (1953, 1955) postulated such an effect for the transfer of material from the surface to the deep sea but data to substantiate the deeper end of this ladder are extremely suspect (see for example Longhurst 1976). Apart from the occasional midwater capture of individual benthic animals there is no evidence that either process is significant in an upward direction. It is impossible to ascertain the movements of individuals within populations, or even the movements of populations distributed in small numbers over wide depth ranges (Roe 1974, Pearre 1979). Consequently one cannot determine whether, for example, individual A. micropthalma move through a depth range >2000m, and if so, with what frequency. Similarly there is no evidence for an upward migratory ladder in the deep sea, and material would have to rise to a depth of at least 1700m before it came within the range of known diel vertical migrants.

Hargreaves (1985a) analysed the distributions of decapods, euphausiids and mysids at 42°N 17°W and found no direct faunistic links between abyssopelagic and mesopelagic communities. The same is true of the micronekton at GME. The decapod Hymenodora gracilis had the most consistent bathy/abyssopelagic distribution and occurred in small numbers between 1910-5233m. Even within this vast vertical range it remained outside the zone of active vertical migration and outside the direct influence of the benthos. Furthermore it is a typical flimsy deep-sea decapod, and there is no evidence that it eats any large or active prey.

Two subsidiary methods of feeding transport may also occur at GME. The parasitic isopod cryptoniscid C (Section 14) was caught between 1400m and the bottom. This parasite could be associated with the decapods A. micropthalma or H. glacialis - the only appropriate pelagic species at GME with depth ranges approaching those of the parasite. Similar parasitic transport could occur via the pelagic holothurian S. herringi which may be parasitized by nematodes (Billett et al 1985). Possible transport of radionuclides by parasites is an interesting, though probably irrelevant, aside.

Finally, dirty feeding, or the rising-particle hypothesis of Yayanos and Nevenzel (1978), could operate at GME. This hypothesis supposes that oil globules or lipid particles could rise up rapidly through the water column. They could therefore act as a pathway for shortlived radionuclides - as has been suggested for fish eggs (see below), but the process has yet to be demonstrated.

Apart from feeding, biological transport may also occur via reproductive processes, larval development and dispersal. Indeed GESAMP (1983), Needler (1986) and Rowe *et al.*, (1986) specifically addressed the potential pathway produced by the release of bouyant eggs from the bottom. They concluded that this mechanism may be more important than slow physical processes for the transfer of short-lived radionuclides to the surface.

Much of the previous modelling and assessment associated with biological aspects of oceanic radioactive waste disposal has focussed on demersal macrurids, especially on *C. armatus*. This species may be of potential commercial interest in the temperate continental rise areas of the NE Atlantic, and a single specimen was caught at GME. There are few collections of the early life history stages of macrurid and abyssobenthic ipnopod fish, and most of these have been taken at epi and mesopelagic depths (e.g. Merrett 1978, Okiyama 1986). However, practically nothing is known of the reproductive strategies of these animals (summarised by Mead, Bertelsen, and Cohen 1964); their larval taxonomy is poorly understood and whether or not a pelagic larval phase is the norm is very much open to question (Merrett in press).

Pelagic development does occur in some benthic groups at GME. In the echinoderms egg size indicates likely development. Eggs have been examined in a variety of species and larvae/juveniles were caught at various depths (Sections 19,28). The echinoid *Plesiodiadema* probably has a pelagic larva, and the asteroids *Hyphalaster* and *Styracaster* probably produce larvae having limited powers of dispersal. Asteroid and ophiuroid larvae were caught in midwater at GME but these probably originated from shallow living species and were advected into the area. The benthic holothurians *Synallastes*, *Mesothuria*, *Peniagone*, and *Pseudostichopus* probably have abbreviated larval development or direct *in situ* development. In contrast, juveniles of the benthic *Benthodytes* were caught at depths of up to 4000m above the bottom. Adult *Benthodytes* were not caught at GME - suggesting horizontal as well as extensive vertical dispersion. Adults of the related genus *Psychropotes* were taken, and these probably have a pelagic juvenile stage similar to that of *Benthodytes*. Of the pelagic holothurians, a single juvenile *Enypniastes diaphana* was caught 2500m above the bottom and it is assumed that *Scotothuria herringi* has a similar pelagic development.

The benthic gastropod *Benthonella* occurred at GME and its pelagic larvae were caught about 2000m above the bottom - possibly *en route* from the surface to the sea bed. Larvae of deep-sea turrids and eulimids were caught close to the bottom, suggesting limited dispersal, and the bivalve *Abra profundorum* may have protracted planktonic development (Sections 9, 30). Shallow living gastropod larvae were also caught in midwater at GME and, as with the asteroids and ophiuroids, these were probably advected into the area.

Potentially the most spectacular ontogenic migration is that of the benthic decapod *Plesiopenaeus*. Adults were relatively common in otter trawl catches and a single specimen of the larval genus *Cerataspides* was caught close to the surface. Burkenroad (1936) suggested that *Cerataspides* is the larva of *Plesiopenaeus*, but there is no supporting evidence for this attribution which must be considered doubtful (Section 17). As with echinoderms and molluscs, larvae of relatively shallow living benthic decapods were caught at GME. These must have been transported into the area from neighbouring seamounts or adjacent coasts.

Finally, within midwater, larvae of meso/bathypelagic fish (e.g. *Cyclothone*, *Cerotoscopelus*) and decapods (*Gennadas*, *Sergestes*) were caught at shallower depths than adults (Sections 17, 20). This implies potential ontogenetic migrations of up to ca. 2000m within the mesopelagic/bathypelagic zone. Similar observations have been made previously at GME (Nellen 1973, Rice and Williamson 1977). A reverse mesopelagic migration occurs in *Amphionides* where adults live in surface layers whereas the larvae are deeper (Section 18).

Much of the previous discussion concerns vertical transport. Vertical zonation of biota occurs throughout the water column and, as a result, there are few direct links between the mesopelagic and bathy/abyssopelagic ecosystems. In contrast, most species and groups have very wide horizontal distributions and few (if any) of the animals caught at GME will be restricted to the immediate geographic area. There is therefore the possibility that horizontal exchange within populations could cause widespread dispersal from the area. Extensive horizontal migrations are known e.g. the schyphozoan *Mastigias* (Hamner and Hauri 1981), antarctic Krill *Euphausia superba* (Kanda, Takagi and Seki 1982) and oceanic squid and tuna (e.g. NEA 1985). Vertical migrants crossing current shears may also be transported considerable horizontal distances (e.g. Hardy and

Gunther 1935).

The occurrence of larvae derived from shallow living benthic animals shows that horizontal transport mechanisms exist at GME. In these instances advection is into the area, but presumably similar processes could also take animals away. The prevailing current direction at GME, at least in the mesopelagic, is likely to be south easterly (Stramma 1984, Section 2) and so any near surface dispersal is also likely to be in this direction

Roe (1985) briefly reviewed the zoogeographic context of GME. The site lies to the south and west of the permanent frontal system SW of the Azores (Käse and Siedler 1982, Gould 1985, Siedler, Zenk and Emery 1985). Mesoscale variability occurs in this area (Gould 1985, Fasham, Platt, Irwin and Jones 1985) but there was no evidence for a southerly movement of the front during the present sampling programme. Movements of this front could influence flux rates within the water column at GME and seasonal data are required to evaluate this possibility.

Horizontal migration by demersal animals may be of more potential significance at GME than similar pelagic movements. Extensive fisheries exist on adjacent islands and upon the north-west African slope, but few demersal fish have distributions which extend from the abyssal plain to depths shallower than 2000m (Merrett and Marshall 1980). Similarly there are distinct differences in the composition of the demersal fish faunas to the north and south of the temperate/subtropical Atlantic (Section 29, Merrett in prep.). These differences are thought to reflect differences in surface productivity and seasonality, but they have the effect that any potentially commercial deep-sea fish stocks do not extend into the GME area.

Finally, although a number of separate biological pathways have been found whereby radionuclides could move via the biota from the sea bed to the surface, it is necessary to put these into perspective. The numbers of individuals caught here which could contribute to such transport is extremely small - single specimens of the pelagic holothurians E. diaphana and S. herringi, a single individual of the decapod Cerataspides, three individual larvae of the benthic holothurian Benthodytes and of the gastropod Benthonella, and a few necrophageous amphipods and parasitic isopods. Clearly the biomass involved in this upward transport is infinitessimally small - even the largest animals, the pelagic holothurians, are largely water (96% - Barnes _et al_., 1976) and will therefore contribute little to any dry weight flux. Similar arguments can be applied to the observed horizontal flux which is restricted to larval forms.

32. SUMMARY

1. The structure and composition of the biological communities inhabiting the water column and sea bed at Great Meteor East are analysed and compared with previous observations.

2. Primary production measurements are described.

3. Feeding and reproductive biology of some benthic and benthopelagic species is described and the implications discussed.

4. The physical context of GME is briefly described.

5. The biomass at GME, both in midwater and on the bottom is low. However, the values are probably typical for the depth and latitude.

6. The midwater biomass is underestimated because biota smaller than 0.32mm were not sampled. The <0.32mm size fraction probably contains more biomass than the observed >0.32 size fraction. The missing small size fraction will probably not contribute to individual biological pathways.

7. Similarly the total benthic biomass is underestimated.

8. The exponential decline in midwater biomass with increasing depth compares well with previous observations. The processes controlling deep-sea biomass are probably similar over wide geographic areas and wide size ranges of animals.

9. Direct observations on the rate of change of the sediment surface due to the biota and to currents indicate that any changes are slow.

10. No evidence has been found to suggest that mass biological transfer of radionuclides from the sea bed to the surface will occur at GME.

11. A variety of biological pathways have been found whereby radionuclides could move through the water column via the biota, but the incidence of

these pathways and the biomass involved is exceedingly low.

12. Similarly there is very little evidence of significant horizontal dispersal via the biota at GME.

13. It is emphasised that the present results are based almost entirely upon a single sample set. There is very little data on the effects of variability, repeatability and seasonality on the biological communities at GME.

14. There is no data on the frequency of any of the observed biological movements between abyssal and shallow ecosystems.

15. Further work is needed to verify the present observations and to provide greater seasonal coverage.

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The structure and composition of the biological communities inhabiting the water column and sea bed at Great Meteor East are analysed quantitatively and qualitatively. The results are compared with previous observations. No evidence has been found to suggest that mass biological transfer of radionuclides from the sea bed to the surface will occur at GME. Some biological pathways exist whereby radionuclides cound move through the water column via the biota, but the incidence of these pathways and the biomass involved is extremely low. It is emphasised that the present data are derived from a single set of observations. Further work is needed to verify the present results and to assess the effects of variability and seasonality on the biological communities at Great Meteor East.

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