

The vertical distribution of micronektonic decapod and mysid crustaceans across the Goban Spur of the Porcupine Seabight

Patricia Mary Hargreaves

SARSIA



Hargreaves PM. 1999. The vertical distribution of micronektonic decapod and mysid crustaceans across the Goban Spur of the Porcupine Seabight. *Sarsia* 84:1-18.

The vertical distribution of micronektonic Decapoda and Mysidacea (Crustacea) is examined along a cross-slope transect of stations with soundings ranging from 192 m to 1800 m in the Porcupine Seabight during spring 1994. Eight species were found only at the three deep-water open oceanic stations to the west of the slope, while the horizontal ranges of others extended from deep-water to the outer (lower) slope station. The numbers of species caught at the inner (upper) slope and shelf station were lower than offshore. The species assemblages were broadly different at the deep-water, upper slope and shelf stations with no species occurring continuously across the whole of the transect. Three deep-living species were found in higher concentrations near-bottom over the slope than at similar depths at the adjacent open ocean stations. Factors affecting distribution of species are discussed.

P.M. Hargreaves, Southampton Oceanography Centre (NERC), Empress Dock, Southampton SO4 3ZH, United Kingdom. E-mail: pmh@soc.soton.ac.uk

Keywords: Decapod crustaceans; North Atlantic; Micronekton.

INTRODUCTION

The vertical and horizontal distribution of decapod and mysid crustaceans in open oceanic areas of the North-east Atlantic is reasonably well-known (e.g. Mauchline & Murano 1977; Lagardère 1976, 1977, 1985; Fasham & Foxton 1979; Hargreaves, 1984, 1985a, 1985b). However, there is relatively little information available about their distributions across slope areas of the northern northeastern Atlantic including the Goban Spur, south of the Porcupine Seabight. Merrett (1986) pointed out that a slope area is likely to contain a wider range of ecological niches than occurs in the open ocean and that this may be related to the variety of topography and to enhanced productivity. The latter may result from the mixing effect of oceanic, slope and shelf currents.

Some information is now available about the responses of midwater organisms to the shallowing of the sea floor on the continental slope. Vinogradov (1968) described an exponential decrease of pelagic biovolume with increasing depth. However Wishner (1980) showed that in some areas there was an increase in biovolume close to the sea floor. Omori & Ohta (1981) reported that sergestid shrimps aggregated several metres above the sea floor in Suruga Bay, Japan.

Hopkins & al. (1981) showed that, in the region of the West Florida continental shelf, the extent of the distribution of micronekton upslope was related to its vertical profile offshore, many deep-living oceanic species rarely being found over the shelf.

Bailey (1982) has shown that blue whiting take a

demersal habit as the slope crosses their oceanic optimum depth range. Hargreaves (1984, 1985b) describing the response of decapod and mysid distributions to the shallowing of the sea-floor across the outer slope area of the Porcupine Seabight in the North Atlantic, observed that the numbers of several mid-water oceanic species increased near to the sea floor.

Other investigations have centred on the distribution of upper slope and shelf species in the Mediterranean (e.g. Abelló & al. 1988; Cartes & al. 1994) and off the Galician continental shelf (Fariña & al. 1977). Factors affecting the zonation of species have been shown to include hydrography, types of bottom sediment and predator/prey relationships.

The aim of this study is to describe newly acquired data on the vertical and horizontal distribution of decapod and mysid species which inhabit open ocean, mid-slope, upper-slope and shelf areas across the Goban Spur in the Porcupine Seabight (stations G, F, D-B, soundings 1800 m-192 m). These data are compared to those obtained in the same area during 1979 using similar sampling methods. Factors affecting species distribution are discussed.

MATERIAL AND METHODS

SAMPLING METHODS

In April/May 1994 a series of vertically stratified hauls were made within a period of 18 days at five RRS *Charles Darwin* (cruise 85) station positions G, F, D-B (Table 1, Fig. 1). Samples were collected using a multiple Rectangular Midwater

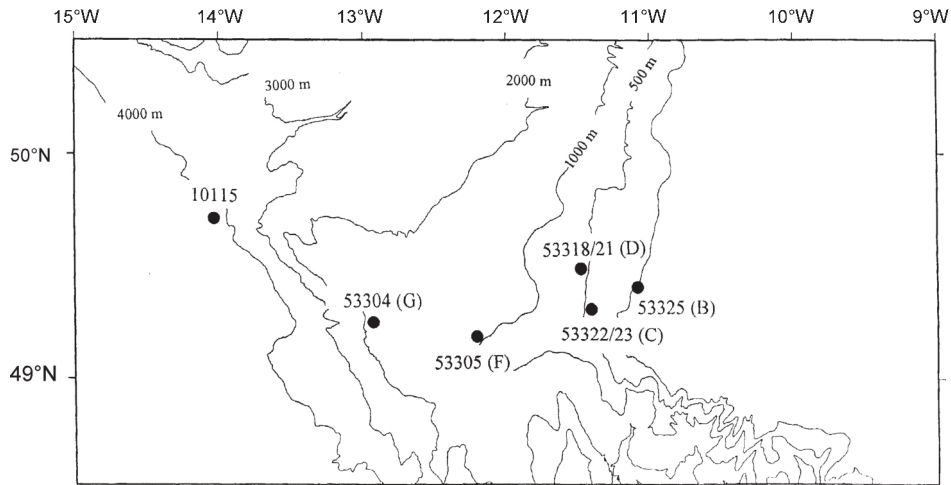


Fig. 1. Positions of station 10115 (1979) and stations 53304, 53305, 53318/21, 53322/23, 53325 (*Charles Darwin* cruise 85, 1994)

Trawl (RMT 1+8M) (Roe & Shale 1979) at a towing speed of 1.05 m s^{-1} . This is an acoustically operated opening/closing net system, which takes three consecutive sets of zooplankton and micronekton samples at adjacent levels. Thus one sample is obtained for each depth range. Decapod and mysid samples from the RMT8M net are the subject of this paper.

At open oceanic deep-water stations G and F discrete hauls were made at two positions centred on $49^{\circ}07'N$ - $49^{\circ}20'N$, $12^{\circ}07'W$ - $12^{\circ}50'W$. At station G samples were taken at 100 m intervals throughout the deep-water column down to within about 200-300 m of the sea floor (a maximum of 1300 m by day and 1100 m by night). A similar sampling strategy was adopted at the slightly shallower station F except that hauls were made to a maximum of 1000 m by day and 1025 m by night.

Two further series of samples were taken over the continental slope at stations D (outer slope) and C (inner slope) which together formed a third and fourth series of day and/or night hauls at 100 m depth intervals throughout the water column. At station D discrete hauls were made to a maximum of 630 m by day and 575 m by night, (sea floor 574-875 m). At station C (sea floor depth 280-376 m) a series of two day-time hauls were made to a maximum of 200 m and three night hauls to a maximum of 300 m. The fifth station B was fished over the

continental shelf (sea floor depth 192 m) where three hauls were made by night to a maximum of 135 m. A full station list is given in Pugh (1995).

The depth of fishing, water temperature, and speed of net through the water were continuously monitored by sensors mounted immediately above the net, and the information was telemetered back to the ship. The RMT8M net, which has a nominal mouth area of 8 m^2 and a mesh size of 4.5 mm, samples crustacean micronekton with carapace lengths (CL) $> 2 \text{ mm}$. Using the data on net speed obtained from the flowmeter, the mean speed of each of the nets was calculated and used to estimate the average net angle (using the formula given by Roe & al. (1980) enabling the numerical and biomass data to be standardised to units of $10\,000 \text{ m}^3$ water filtered. At a towing speed of 1 m s^{-1} , the average volume of water filtered was $28\,000 \text{ m}^3$ per hour. The volume of water filtered during each haul is given in Appendix I. Several CTD casts were deployed during Cruise 85 to the east of the Seabight at $49^{\circ}08'$ - $49^{\circ}25'N$, 11° - $13^{\circ}30'W$, one to a maximum depth of 200-300 m, two to a maximum of 1200 m and one to 1500 m. Unfortunately the CTD cast closest to station D malfunctioned, temperature values were recorded but not salinity.

Previously, during *Discovery* cruise 105 in late August/September 1979, one open oceanic deep-water station was worked

Table 1. Sampling stations across the Goban Spur: station 10115 (RRS *Discovery* cruise 105); stations 53304, 53305, 53318/21, 53322/23, 53325 (RRS *Charles Darwin* cruise 85).

Station	Code	Mean Position	Description	Total sampling depth (m)		Est. depth range of deepest haul above bottom (mab)		Depth of sea-floor (m)	Date
				day	night	day	night		
10115	-	$49^{\circ}45'N$ $14^{\circ}04'W$	Deep-water	10-1500	10-900	>2000	>2000	4000	Sept. 1979
53304	G	$49^{\circ}15'N$ $12^{\circ}48'W$	Deep-water	10-1300	10-1100	>300	>250	1350-1800	April 1994
53305	F	$49^{\circ}10'N$ $12^{\circ}15'W$	Deep-water	10-1000	10-1025	>100	25-52, 10-25	1038-1109	April 1994
53318-21	D	$49^{\circ}30'N$ $11^{\circ}30'W$	Outer slope	10-630	10-575	10-28, 25-89	26-72	574-875	May 1994
53322-23	C	$49^{\circ}20'N$ $11^{\circ}22'W$	Inner slope	22-200	20-300	> 80	>50	280-376	May 1994
53325	B	$49^{\circ}29'N$ $11^{\circ}04'W$	Shelf	-	18-135	-	>57	192	May 1994

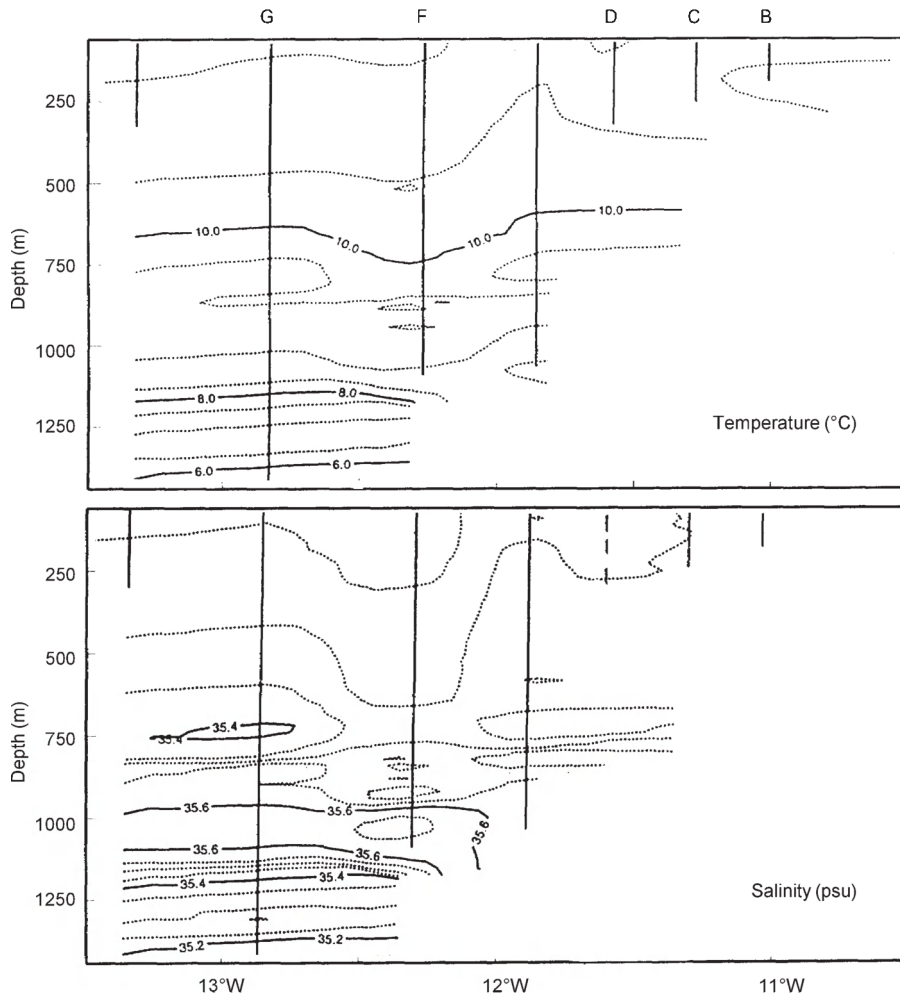


Fig. 2. Temperature/Salinity sections from stations G and F across to slope stations D and C and shelf station B.

in the same area on the outer slope of the Goban Spur (station 10115) (Fig. 1). The sampling gear was similar to that deployed during the recent RRS *Charles Darwin* cruise 85. A summary of the sampling is given in Table 1. Full sampling details of this previous cruise are given in Herring (1979) and Hargreaves (1984).

LABORATORY WORK

All samples were preserved initially in 5% neutralized formaldehyde in seawater and the preservative was changed within 24-48 hours back in the laboratory when the total sample was volumed to estimate biomass (biovolume) and then transferred to Steedman's preserving fluid (Steedman 1976) prior to sorting. The wet displacement volumes of major taxa were measured after sorting, when any post-preservation changes in volume would have been complete.

STATISTICAL TREATMENT

A factor analysis based on principal components using a correlation matrix for extraction was performed on each of the sets of day and night decapod and mysid data from the Goban Spur deep-water hauls at station 10115 (Autumn 1979) and the recently worked stations G, F, D-B (53304, 53305, 53318/21, 53322/23 and 53325 (night data only). Only species occurring more than twice throughout the samples were included in the analyses. Most day hauls above 450 m at the open oceanic stations were excluded from the analysis as there were only a few unidentifiable post-larval specimens in these hauls. At station 10115 day data were available to a maximum of only 900m. Included in the analysis were all decapod and mysid species with the exception of very rare species or unidentifiable post-larvac/juveniles. Full details of the methods are given in the Systat handbook (1996). Rotated factor loadings were used to

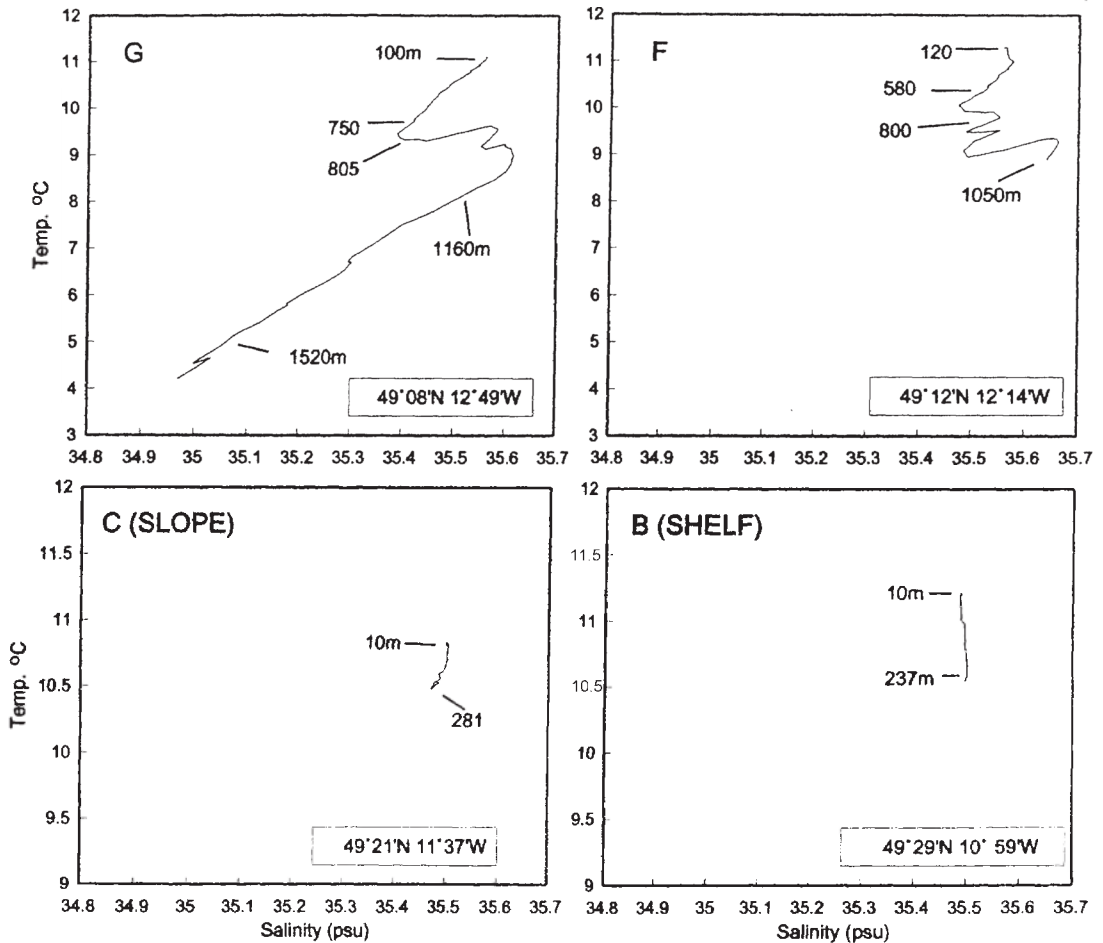


Fig. 3. T-S profiles taken near oceanic deep-water, slope and shelf stations in the region of 49°08'-49°29'N, 10°59'-12°49'W during *Charles Darwin* cruise 85 (1994).

classify the hauls into groups associated with each factor and the group number plotted at the appropriate relative location and depth horizon for each haul. Day data included those from open oceanic deep-water stations 10115, G and F and also lower slope station D. Night data included those from the open oceanic deep-water stations, slope stations D and C and outer shelf station B.

RESULTS

HYDROGRAPHY

Temperature/Salinity (T-S) sections from station G across the slope, derived from CTD data are given in Fig. 2. The section adjacent to the slope close to station D is derived from extrapolated data. Separate T-S profiles at positions across the slope and at the open oceanic deep-water stations are shown in Fig. 3. At station G from 100 m to 750 m the characteristics were similar to those

of North Atlantic Central Water (NACW – see Sverdrup & al. 1942) with a potential temperature $> 9.7^{\circ}\text{C}$, salinity > 35.42 psu at 700 m. From 750 m to 1080 m mixing with highly saline Gulf of Gibraltar (GGib) water occurred (see Cooper 1952; Wright & Worthington 1970). Below 1100 m the T-S characteristics were close to those of mixed GGib water, T-S values declining to 7°C , 35.4 psu at 1200 m. Broadly similar T-S profiles occurred at station F. During Autumn 1979 at open oceanic station 10115, a similar T-S profile was apparent with T-S characteristics close to those of NACW in the surface 650 m. From 750 m to 950 m increased mixing with GGib water occurred while below 1000 m there was a gradual increase in salinity. At 1900 m the T-S characteristics were close to those of Labrador Sea Water.

The April/May 1994 T-S profiles taken over slope and shelf areas in the region of 49°21'N-49°30'N, 11°-

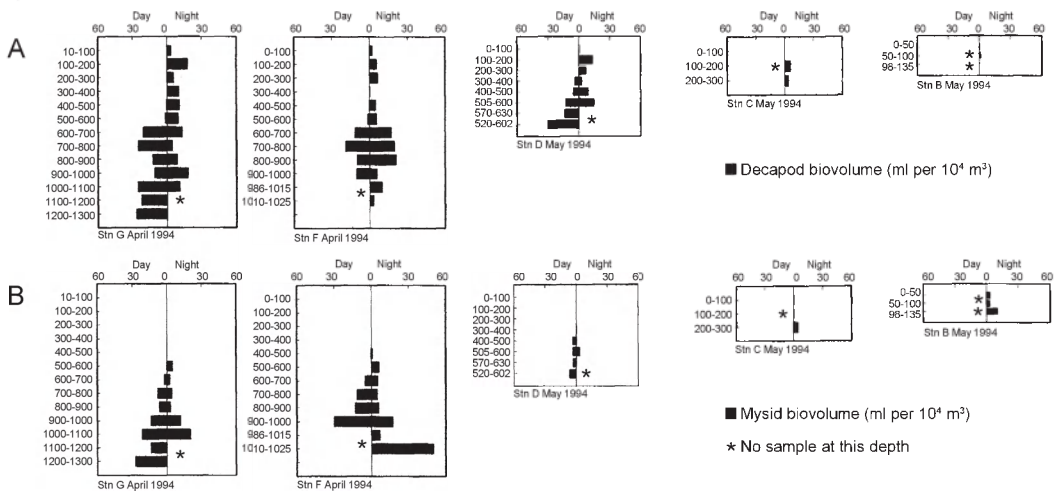


Fig. 4. Total micronektonic biovolumes of (A) decapods and (B) mysids sampled with the RMT8M and expressed as wet displacement volume ($\text{ml per } 10^4 \text{ m}^3$). An asterisk indicates given depth ranges where samples were not taken.

$11^{\circ}30'W$ close to station C at depths above 290 m, were typical of those of NACW (Fig. 3) with temperature values ranging from 10.5°C – 11.2°C , respectively and with salinity values approximately 35.5 psu throughout most of the water column. These values are in accordance with those given by McMahon & al. (1995) who recorded near-vertical isotherms of 9.8 – 10.4°C (salinity 35.4–35.5) between the surface and 300 m across the Irish Shelf front at a more northerly position (52°N , 11° – $11^{\circ}30'W$) in April 1992. T-S data for depths below 300 m at station D (maximum depth of net sampling 602 m) are not available but it is unlikely that highly saline Gulf of Gibraltar water occurred there. In the Porcupine Seabight a slope current flows in a northwesterly direction along the western Celtic shelf. It is variable in strength but strongest from January to March (Pingree & Le Cann 1989).

BIOVOLUME AND NUMBERS OF DECAPODA AND MYSIDACEA

Total micronektonic biovolumes of decapods and mysids sampled with the RMT8M and expressed as wet displacement volume ($\text{ml per } 10^4 \text{ m}^3$) are shown in Figs 4A and 4B (An asterisk indicates that samples were not taken at given depth ranges). At the open oceanic deep-water stations G–F decapod biovolume was greatest by day below 600 m reaching maxima of $> 25 \text{ ml per } 10^4 \text{ m}^3$ at 600–800 m and 1000–1300 m at station G. By night there was a marked diel vertical migration by some species into the top 600 m but several species remained below 600 m. A broadly similar profile was observed by day and night at lower slope station D down to the limit of sampling at approximately 600 m. Here a marked increase in biovolume occurred in the daytime sample

fished within 28 m of the sea-floor (mean = 19 m above the bottom (m a.b.)). At the upper slope station C hardly any decapods were caught by day. By night decapod biovolume concentrations reached a maximum of $6 \text{ ml per } 10^4 \text{ m}^3$ at the upper slope station and $2 \text{ ml per } 10^4 \text{ m}^3$ at the shelf station the latter of which was sampled only by night.

At the oceanic deep-water and lower slope stations mysids rarely occurred by day above 600 m. At station G mysid biovolume concentration was relatively high by day at 900–1300 m (13 – $30 \text{ ml per } 10^4 \text{ m}^3$). By night there were indications of a slight diel vertical migration by a small part of the population into the 500–600 m depth stratum. Similar profiles occurred at station F but there was a marked increase in biovolume in the 1010–1025 m night haul taken within 25 m of the sea-floor (mean = 20 m above the bottom) where a biovolume of $50 \text{ ml per } 10^4 \text{ m}^3$ was recorded as a result of particularly large numbers of *Eucopia unguiculata*.

At the lower slope station D mysid biovolume values were much lower with a maximum of $7 \text{ ml per } 10^4 \text{ m}^3$ (i.e. at a mean of 19 m above the bottom by day). At station C no mysids were caught by day and standardised values of night samples did not reach more than $6 \text{ ml per } 10^4 \text{ m}^3$ in any haul. At shelf station B (night hauls only) standardised mysid biovolume increased to $> 10 \text{ ml}$ at 135 m.

DISTRIBUTION OF SPECIES ACROSS THE GOBAN SPUR

A total of 1838 decapods and over 6000 mysids were examined. These were attributed to total of 17 decapod species and 12 mysid species. A full list of species caught and their authorities are given in Appendix 2.



Table 2A. Summary of the distribution of decapod species across the Goban Spur by day (ind per 10^4 m^3). mab = metres above the bottom.

	<i>G. elegans</i>	<i>S. robustus</i>	<i>A. pelagica</i>	<i>S. debilis</i>	<i>P. multidentata</i>
	<i>S. arcticus</i>	<i>P. sulcatifrons</i>	<i>A. purpurea</i>	<i>E. figueirae</i>	
Station 53304 (G)					
Approximate depth (m)					
10-100					
100-200					
200 - 300					
300 - 400					
400 - 500				0.3	0.3
500 - 600		0.3		3.7	
600 - 700	4.0	8.4	0.2	4.9	1.1
700 - 800	10.3	8.7		1.1	
800 - 900	13.2	1.3		1.4	
900 - 1000	5.6	0.3	0.9		1.0
1000 - 1100	8.5	0.9	0.9		0.9
1100 - 1200	8.9	0.7	1.0		0.6
1200 - 1300	5.1		0.7		0.5
Mean (positive hauls)	7.9	2.9	0.7	2.2	0.9
Std. Dev. (positive hauls)	3.3	3.5	0.3	0.9	1.1
Station 53305 (F)					
Approximate depth (m)					
0-100					
100-200					
200 - 300					
300 - 400					
400 - 500					0.3
500 - 600				2.9	0.7
600 - 700	6.2	3.1		2.4	1.7
700 - 800	22.9	1.3	0.3	0.3	0.3
800 - 900	11.1	0.3	0.3	0.3	0.3
900 - 1000	6.2	0.4		0.3	1.1
Mean (positive hauls)	11.6	1.3	0.3	2.7	0.3
Std. Dev. (positive hauls)	7.9	1.3	0.0	0.7	1.9
Station 53318/21 (D)					
Approximate depth (m)					
0 - 100					
100 - 200					
200 - 300					
300 - 400		1.8		0.9	0.4
400 - 500	1.3	3.4		1.3	
505 - 600		3.4	0.3		6.5
570-630 (25-89 mab)		4.1	0.7		7.0
520-602 (10-28 mab)		25.8			58.6
Mean (positive hauls)	1.3	7.7	0.5	1.1	18.2
Std. Dev. (positive hauls)		10.2	0.2	0.3	27.1

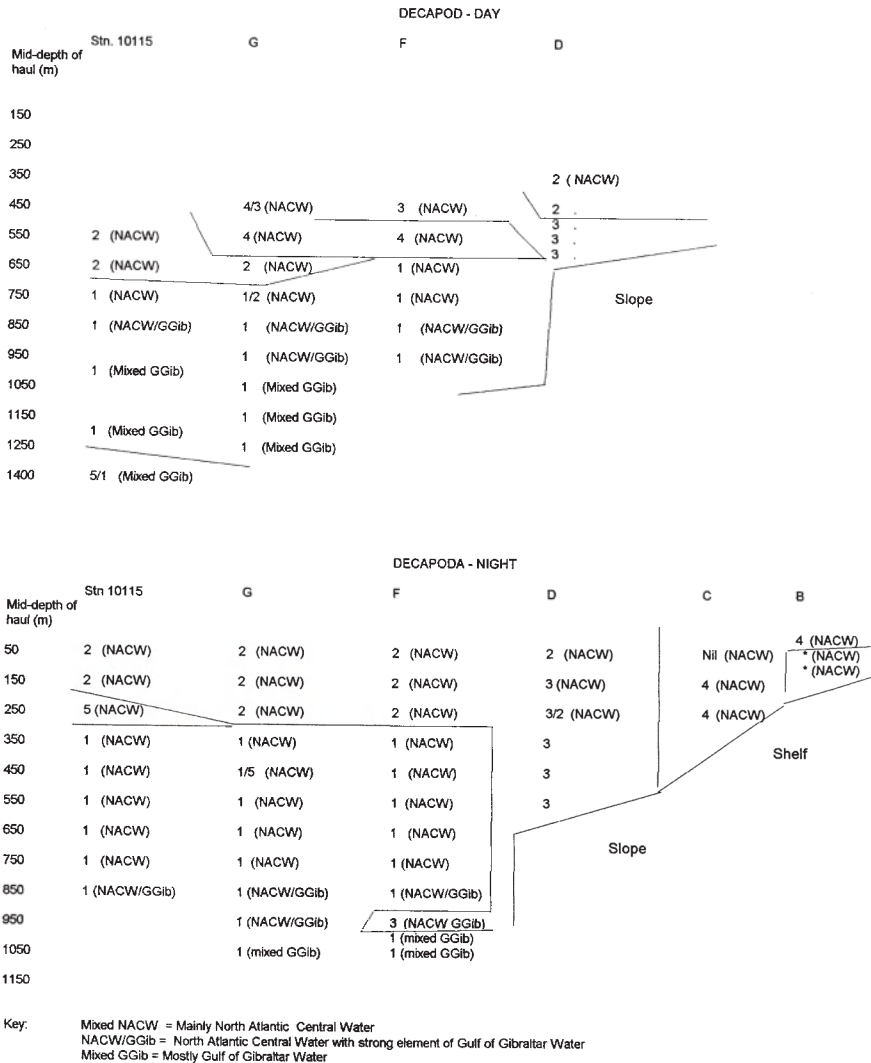


Fig. 5. A summary of the zonations resulting from a factor analysis. A (this page). Day and night decapod distributions. B (next page). Day and night mysid distributions. Also shown is the type of water at each station based on CTD profiles.

Table 3. Mean carapace length (mm) of *Sergestes arcticus* by day in the Porcupine Seabight.

Depth (m)	Station			
	10115	53304 (G)	53305 (F)	53318/21 (D)
400-500	5.8	-	-	-
500-600	7.2	9.0	11.6	10.7
600-700	8.3	10.1	11.2	-
700-800	8.9	11.5	12.5	-
800-900	9.6	14.0	17.0	-
900-1100	9.7	16.0	14.0	-
1100-1300	12.0	14.7	-	-
1300-1500	13.1	-	-	-

Decapoda

Numbers of decapods at the open oceanic, slope and outer shelf stations are shown in Table 2A (day) and 2B (night). In addition to those listed there were several infrequently-occurring species. All species at stations F, G, and D were mesopelagic whilst those at stations C and B were primarily bottom-living, some having a pelagic phase. Some species were found mainly at one or both of the two open oceanic deep-water stations G and F, i.e. *Gennadas elegans*, *Acanthephyra pelagica*, *Ephyrina figueirae*, *Parapasiphaea sulcatifrons*. Other species e.g. *Sergia robustus* and *Systellaspis debilis* tended to occur

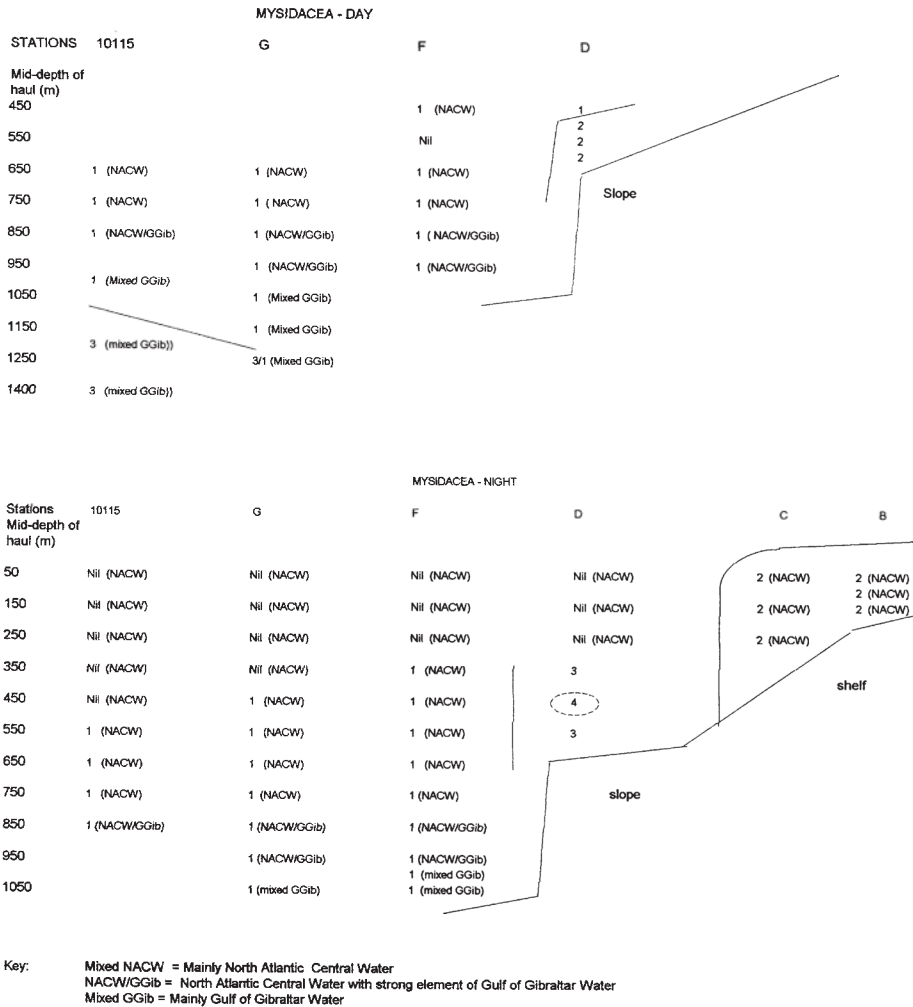


Fig. 5. A summary of the zonations resulting from a factor analysis. A (previous page). Day and night decapod distributions. B (this page). Day and night mysid distributions. Also shown is the type of water at each station based on CTD profiles.

at the open oceanic deep-water stations and also in moderate to low numbers at the outermost slope station (D) though not at the upper slope and shelf stations. Generally species distribution at stations G and F were similar to those taken at station 10115 sampled during Autumn 1979 (cruise 105, Hargreaves 1984) except that the deep-living decapods *Sergia japonicus* and *Hymenodora gracilis* were not recorded.

The distribution patterns of two decapod species are particularly worthy of note i.e. *Sergestes arcticus* and *Pasiphaea multidentata*. The former species occurred at open oceanic stations 10115, G-F and at the lower slope station D. There was some variation in distribution across slope. At the deep-water stations maximum numbers

occurred by day at approximately 600-900 m (> 12 specimens per 10⁴ m³ – station 10115) and at 600-700 m (3-8 specimens per 10⁴ m³ at stations G-F), (Table 2A). *S. arcticus* is known to be a strong diel migrant and was found in the top 300-400 m by night. However at slope station D maximum numbers of 26 specimens per 10⁴ m³ were found within 28 m of the sea floor (mean depth of haul = 19 m above the bottom) in the 520-602 m day haul. Furthermore only part of the population of this species undertook a diel migration towards the surface by night (Table 2B). Near-bottom samples taken during cruise 105 in 1979 also indicated that this species tended to aggregate close to the sea-floor in this slope area (Hargreaves 1984). A comparison of the size range of



Table 4A. Summary of the distribution of mysid species across the Goban Spur by day (ind per 10⁴ m³). mab = metres above the bottom.

	<i>E. unguiculata</i>	<i>E. sculpticauda</i>	<i>E. grimaldi</i>	<i>B. microps</i>	<i>G. zoea</i>	<i>B. arctica</i>	<i>L. fuscus</i>
Stn. 53304 (G)							
Approximate depth (m)							
10-100							
100-200							
200 - 300							
300 - 400							
400 - 500							
500 - 600							
600 - 700	16.8						
700 - 800	27.4						
800 - 900	48.5			0.3			
900 - 1000	74.1		0.6	1.5	1.8		
1000 - 1100	136.8	0.3	2.7	3.5	5.3		
1100 - 1200	68.4	0.5	5.2	5.4	1.7		
1200 - 1300	49.1	3.4	42.3	3.4	3.4		0.3
Mean (positive hauls)	60.2	1.4	12.7	2.8	3.0		0.3
Std. dev. (positive hauls)	39.5	1.7	19.8	2.0	1.7		-
Stn. 53305 (F)							
0-100 (m)							
100-200							
200 - 300							
300 - 400							
400 - 500	1.0						
500 - 600							
600 - 700	35.0						
700 - 800	53.8						
800 - 900	103.1						
900 - 1000	260.1	1.1			1.1		
Mean (positive hauls)	90.6	1.1			1.1		
Std. dev. (positive hauls)	101.7	-			-		
Stn. 53318-21 (D)							
0-100 (m)							
100 - 200							
200 - 300							
300 - 400							
400 - 500	2.1						
505 - 600	1.3				3.7	0.6	
570 - 630 (25-89 mab)	5.1				39.2		
520 - 602 (10-28 mab)	5.2				45.0	14.6	
Mean (positive hauls)	3.4				29.3	7.6	
Std. dev. (positive hauls)	2.0				22.4	9.9	
Stn. 53322-23 (C)							
No specimens in day hauls							

Table 4B. Summary of the distribution of mysid species across the Goban Spur by night (ind per 10⁴ m³). mab = metres above the bottom.

	<i>E. unguiculata</i>	<i>E. sculpticauda</i>	<i>B. microps</i>	<i>K. oceanae</i>	<i>B. arctica</i>
	<i>E. grimaldii</i>	<i>L. typicus</i>	<i>G. zoea</i>	<i>B. megalops</i>	<i>B. tridens</i>
Stn. 53304 (G)					
Approximate depth (m)					
10-100					
100-200					
200 - 300					
300 - 400					
400 - 500	0.3				
500 - 600	18.2				
600 - 700	16.7				
700 - 800	33.9		0.4	0.4	
800 - 900	50.6	3.8		0.3	
900 - 1000	98.8		1.6	2.9	
1000 - 1100	124.9		2.1	4.5	
Mean (positive hauls)	49.0		1.3	2.0	
Std. dev. (positive hauls)	46.2		0.9	2.0	
Stn. 53305 (F)					
0-100 (m)					
100-200					
200 - 300					
300 - 400	0.3				
400 - 500	9.0				
500 - 600	18.7				
600 - 700	34.9				
700 - 800	43.7				
800 - 900	97.8			0.4	
900 - 1000	68.8				4.8
986-1015 (25-52 mab)	52.0			1.0	
1010-1025 (10-25 mab)	283.2	2.4		2.1	0.7
Mean (positive hauls)	67.6	2.4		1.1	0.7
Std. dev. (positive hauls)	86.3	-		0.9	-
Stn. 53318-21 (D)					
0-100 (m)					
100 - 200					
200 - 303					
300 - 400				0.6	
400 - 500				0.6	1.2
510-575 (26-72 mab)	0.7			5.3	0.4
Mean (positive hauls)	0.7			2.2	0.8
Std. dev. (positive hauls)	-			2.7	0.6
Stn. 53322-23 (C)					
0-100 (m)		0.9			0.6
100 - 200		2.2			0.3
200-300		20.1			5.4
Mean (positive hauls)		7.7			2.1
Std. dev. (positive hauls)		10.7			2.9
Stn. 53325 (B)					
18-50 (m)		84.4			
50-100		34.6			
100-150		20.7			
Mean (positive hauls)		46.5			
Std. dev. (positive hauls)		33.5			



these species sampled during 1979 and 1994 is given in Table 3. Both sets of samples indicated that an ontogenetic migration had occurred and that the larger individuals tended to live closest to the sea-floor. However individuals sampled in April 1994 tended to be larger than those sampled in October 1979.

Pasiphaea species, although occurring in low numbers at the deep-water stations were recorded in higher numbers at the slope station D (maximum of 58 specimens per 10^4 m³). Most specimens were small juveniles identified as *Pasiphaea multidentata*. Part of the population showed some diel migration at deep-water station G and at slope station D but not at station F where numbers were low. The species did not occur at the inner slope or shelf stations. In contrast juveniles of *Pasiphaea* cf. *sivado* were found mainly at the upper slope station C. There were few other decapods recorded at this station.

Mysidacea

Numbers of Mysidacea at the open oceanic deep-water stations and the slope and outer shelf stations are shown in Table 4A and 4B (day and night data). Some species were found only at one or both of the two open oceanic stations e.g. *Eucopia sculpticauda*, *Eucopia grimaldii* and *Boreomysis microps*. *Eucopia unguiculata* tended to occur at the open oceanic deep-water stations below 300 m. Numbers were very abundant near-bottom at station F but moderate to low at station D. *Gnathophausia zoea* was

also found in moderate numbers at open oceanic stations G and F and in large numbers at slope station D.

The small, fragile mysid genus *Boreomysis* showed a clear partition of species across the slope. The pelagic species *B. microps* was found only at the oceanic deep-water stations 10115 and G mainly below 700 m (both by day and night). It was not found at station F or at slope stations D or C. It seems that it was replaced at the outer slope station (D) by the closely-related species *Boreomysis arctica* and at the inner slope station (C) by *B. megalops*. Several *B. tridens* occurred at deep-water station F. At shelf station (B) there were very few mysid species. Most of the *Boreomysis* species found over the upper slope and shelf tended to be suprabenthic, sometimes having a pelagic phase. This applied also to the numerically dominant *Lophogaster typicus* which was found only at the stations B and C. This species is known to inhabit Norwegian fjords by day but has been recorded there in greater numbers (see Fosså & Brattegard 1990). It tends to inhabit muddy deposits on the sea floor for part of its life cycle but may be planktonic when immature. The RMT8M net was fished throughout the whole of the water column at each station but usually at least 10 m from the bottom, thus it may not have taken a representative sample of these or other benthic or suprabenthic species. The distribution of numerically dominant species of both decapods and mysids at the open oceanic, slope and shelf stations is summarised in Table 5.

Table 5. A summary of the distribution of numerically dominant decapod and mysid species at the deep-water, slope and shelf stations during *Charles Darwin* cruise 85. * species present at station in low numbers; ** 9-19 ind.; *** > 19 ind. per 10^4 m³ in any haul.

Species	Stations				
	G	F	D	C	B
<i>Eucopia grimaldi</i>	***				
<i>Boreomysis microps</i>	*				
<i>Eucopia sculpticauda</i>	*	*			
<i>Gennadas elegans</i>	**	***	*		
<i>Acantheephyra pelagica</i>	*	*			
<i>Acantheephyra purpurea</i>	*	*			
<i>Ephyrina figueirae</i>	*	*			
<i>Eucopia unguiculata</i>	***	***	**		
<i>Sergia robustus</i>	*	*	*		
<i>Parapasiphaea sulcatifrons</i>	*	*	*		
<i>Systellaspis debilis</i>	*	*	*		
<i>Sergestes arcticus</i>	***	*	***	*	
<i>Gnathophausia zoea</i>	*	*	***		
<i>Pasiphaea cf multidentata</i>	*	*	***		
<i>Pasiphaea cf sivado</i>				**	*
<i>Lophogaster typicus</i>				***	***
<i>Boreomysis megalops</i>				**	
<i>Boreomysis arctica</i>			**		
<i>Boreomysis tridens</i>		*			



DISTRIBUTIONAL SIMILARITIES

Factor analyses were undertaken and hauls were classified into groups on the basis of rotated factor loadings. Values of < 0.5 were not used in the classification. The resulting zonations are summarised in Figs 5A (day and night decapod distributions) and 5B (day and night mysid distributions). Where a haul was intermediate between two factor groups, the one with the highest loading is given first. In addition the characteristics of the water mass is shown in brackets. The percentage of total variance explained in each of the decapod and mysid day and night analyses is shown in Appendix 3. The factor analysis based on decapod day hauls at the deep-water stations 10115, G and F (below 600 m) showed four clear groups of species. Dominant species within the groups to which the hauls have been assigned are summarised in Table 6.

Most decapod day hauls below 700 m at the open oceanic stations were assigned to group 1. Here the species assemblage was composed mainly of *G. elegans* together with *S. robustus* and/or *A. pelagica* and *S. arcticus*. At station 10115, day hauls at 500-700 m were assigned to group 2 as was the 600-700 m day haul at station G and the 300-400 m and 400-500 m hauls at station D. These hauls were composed mainly of *S. arcticus* and *S. debilis* (Table 6). Several shallow day hauls at the open oceanic stations and one over the slope in which *S. debilis* was dominant were assigned to group 4. Three near-bottom hauls at station D and the shallowest haul at station F in which *P. multidentata* and *S. arcticus* were numerically dominant were assigned to group 3. There were no day data for stations C and B.

With one exception decapod night hauls below 300 m at the open oceanic stations were all assigned to group 1. These had a broadly similar species assemblage to that of 600-1000 m day-time hauls. Most shallow hauls at the deep-water stations and the shallowest at slope station D, containing *S. arcticus* and *S. debilis*, were assigned to group 2. Deeper hauls at station D were assigned to group 3 (mainly *P. multidentata* and *S. arcticus*). Further zonation was apparent at 200-400 m at slope station C where *P. sivado* was the main species (assigned to Group 4) as was the near-surface haul at station B. The 55-135 m hauls at station B in which there were small numbers of *Pontophilus* and *Hymenopenaeus* species were unclassified.

Most day and night mysid hauls at the open oceanic stations in which *E. unguiculata* were numerically dominant were assigned to group 1, while two deep day hauls in which there were also occurrences of *E. grimaldi* were assigned to Group 3. Day and night hauls over the slope floor at station D where *G. zoea* was numerically dominant was assigned to groups 2 and 3 respectively except

for the day haul at 400-500 in which there were low numbers of mysids, mainly *B. arctica*. At shelf stations B and C where *L. typicus* was the dominant species by night hauls were all assigned to Group 2. Thus the zonation of hauls derived from the principal component analysis suggests that station D is a transition zone, characterised mainly by several deep-water species known to be common further offshore.

RELATIONSHIP OF SPECIES TO THE HYDROGRAPHY

A comparison of the T-S characteristics and daytime profiles of decapod and mysid species showed that most species at the open oceanic stations were within the T-S envelope for mixed North Atlantic Central Water (NACW) and Gulf of Gibraltar (GGib) Water. Most of the highly saline GGib water occurred from 900 m to at least 1400 m and the only decapod found solely in such hauls was the genus *Ephyrina*. *A. pelagica* and *Parapasiphaea sulcatifrons* were present in mixed Gulf of Gibraltar water (but also in less saline NACW/GGib water). *S. debilis* tended to remain in NACW but has also been recorded previously in mixed NACW/GGib water (Hargreaves 1985a). Of the mysids, only *Eucopeia sculpticauda* and *E. grimaldi* were found to be mainly in mixed Gulf of Gibraltar water. Most other open oceanic, deep-water species were not confined to a particular water mass. With regard to the shallow-living species recorded at the two inshore stations, we have few hydrographic data for this area but it is likely that it was dominated by North Atlantic Central Water.

Table 6. The species which contributed the greatest proportion to the catch assigned to given factors.

Decapods		Day	Night
Factor 1	<i>G. elegans</i>	Factor 1	<i>G. elegans</i>
Factor 2	<i>S. arcticus</i>	Factor 2	<i>S. arcticus</i> <i>S. debilis</i>
Factor 3	<i>P. multidentata</i> <i>S. arcticus</i>	Factor 3	<i>P. multidentata</i> <i>S. arcticus</i>
Factor 4	<i>S. debilis</i>	Factor 4	<i>P. sivado</i>
Factor 5/1	<i>G. elegans</i> <i>H. gracilis</i>	Factor 5	<i>S. robustus</i> <i>G. elegans</i>
Mysids		Day	Night
Factor 1	<i>E. unguiculata</i>	Factor 1	<i>E. unguiculata</i>
Factor 2	<i>G. zoea</i>	Factor 2	<i>L. typicus</i>
Factor 3	<i>E. unguiculata</i> / <i>E. grimaldii</i>	Factor 3	<i>G. zoea</i>
		Factor 4	<i>B. arctica</i>



DISCUSSION

Most decapod and mysid species identified from the samples have been recorded previously in open North Atlantic water (Mauchline & Murano 1977; Fasham & Foxton 1979; Hargreaves 1984a, 1985a, 1985b). The decapod and mysid species composition at the open oceanic stations sampled during 1979 and again in 1994 seems remarkably similar. For example previously the mysid *G. zoea* was also found to be abundant within 50 m of the sea floor at two near-bottom stations (10108-10109) also sampled during cruise 105 in 1979 (see Hargreaves 1985b).

The factor analyses confirmed that a transition in species occurrence between open oceanic deep-water stations 10115, G and F on the one hand and up-slope/shelf species on the other. Abelló & al. (1988) and also Fariña & al. (1997) have shown that, in slopes off the Catalan coast and Galician continental shelf respectively, spatial separation of some groups of crustacean decapods is related to changes in oceanography and sediment along the continental margin. Abelló & al. found that a transition zone between up-slope fauna and offshore bathyal fauna occurred at approximately 400 m, the location of the transition zone appearing to be determined partly by hydrographic conditions, partly by fluctuations in water temperature and partly by bottom sediment structure associated with steepness of the bottom. Cartes & al. (1994) sampling bathyal decapods in the Catalan Sea with bottom trawls also identified three separate decapod communities i.e. shelf, upper, and middle slope and a fourth community in the vicinity of submarine canyons.

Most of the abundant decapod species identified during the present survey from the deep-water column in the Porcupine Seabight are widespread in the North Atlantic, many also having been recorded in the Mediterranean Sea (e.g. Cartes & al. 1994; Sardou & al. 1996). A comparison of previous records from this, and adjacent areas confirmed that none of the species at the offshore stations or on the outer slope were outside of their normal geographic limits. Most of the species identified are well-known inhabitants of the deep mesopelagic regions in the open ocean e.g. the decapod species: *Ephyrina figueirae*, *G. elegans*, *Sergia robustus*, *Sergestes arcticus* and the mysid species *Eucopia unguiculata* and *Gnathophausia zoea*.

At the two open oceanic stations F and G species composition was relatively uniform and there was little evidence that most mesopelagic species altered their range vertically between the two stations. Few pelagic species were recorded up-slope at station C and shelf station B where near-bottom species predominated. Station D represented a transition zone where numbers of open oceanic species were low except for *S. arcticus*, *Pasiphaea*

multidentata and *G. zoea* which, although broadly maintaining a presence in mid-water over the slope, accumulated in relatively large numbers near to the bottom.

The timing of diel vertical migration is related to diurnal changes in light intensity (Omori 1974; Roe 1984). Our data provide clear evidence for such behaviour in oceanic species. Vertical migration at the open oceanic stations was apparent in the decapods *Gennadas elegans*, *Sergestes arcticus*, *S. robustus*, *Acanthephyra purpurea* and *Systellaspis debilis*. This may represent predator avoidance behaviour (see Bollens & Frost 1991; Loose & Dawidowicz 1994). Although *S. arcticus* was abundant at outer slope station D by day and night, the numbers migrating to the upper 200-300 m by night tended to be reduced compared to that at the deep-water stations. On the other hand part of the population of *Pasiphaea multidentata* at station D also showed a clear diel migration. Most mysid species did not undertake extensive diel migrations except possibly the inshore species *Lophogaster typicus* for which we have mainly night data.

The present data demonstrates that a separation of mesopelagic species from inshore pelagic and bottom-living species occurs at the upper slope. The reasons for this discontinuity are unclear but it may be linked to hydrographic conditions across the slope and shelf and also with other factors such as topography and predation. Clearly the mesopelagic species offshore inhabit both North Atlantic Central Water and mixed Gulf of Gibraltar Water. However, the hydrographic structure of the area is complex, its variability accentuated in the slope and shelf area (see McMahon & al. 1995). The north-westerly currents as described by Pingree & Le Cann (1989) may be implicated but as yet the seasonal and annual variability of such current systems is unclear. It is known that vertical mixing occurs over the upper slope and shelf to the north of stations C and B but we have insufficient data to determine whether a frontal system exists in that region. There was little evidence that highly saline water (35.6 psu) present offshore below 900 m during the period of sampling extended to the upper slope or shelf (salinity < 35.5). In this region the temperature remained at approximately 10.5-11 °C at depths of 10 m to 250 m, the 10 °C isotherm remaining below 600 m at the open oceanic stations G and F. Although temperature values remained similar at stations C and B there was a difference in species composition between these stations. At station C the pasiphaeids were represented by a pelagic species *Pasiphaea sivado* and the mysids by *Boreomysis megalops* and *L. typicus*, the latter species of which tends to be found near-bottom by day but migrates up into the water column by night. *L. typicus* was found also at station B together with two



bottom-living decapod genera *Hymenopenaeus* and *Pontophilus*.

There are a great many factors which may determine the distribution of species particularly across slope areas where pelagic, suprabenthic and benthic species inhabit adjacent areas. In addition to hydrographic conditions such factors include topography, food availability, predation, competition for space, ambient light and type of bottom sediments. For example Kaartvedt (1989) and Fosså & Brattegard (1990) show that the distributions of some bottom-living mysids in the relatively homogeneous hydrographic conditions of Norwegian fjords are related to bottom topography rather than to hydrography.

Food availability is also an important factor which affects crustacean distribution. For example several authors including Lagardère (1976) have shown that, over European continental slopes, spatial separation of *P. multidentata* and *P. sivado* may occur and that there is little trophic competition between these species. It is also known that *P. multidentata* and *P. sivado* inhabit the benthopelagic domain on the Western Mediterranean slope, both species feeding on benthic prey items such as amphipods by night and some mesopelagic items by day but also apparently with no dietary overlap (Cartes 1993). The diet of *P. multidentata* may change with increasing depth due to changes in bathyal communities. Cartes (1993) found that one of the major prey items of *P. multidentata* was *B. arctica* (which has a suprabenthic and a pelagic phase), both species of which were recorded during the present sampling at station D.

The lack of open-oceanic species at the two shallow stations C and B and accumulation of several species that tend to occur near-bottom there may also be related to predator avoidance. Most of the deep-water mesopelagic species recorded offshore were living in conditions of low ambient light both by day and by night. We have hardly any daytime data for species inhabiting the shallow upper slope and shelf in conditions of increased light penetration. Relatively shallow-living species living in such conditions may need to retain a benthic existence during the hours of daylight to escape predation. Deep-living pelagic species offshore may be subject to greater predation pressures if they move up-slope towards such areas of increased ambient light. Macquart-Moulin & Maycas (1995) studying the nocturnal migratory activity of benthopelagic mysids off the European coast found that nocturnal distribution of some species becomes deeper as the clarity of the water increases. Kaartvedt & al. (1996) showed that the vertical distribution of acoustic scattering layers of fish and krill close to the Norwegian shelf was determined partly by the ambient light levels (associated with fluorescence) across a front.

Advective current systems may also affect not only

the horizontal distribution but also the vertical distribution of species. Behavioural adaptations resulting in a reduction in diel migratory activity in strong currents may reduce the possibility of advection and dispersion (Clutter 1967, 1969; Mauchline 1980; Jahn & Lavenberg 1986). It is known that some species of mysid are able to maintain a population partly by behavioural mechanisms. Kaartvedt (1989) examining distribution patterns of mysids, including *L. typicus* and *B. megalops*, in Norwegian fjords concluded that during periods of strong currents, maintenance of suprabenthic mysid populations within a given geographic locality is not possible if individuals, performing upward diel migrations by night, drift passively in the pelagic zone. Rather they may need to modify their diel vertical migrations. O'Brian (1988) suggests that clustering may not only help some mysid species to maintain their position in the environment but that it also acts as an anti-predation measure, the maintenance of the position of the cluster varying with substrate attraction and hydrographic conditions.

The distribution of the mysid genus *Boreomysis*, although not numerically dominant in the hauls, provided further examples of species separation related to depth distribution which may be relevant also to bottom sedimentation, food availability or anti-predation. It is known that these species may also occur in suprabenthic hauls taken across the slope in this area at 60–120 cm above the bottom, often in large numbers (e.g. Fosså 1985; Fosså & Brattegard 1990; Cartes & Sorbe 1995; Hargreaves 1997). For example Cartes & Sorbe (1995) found large numbers of *B. arctica* (up to 175 ind. per 100 m³) in suprabenthic hauls taken over the Catalan Sea slope. It is likely that the RMT8M sampled only a small proportion of each population. Lagardère (1985) and Elizalde & al. (1991), examining samples from the continental slope of the Bay of Biscay, found some correlation with the distribution of *B. arctica* and *B. megalops* and the type of sedimentation of the sea-floor.

There may be several reasons for accumulation near-bottom in mesopelagic species such as *P. multidentata*, *S. arcticus* and *G. zoea* as recorded at station D. Factors which may influence vertical distribution of such species may include availability of food or clustering behaviour. In turn the distribution of their prey items such as *B. arctica* may have been affected by the type of sea-floor sediment.

In summary, both the decapod and mysid sets of data suggest that species composition from deep oceanic water across to the lower slope station depends greatly on the optimum depth range tolerated by each given species and that in the Seabight, outer-shelf, slope and open oceanic offshore distributions of given species tend to be depth-dependent. Most open oceanic species inhabit a broad depth range. With few exceptions, mesopelagic,



deep-living, open oceanic species do not generally move into shallow water in large numbers. Reasons for this may include hydrographic conditions, predator avoidance or food availability. The present data suggests that in some of those species which are able to inhabit lower slope areas where the water depth becomes shallower, part of the population may accumulate near the sea-floor. Cartes & al. (1994) investigating deep-water communities in the Northwestern Mediterranean also found that mesopelagic species were numerically dominant in bathyal communities but were usually not found over the upper slope or shelf transition zone.

Our findings accord also with those of Hopkins & al. (1981) who showed that many deep-living oceanic species off Florida are rarely found inshore over the shelf. They also support the observations of Merrett (1986) who, providing data on ichthyofauna, found that the continental slope may truncate the distribution of oceanic meso- and bathypelagic species.

ACKNOWLEDGEMENTS

I wish to thank the many colleagues who participated in the collection and sorting of the samples.

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Accepted 15 July 1998 – Printed 16 April 1999
Editorial responsibility: Tore Høisæter

Appendix 1. Volume of water filtered (m³) by the RMT8M net for each sample. (NS = no sample)

Station 53304			Station 53305			Station 53318/21			Station 53322/23			Station 53325		
Depth (m)	Day Volume filtered	Night Volume filtered	Depth (m)	Day Volume filtered	Night Volume filtered	Depth (m)	Day Volume filtered	Night Volume filtered	Depth (m)	Day Volume filtered	Night Volume filtered	Depth (m)	Day Volume filtered	Night Volume filtered
0 - 100	36957	36758	0 - 100	33997	33173	0 - 100	15107	33725	0 - 100	32891	30214	0 - 50	NS	30831
100 - 200	25031	34549	100 - 200	31908	31734	100 - 200	15062	29597	100 - 200	32006	32397	50 - 100	NS	30124
200 - 300	29638	29691	200 - 300	29498	22965	200 - 300	13745	29585	200 - 300	NS	23838	100 - 150	NS	12124
300 - 400	34530	32891	300 - 400	30831	30831	300 - 400	22819	34265						
400 - 500	33095	32397	400 - 500	29585	30977	400 - 500	23528	32702						
500 - 600	29751	30831	500 - 600	30772	28817	505 - 600	29063	28527						
600 - 700	45371	30562	600 - 700	28868	27534	570 - 630	26995	NS						
700 - 800	35804	28647	700 - 800	31436	31135	520 - 602	30214	NS						
800 - 900	31740	30831	800 - 900	29781	28524									
900 - 1000	34265	30562	900 - 1000	26641	28944									
1000 - 1100	33997	29232	986 - 1015	NS	30786									
1100 - 1200	40480	NS	1010 - 1025	NS	29063									
1200 - 1300	29309	NS												

Appendix 2. Decapod and mysid species recorded during RRS *Charles Darwin* Cruise 85.

DECAPODA

Caridea

<i>Acanthephyra pelagica</i>	Risso, 1816
<i>Acanthephyra purpurea</i>	Milne Edwards, 1881
<i>Ephyrina figueirae</i>	Crosnier and Forest, 1973
<i>Hymenodora gracilis</i>	Smith, 1887
<i>Parapasiphaea sulcatifrons</i>	Smith, 1884
<i>Pasiphaea sivado</i>	(Risso, 1816)
<i>Pasiphaea multidentata</i>	Esmark, 1866
<i>Pontophilus spinosus</i>	(Leach, 1815)
<i>Philocheras trispinosus</i> *	Hailstone, 1835
<i>Systemaspis debilis</i>	(Milne Edwards, 1881)

Penaeidea

<i>Gennadas elegans</i>	Smith, 1882
<i>Gennadas valens</i> *	Smith, 1884
<i>Hymenopenaeus</i> sp.	Smith, 1882
<i>Sergia japonicus</i>	Bate, 1881
<i>Sergia robustus</i>	Smith, 1882
<i>Sergestes arcticus</i>	Kroyer, 1859
<i>Sergestes sargassi</i> *	Ortmann, 1893

MYSIDACEA

Lophogastrida

<i>Eucopia unguiculata</i>	(Willemoes-Suhm, 1875)
<i>Eucopia grimaldii</i>	Nouvel, 1942
<i>Eucopia sculpticauda</i>	Faxon, 1893
<i>Gnathophausia zoea</i>	Willemoes-Suhm, 1873
<i>Lophogaster typicus</i>	M. Sars, 1857

Mysida

<i>Boreomysis microps</i>	G.O. Sars, 1883
<i>Boreomysis arctica</i>	Kroyer, 1861
<i>Boreomysis tridens</i>	G.O. Sars, 1870
<i>Boreomysis megalops</i>	G.O. Sars, 1872
<i>Boreomysis bispinosa</i> *	O. Tattersall
<i>Longithorax fuscus</i> *	Hansen, 1908
<i>Katerythrops oceanae</i> *	Holt and Tattersall, 1905

* Not included in the factor analyses

Appendix 3. Percentage of total variance explained by rotated components in factor analyses of decapod and mysid species.

Factor	1	2	3	4	5	Total
Decapod						
Day	45	20	16	14	3	98
Night	44	20	13	6	6	89
Mysid						
Day	76	13	10			99
Night	68	20	3	3		94