

## Species composition and distribution patterns of early life stages of cephalopods at Great Meteor Seamount (subtropical North-east Atlantic)

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### Abstract

The distribution of early life stages of cephalopods was studied during a cruise of RV Meteor in September 1998 at Great Meteor Seamount, an isolated flat-topped seamount in the subtropical eastern North Atlantic. Zooplankton sampling was conducted with a multi-opening-closing net (modified MOCNESS, 1 m<sup>2</sup> net opening, 335 µm mesh size) in seven depth strata between 290 m depth and the surface. 1180 early life stages of cephalopods were collected, representing at least 18 families and 31 mainly oceanic species. Most of the identified cephalopods comprised mesopelagic species (*e. g.*, representatives of the families Enoploteuthidae and Pyroteuthidae) that showed diel vertical migration patterns. Hydrographic measurements parallel to zooplankton sampling revealed slow anticyclonic recirculation around the seamount forming a Taylor column and, thus, some retention potential for passive particles. Nevertheless, multivariate statistical analysis revealed no differences in the cephalopod community between the area in the proximity of the summit and the adjacent oceanic region. This was partly related to the depth of the plateau (< 300 m), which resulted in only slightly enhanced primary production, as well as to the low retention potential for active vertical migrators. However, reduced numbers of cephalopods were observed over the summit in night-time sampling, indicating gap formation above the seamount.

### Kurzfassung

#### Artenzusammensetzung und Verteilungsmuster früher Lebensstadien von Cephalopoden an der Großen Meteorbank (subtropischer Nordostatlantik)

Die Verteilungsmuster früher Lebensstadien von Cephalopoden wurden im September 1998 an der Großen Meteorbank, einem isolierten Seeberg mit einem ausgeprägt flachen Plateau im subtropischen Nordostatlantik, untersucht. Zooplanktonprobennahmen wurden mit Hilfe eines vertikal auflösenden Mehrfachschlieβnetzes (modifiziertes MOCNESS, 1 m<sup>2</sup> Netzöffnung, 335 µm Maschenweite) in sieben Tiefenhorizonten von 290 m Tiefe bis zur Oberfläche durchgeführt. Insgesamt wurden 1180 frühe Lebensstadien von Cephalopoden gefangen, die zu mindestens 18 Familien und 31 Arten zu zählen waren. Die meisten Individuen gehörten zur mesopelagischen Cephalopodenfauna, wie z. B. Vertreter der Familien Enoploteuthidae und Pyroteuthidae, deren frühe Lebensstadien bereits ausgeprägte Vertikalwanderungen zeigten. Parallel durchgeführte hydrographische Messungen ergaben eine langsame antizyklonale Strömung um den Seeberg, die eine sogenannte Taylor-Säule bildete, so dass passive Partikel einem gewissen Retentionspotential unterlagen. Multivariate statistische Verfahren lie-

ßen allerdings keine Unterschiede in der Cephalopodengemeinschaft zwischen dem Gebiet über dem Plateau des Seeberges und dem angrenzenden offenen Ozean erkennen. Dies wurde teilweise auf die Tiefe der Seebergkuppe (~ 300 m) und der damit verbundenen nur gering erhöhten Primärproduktion als auch auf das geringere Retentionspotential für aktive Vertikalwanderer zurückgeführt. Es wurden jedoch Hinweise gefunden, die auf einen Seebergeffekt im Sinne einer Ausdünnung von Tintenfischlarven über dem Plateau während der nächtlichen Probennahme hindeuteten.

## Introduction

Seamounts are striking features in all oceans contrasting with the vast surrounding abyssal plains. They attract biological oceanographers because they are assumed to increase productivity and, therefore, host comparatively large stocks of pelagic and benthic organisms in regions that are commonly regarded as oceanic deserts (Boehlert and Genin 1987; Koslow 1997; Rogers 1994). Seamounts are elevations of more than 1000 m that are mainly of volcanic origin (Epp and Smoot 1989). Approximately 30 000 seamounts are assumed to exist worldwide but only a few of them have been studied in detail (Rogers 1994). Seamounts are known to affect prevailing oceanic circulation patterns (Beckmann 1999; Roden 1987). On a meso-scale spatial level, they can enhance the formation of trapped waves (Brink 1990), deflect ocean currents along isobaths, amplify tidal currents (Eriksen 1991), and produce eddies that may form closed circulation cells, so-called Taylor columns or Taylor caps (*e. g.*, Chapman and Haidvogel 1992; Lueck and Mudge 1997).

Hydrographic conditions such as recirculating currents appear to be important for the retention of planktonic larval stages and may even support speciation and endemism of faunal components (Calder 2000; Mullineaux and Mills 1996; Richer de Forges *et al.* 2000). In contrast, topography and hydrography may also act as dispersal mechanisms (Dower *et al.* 1992; Leal and Bouchet 1991; Parker and Tunnicliffe 1994). Recently, exploratory fisheries at seamounts have revealed large and economically valuable fish stocks (Koslow *et al.* 1994; Moore 1999; Uchida and Tagami 1984). Whether these comparatively large stocks of demersal fish are a consequence of higher productivity or better transfer efficiency compared to the adjacent open ocean is still under discussion (Comeau *et al.* 1995; Dower and Mackas 1996; Haury *et al.* 2000; Mouriño *et al.* 2001; Rogers 1994) and depends on local conditions, *e. g.*, the varying minimum depth of the seamount plateau, lateral extent of the summit, steepness of the slope, and the degree of isolation from the continental shelf and major oceanic currents.

One of the most striking isolated submarine features in the North-east Atlantic is Great Meteor Seamount (GMS), located east of the mid-Atlantic Ridge at approximately 30° N and 28.5° W. This seamount rises from depths of almost 4800 m to about 275 m below sea level. GMS is characterised by an elliptical base, a steep slope with a gradient of up to 45°, a relatively flat and large plateau area of about 1130 km<sup>2</sup>, and an average depth of 330 m. In 1998 an interdisciplinary research cruise was conducted to study biological and hydrographical features at GMS. One focus of the sampling was the investigation of the influence of topography on the pelagic fauna, from microzooplankton to macronekton. Cephalopods are one component of the pelagic fauna, and they form an important link in oceanic food webs (Piatkowski *et al.* 2001). Most oceanic species have in common that their hatchlings develop within the plankton, mainly in the upper layers. The early life stages are thus susceptible to zooplankton sam-

pling, and can be caught more quantitatively than their fast-swimming adult stages, which are difficult to sample representatively even with large pelagic trawls (Piatkowski 1998). This may be a reason why relatively few studies on cephalopods in the open ocean, and especially at seamounts, have been conducted (Nesis 1994; Parin *et al.* 1988). Nesis (1993a) provided an overview of the various association modes of cephalopod species at seamounts, but specific distribution patterns remained unclear. In the present study we investigate the cephalopod fauna at GMS for the first time and relate the distribution of the early life stages to topography and special hydrographic features. Corresponding to recent findings on seamount-specific zooplankton and demersal fish communities (Dower and Mackas 1996; Fock *et al.* 2002), the main objective was to demonstrate whether a characteristic cephalopod fauna exists at GMS and to what extent the seamount influences distribution patterns and dispersal strategies of the early life stages of cephalopods. Furthermore, we describe specific vertical distribution and diel migration patterns.

## Material and Methods

### Sampling

Cephalopod specimens were obtained from zooplankton samples collected at Great Meteor Seamount (GMS) in September 1998 during cruise 42/3 of the German research vessel Meteor. Sampling was carried out with a BIOMOC, *i. e.*, a modified MOCNESS (Wiebe *et al.* 1976) with a 1 m<sup>2</sup> net opening that allows consecutive opening and closing of nine nets during one haul. The gear was equipped with an electronic flowmeter to estimate the net specific filtered volume. The nets had a length of 6 m and a mesh size of 335 µm.

In total, 22 stations were sampled, covering the flat-topped summit of the seamount, the slope, and the surrounding oceanic region (Table 1). At each station sampling was conducted from 290 m depth to the surface in 7 depth strata (290 to 250 m, 250 to 200 m, 200 to 150 m, 150 to 100 m, 100 to 50 m, 50 to 10 m, 10 to 0 m). The net was towed in each water layer in a three-fold oblique tow at a ship's speed of approximately 3 knots. On the average, 1500 m<sup>3</sup> of water were filtered in each depth stratum. All samples were initially preserved on board in sodium borate buffered formalin, diluted in seawater to 4 %.

Cephalopods were sorted and identified to the lowest feasible taxonomic level. For each station, cephalopod species densities

Table 1: Numbers of stations sampled with BIOMOC net above the summit, the slope, and in the adjacent deep sea at Great Meteor Seamount during RV Meteor cruise 42/3 in September 1998. Listed are the corresponding water depth, time of sampling, and haul numbers. Haul numbers sampled at «shallow» and «deep-water» stations correspond to the same sampling but to a different categorisation applied within parts of the analysis. At all stations depth-stratified tows were conducted from 290 m depth to the surface.

Location	Water depth [m]	No. of tows		
		Day	Twilight	Night
Plateau	< 350	5	1	4
Slope	350–1500	0	2	3
Deep-Sea	> 1500	2	2	3
Shallow	< 350	5		4
Deep water	> 1000	2		2

(N/1000 m<sup>3</sup>) were calculated per depth stratum and integrated for the entire water column. Water column densities (0 to 290 m) were calculated for each station by weighting the samples according to the extent of the corresponding depth stratum (equal to numerical integration). Only water-column densities were used in the initial species-station table for the spatial analysis of the cephalopod community.

### ***Hydrography***

GMS is positioned within the flow system of the wind-driven subtropical gyre of the North-east Atlantic. Hydrographical measurements performed on the M42/3 cruise of RV "Meteor" revealed that the seamount lies within a weak south-westerly current, and it is strongly influenced by diurnal and semidiurnal tides (Mohn and Beckmann 2002). These authors also detected a Taylor cap formation above the seamount. Furthermore, Mohn and Beckmann (2002) and Beckmann and Mohn (2002) developed a numerical model simulating the three-dimensional circulation at GMS. In separate experiments, passive tracers and Lagrangian trajectories with passive floats and actively vertically migrating particles were used. They concluded that the region hydrographically influenced by GMS extends to about 4 times the area of the summit plain and generally includes an area delineated by a water depth of less than 4400 m. They defined an inner (circumscribed by the 1500 m depth contour) and an outer seamount regime (covering an area from 1500 to 4400 m water depth). A strong retention potential of passive tracers was confined to the summit area, delimited by the 350 m depth contour.

### ***Data analysis***

Zooplankton stations were categorised according to different abiotic variables (sampling time of day, position in relation to the seamount or distance from the plateau margin, water depth). Three different time periods were distinguished: Day, night and twilight (dusk/dawn), with the concurrent global radiation measured on board RV Meteor as a proxy. The positions of the stations were assigned as plateau (< 350 m water depth), slope (350 to 1500 m water depth), and deep sea stations (> 1500 m water depth) according to the findings of Beckmann and Mohn (2002) (Table 1).

Multivariate statistical analyses were performed to examine differences in species composition and abundances of cephalopods at the sampling sites. For this purpose, families that mainly comprised specimens that could not be identified to species level were treated as entities. Species/group densities (N/1000 m<sup>3</sup>) were calculated for each station (integrated over the water column). Densities were fourth-root transformed in order to reduce the effect of dominating species/groups and to increase the importance of rare ones (Field *et al.* 1982). Similarity between stations was calculated by means of the Bray-Curtis coefficient (Bray and Curtis 1957). Samples were classified by hierarchical agglomerative cluster analysis using the group-average linking method (CLUSTER; Field *et al.* 1982) and ordinated by non-metric multidimensional scaling (nMDS; Kruskal and Wish 1978). Two-dimensional ordination plots were performed on the resulting similarity matrix to illustrate the relationships among cephalopod assemblages at the various stations around the seamount. Relationships between cephalopod assemblages and various subsets of environmental variables were examined using the BIOENV procedure (Clarke and Ainsworth 1993). Light intensity at sea level (indicating time of day), distance from the plateau margin, and water depth were

applied as continuous variables possibly influencing distribution patterns. Measures of light intensity were log transformed to validate the use of normalised Euclidean distances for the calculation of a similarity matrix based on abiotic information. The Spearman rank correlation was used as a measure of agreement between each of the abiotic matrices and the biotic Bray-Curtis similarity matrix (Clarke and Ainsworth 1993). The above non-parametric multivariate techniques are included in the PRIMER software package (Clarke and Warwick 1994).

For species occurring in sufficient numbers in zooplankton catches at different times of the day (> 10 individuals per time of day) the weighted mean depth (WMD) was calculated as  $WMD = \sum n_i d_i / \sum n_i$ , where  $n_i$  is species/family density (N/1000 m<sup>3</sup>) at depth  $d_i$  (Bollens and Frost 1989). WMD's were not compared statistically between different times of the day due to the low number of stations. In a second approach differences between the average day and night distribution patterns of the most abundant species were investigated by the Kolmogorov-Smirnov two-sample test, as this test is known to be robust against so-called shift alternatives (Darling 1957).

In order to investigate the effect of the topographic elevation on the densities of early life stages of cephalopods two different approaches were chosen. Specimens of all cephalopod species were summed up, as numbers at the species level would be too low for statistical analysis. Because of the pronounced diel vertical migration of some cephalopod groups, day and night samples were considered separately. Firstly, the depth variation in cephalopod density between plateau (< 350 m water depth) and deep-water stations (> 1000 m water depth) (Table 1) was examined by using a two-way ANOVA; original data were log (x + 1) transformed to achieve homogeneous variances (Bartlett's test,  $p > 0.05$ ). Normal distribution of data could not be tested directly because of the low number of stations. Therefore, data were pooled after using a z-transformation and investigated graphically and statistically for deviations from normal distribution (Kolmogorov-Smirnov test,  $p > 0.2$ ). Secondly, the mean vertical distribution of cephalopods above the plateau and in deep water was analysed by the Wilcoxon matched pairs test, by comparing the mean densities in each depth stratum. As no differences between the distribution patterns were detectable, the requirements for the test were met. All statistical tests were considered to be significant at a probability level of  $p < 0.05$ .

## Results

### *Species composition*

22 BIOMOC hauls yielded a total of 1180 early life stages of cephalopods, comprising 18 families and 31 species (Table 2). All specimens belonged to the order Oegopsida and the octopod sub-order Incirrata. Since many specimens could not be identified to species level the total number of species must be considered to be a minimum number. As an example, morphological characters of rhynchoteuthion larvae indicated 4 different species of the family Ommastrephidae in the collection that can be reliably distinguished only into two different larval types (Vecchione *et al.* 2001), rhynchoteuthion type A' (probably representing *Ommastrephes bartramii*) and type B' (including paralarvae of *Hyaloteuthis pelagica*, *Stenoteuthis pteropus*, and *Ornitoteuthis antillarum*). Densities per family, integrated over 0 to 290 m

Table 2: Early life stages of cephalopods collected by BIOMOC net during RV Meteor cruise 42/3 in September 1998. Numbers for higher taxa only include specimens that could not be further identified. Identification of Ommastrephidae into rhynchoteuthion types was performed according to Vecchione *et al.* (2001).  $N_{\text{abs}}$  = total catch in numbers;  $N/1000 \text{ m}^3$  = (I.) average species density in specimens per 1000  $\text{m}^3$  filtered water volume and (II.) average family density (as before). Percentage of positive tows indicates the frequency of species at the 22 stations.

Order. Family	Species	$N_{\text{abs}}$	$N/1000 \text{ m}^3$	$N/1000 \text{ m}^3$ per family	Positive tows [%]
<b>Order Oegopsida</b>	Oegopsida indet.	183	13.42		
Family Enoploteuthidae	Enoploteuthidae indet.	136	23.71		
	<i>Abralia veranyi</i>	1	0.12	33.31	4.5
	<i>Abraliopsis pfefferi</i>	86	8.81		86.4
	<i>Enoploteuthis leptura</i>	7	0.67		18.2
Family Onychoteuthidae	Onychoteuthidae indet.	6	0.89		
	<i>Onychoteuthis banksii</i>	194	19.78	21.85	81.8
	<i>Onykia carriboea</i>	14	1.18		27.3
Family Pyroteuthidae	Pyroteuthidae indet.	28	3.54		
	<i>Pterygioteuthis giardi</i>	2	0.14	13.84	4.5
	<i>Pyroteuthis margaritifera</i>	77	10.16		81.8
Family Lycoteuthidae	Lycoteuthidae indet.	8	0.94		
Subfamily Lycoteuthinae	<i>Selenoteuthis scintillans</i>	54	6.47	7.41	68.2
Family Ancistrocheiridae	<i>Ancistrocheirus lesueuri</i>	70	7.30	7.30	72.7
Family Cranchiidae	Cranchiidae indet.	10	1.45		
Subfamily Cranchiinae	Cranchiinae indet.	8	0.71		
	<i>Cranchia scabra</i>	4	0.55		13.6
	<i>Leachia</i> sp.	1	0.03		4.5
	<i>Liocranchia reinhardti</i>	2	0.18		9.1
Subfamily Taoninae	Taoninae indet.	5	0.40	6.72	
	<i>Bathothauma lyromma</i>	3	0.23		13.6
	<i>Helicocranchia</i> sp.	3	0.30		
	<i>Helicocranchia papillata</i>	21	2.26		50.0
	<i>Helicocranchia pfefferi</i>	4	0.24		9.1
	<i>Liguriella</i> sp.	3	0.36		9.1
Family Ommastrephidae	Ommastrephidae indet.	7	0.78		
Subfamily Ommastrephinae	<i>Rhynchoteuthion Type A</i>	38	3.93	5.85	50.0
	<i>Rhynchoteuthion Type B</i>	17	1.14		40.9
Family Ctenopterygidae	<i>Ctenopteryx sicula</i>	52	5.19	5.19	72.7
Family Chiroteuthidae	Chiroteuthidae indet.	2	0.34		
	<i>Chiroteuthis</i> sp.	11	1.77	2.65	36.4
	<i>Valbyteuthis</i> sp.	8	0.54		18.2
Family Thysanoteuthidae	<i>Thysanoteuthis rhombus</i>	8	0.93	0.93	22.7
Family Brachiooteuthidae	<i>Brachiooteuthis</i> sp.	5	0.35	0.35	13.6
Family Mastigoteuthidae	<i>Mastigoteuthis</i> sp.	3	0.24	0.24	13.6
Family Histiooteuthidae	<i>Histiooteuthis</i> sp.	1	0.15		4.5
	<i>Histiooteuthis celetaria celetaria</i>	1	0.09	0.24	4.5
Family Cycloteuthidae	<i>Discoteuthis</i> sp.	3	0.13	0.13	4.5
<b>Order Octopoda</b>	Octopoda indet.	1	0.14		
Family Argonautidae	<i>Argonauta argo</i>	21	2.57		50.0
Family Bolitaenidae	<i>Bolitaena pygmaea</i>	43	4.43	9.71	72.7
Family Octopodidae	Octopodinae sp.	27	2.29		40.9
Family Tremoctopodidae	<i>Tremoctopus violaceus</i>	2	0.28		9.1
<b>Sum</b>		1180			

water depth (N/1000 m<sup>3</sup>) (Table 2) showed a dominance of two families, the Enoploteuthidae (25.8 % of the total catch) and the Onychoteuthidae (16.9 %; Figure 1). The two families were each mainly represented by one species: *Abraliopsis pfefferi* (Enoploteuthidae) and *Onychoteuthis banksii* (Onychoteuthidae), respectively. Other moderately abundant groups were small-bodied mesopelagic squids of the families Pyroteuthidae (10.7 %), Ancistrocheiridae (5.7 %), and Lycoteuthidae (5.7 %). The meso- to bathypelagic Cranchiidae amounted to 5.2 % of the total catch. Besides the Ommastrephidae (4.5 %) and the Ctenopterygidae (4.0 %), all other oegopsid families contributed less than 2.5 % to the overall abundance of cephalopods (Figure 1). The Octopoda (7.5 %) were represented by at least four families, three of them comprising pelagic species (*Argonauta argo*, *Bolitaena pygmaea*, *Tremoctopus violaceus*). Specimens belonging to the Octopodidae were probably hatchlings of the deep-water species *Scaevurgus unicolor*, as benthic juveniles and adults were caught four times by concurrent bottom trawl hauls and bottom traps during the Meteor expedition at GMS (Diekmann, unpublished data).

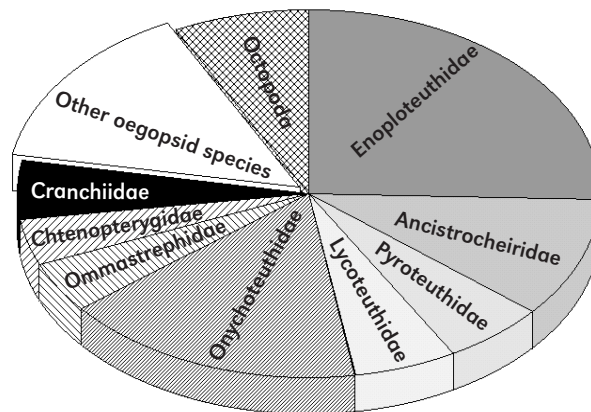


Figure 1: Catch composition of cephalopods as percentage of the total relative abundance of major cephalopod groups from BIOMOC samples at Great Meteor Seamount during RV Meteor cruise 42/3 in September 1998. Unidentified specimens and oegopsid species/families that contributed less than 2.5 % to the total cephalopod abundance were summarised as «other oegopsid species».

### ***Cephalopod distribution in relation to GMS***

Cephalopod densities in BIOMOC hauls standardised to 290 m water depth varied between 1.5 and 16.7 specimens per 1000 m<sup>3</sup> (Figure 2). Night and twilight sampling yielded up to 200 % more specimens compared to daytime sampling. When diurnal patterns were not taken into account, densities were higher in the south-western region, *i. e.*, leeward of the seamount, than above its summit (Figure 2). Separate consideration of day and night hauls revealed differences between shallow (< 350 m water depth) and deep-water stations (> 1000 m water depth) in average densities and vertical distribution of early life stages of cephalopods. During daytime, lower densities were measured at deep-water stations compared to stations above the summit (Figure 3); in all seven depth strata lower densities were

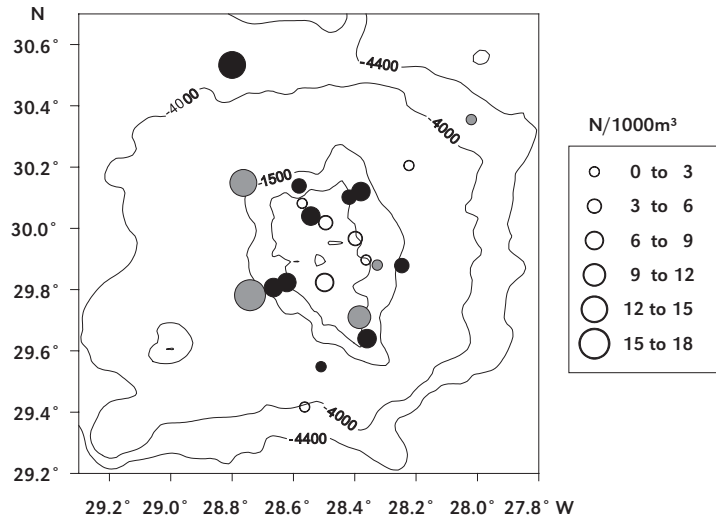


Figure 2: Cephalopod densities (N/1000 m<sup>3</sup>) in BIOMOC samples from 290 m depth to the surface, collected during the RV Meteor cruise 42/3 in September 1998 at Great Meteor Seamount. Bathymetry of Great Meteor Seamount is displayed in 350 m, 1500 m, 4000 m, and 4400 m depth contours. Diameters of the circles, representing cephalopod densities, increase linearly from 0 to 18 specimens/1000 m<sup>3</sup> filtered water volume. Shading of circles indicates time of day during sampling (open circles: day; grey circles: twilight; black circles: night).

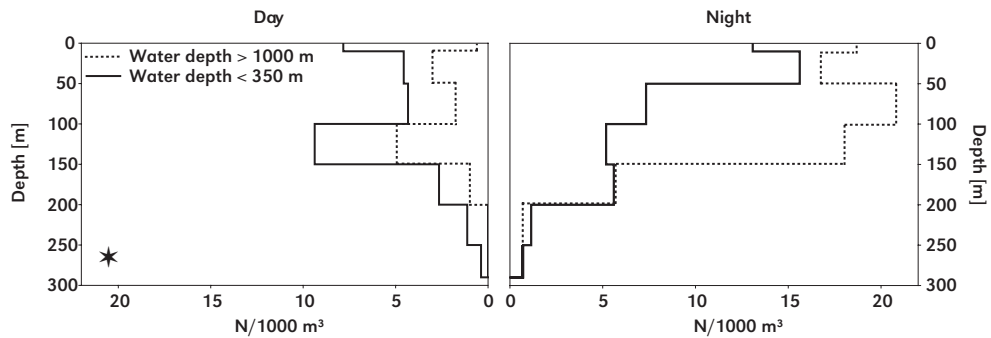


Figure 3: Vertical distribution of early life stages of cephalopods in seven discrete depth strata sampled by BIOMOC net at Great Meteor Seamount during RV Meteor cruise 42/3 in September 1998. Distribution patterns between stations sampled above the summit (< 350 m water depth, solid line) and in deep waters (> 1000 m water depth, dotted line) are compared separately for day and night sampling. \* indicates significant difference between two sampling series at the 0.05 probability level (Wilcoxon matched pairs test).

found at deep-water stations and differences were statistically significant ( $p < 0.05$ ; Wilcoxon matched pairs test). At night the reverse pattern was observed. Higher densities were measured in deep-water hauls compared to sampling above the summit. However, below 200 m water depth, densities were generally low and even fewer specimens were caught at deep-water sta-



tions than above the plateau. Thus, no statistical difference was revealed ( $p > 0.05$ ; Wilcoxon matched pairs test). The same results were obtained using densities per depth stratum separately for each station (two-way ANOVA, Table 3). Densities were significantly different ( $p < 0.05$ ) between shallow- and deep-water stations by day, but not at night. Significant differences between depth strata were demonstrated at any sampling time.

Hierarchical, agglomerative classification (CLUSTER) and ordination (nMDS) of species densities at BIOMOC stations indicated three different groups, separated at an arbitrary level of 53 % dissimilarity, and one ungrouped station (Figure 4). The largest group contained 14 of the 22 stations. When additional information on position (plateau, slope, deep sea) and time of day (day, twilight, night) were superimposed on the graph no direct de-

Table 3: Results of two-way ANOVA testing for differences in density of cephalopod early life stages by position (shallow stations: < 350 m water depth, deep stations: > 1000 m water depth) and sampling depth (7 depth strata from 290 m depth to the surface). Day and night distributions were tested separately. Significant differences ( $p < 0.05$ ) are in italics. Sampling was performed by BIOMOC net during RV Meteor cruise 42/3 in September 1998.

Source of variation	df	MS	F-ratio	p-value	Number of vertical series
<b>Day</b>					
Position	1	0.716	7.899	<i>0.00805</i>	
Depth stratum	6	0.394	4.347	<i>0.00222</i>	7
Position $\times$ depth	6	0.044	0.488	0.81255	
Error	35	0.091			
<b>Night</b>					
Position	1	0.001	0.018	0.894	
Depth stratum	6	0.792	12.903	<i>0.000</i>	6
Position $\times$ depth	6	0.082	1.336	0.275	
Error	28	0.061			

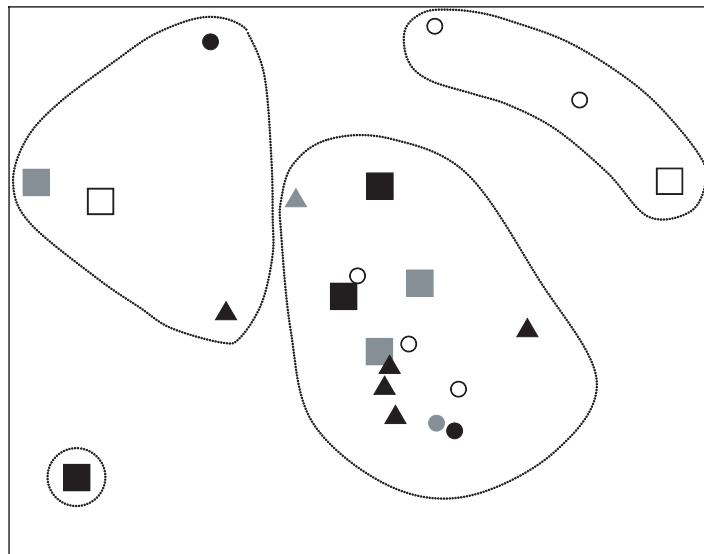


Figure 4: Ordination of the 22 BIOMOC stations according to cephalopod assemblages, sampled at Great Meteor Seamount during RV Meteor cruise 42/3 in September 1998. Symbols represent stations categorised as plateau (circles), slope (triangles), and deep-sea stations (squares). Colour of the symbols represent the time of sampling (white: day; grey: twilight; black: night). Grouping (dotted lines) was indicated by cluster analysis. Stress = 0.12.

pendence on any factor was obvious (Figure 4). This observation was additionally tested by the BIOENV procedure, using continuous data for water depth, light intensity, and distance from the plateau margin. A maximum of 15.8 % correlation to the similarity matrix based on species abundances could be achieved combining all three factors, indicating no detectable interrelation between cephalopod community structure and the tested abiotic variables.

### *Diel vertical migration patterns*

The comparison of the weighted mean depth (WMD) between different times of the day resulted in similar vertical migration patterns for most investigated species groups. For major cephalopod species/families and for the total of all early life stages of cephalopods, the WMD by day was found to be deeper than at night (Table 4). The biggest differences between day and night distributions were observed for Enoploteuthidae ( $\pm 43$  m), Ancistrocheiridae ( $\pm 30$  m) and Pyroteuthidae ( $\pm 29$  m), of which the latter additionally showed the deepest distribution of all investigated cephalopod groups. However, the variability within stations sampled at the same time of day was high. Migration magnitudes may have been underestimated, as the samples were not necessarily obtained when specimens were at their maximum or minimum depth distribution.

Table 4: Average weighted mean depth (WMD) at day, twilight, and night of all early life stages of cephalopods and the most abundant species/families sampled with BIOMOC net at Great Meteor Seamount during RV Meteor cruise 42/3 in September 1998. Additionally listed are one standard deviation (s) of the WMD and the total number of specimens (n), on which the analysis was based.

Species group	Daytime	WMD	s <sub>WMD</sub>	n
All species	Twilight	95.0	21.5	354
	Day	101.9	18.2	230
	Night	93.8	20.7	585
Enoploteuthidae	Twilight	68.6	8.2	67
	Day	109.6	33.4	47
	Night	66.8	26.8	111
Ommastrephidae	Day	46.5	25.3	18
	Night	64.9	18.9	23
<i>Onychoteuthis banksii</i>	Twilight	73.6	26.1	77
	Day	78.4	22.2	45
	Night	61.7	22.7	73
Pyroteuthidae	Twilight	150.2	33.7	20
	Day	165.1	67.0	14
	Night	135.9	40.7	64
<i>Ancistrocheirus lesueuri</i>	Twilight	51.5	7.1	21
	Day	85.0	35.1	15
	Night	55.2	32.2	24
<i>Selenoteuthis scintillans</i>	Twilight	92.5	76.9	11
	Day	70.3	4.4	14
	Night	94.6	47.1	37
Cranchiidae	Twilight	102.8	16.7	14
	Day	138.4	43.3	12
	Night	112.9	43.8	35

Twilight sampling mostly resulted in an intermediate depth distribution except for Ancistrocheiridae and Cranchiidae. No upward migration at night could be demonstrated for Ommastrephidae and *Selenoteuthis scintillans* (Lycoteuthidae). Both occurred in shallower mean depths during the day than at night (Table 4). However, the vertical distribution patterns did not confirm this observation (Figure 5). The Ommastrephidae were exclusively found in the upper 150 m of the water column without any upward migration at any time of the day. The same was observed for *Selenoteuthis scintillans* and partly for *Onychoteuthis banksii*, although for this

Early life stages of cephalopods

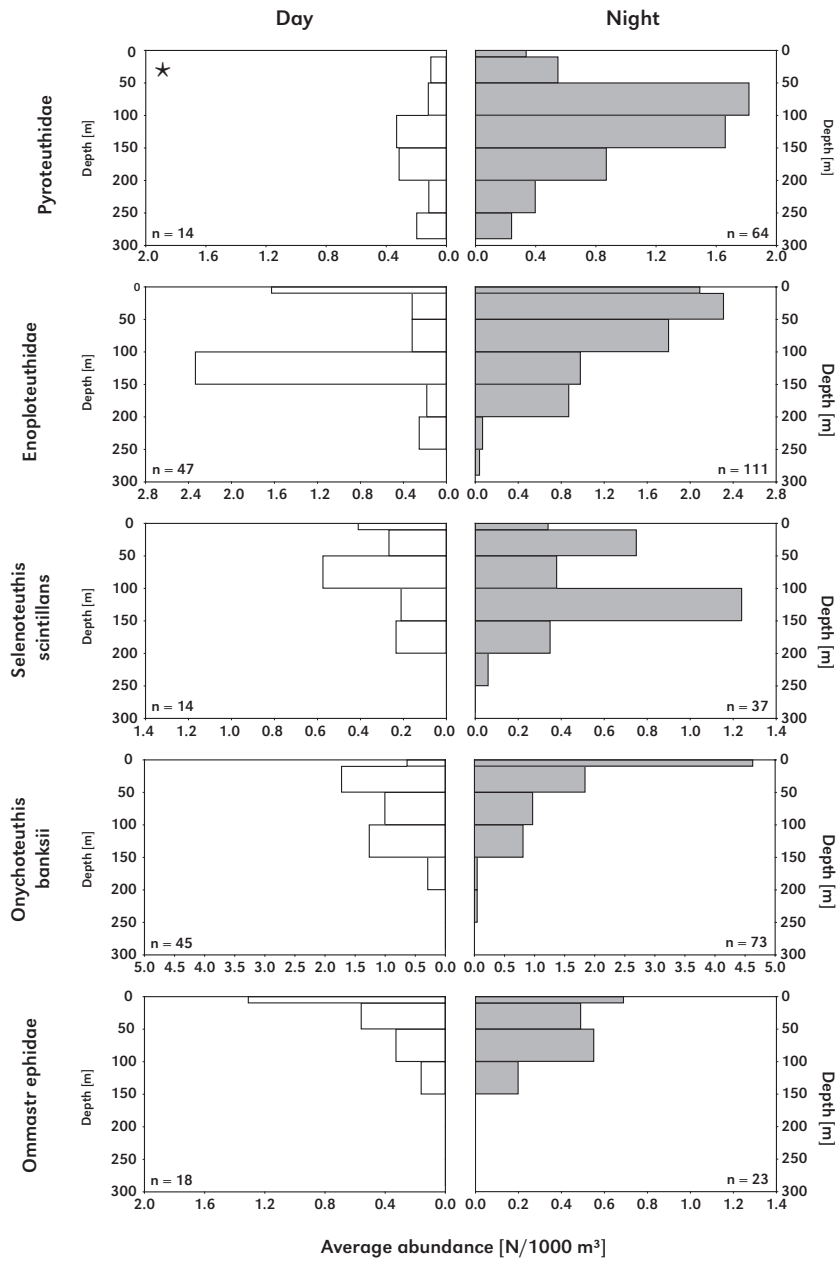


Figure 5: Vertical distribution of the most abundant cephalopod species/families sampled by BIOMOC net at Great Meteor Seamount during RV Meteor cruise 42/3 in September 1998. Bars are mean abundances per 1000 m<sup>3</sup> at each depth interval of 7 day (clear bars) and 10 night (shaded bars) vertical series of samples. \* indicates significant difference between day and night distribution at the 0.05 probability level (K-S test).

species abundance increased during the night in the near-surface layer. An upward migration at night was revealed for the Enoploteuthidae, the most abundant family in the samples, and for the Pyroteuthidae, although only the latter showed statistically significant differences between day and night vertical distribution patterns.

## Discussion

In the present study the cephalopod fauna at Great Meteor Seamount (GMS) and its surrounding water masses was investigated for the first time. The sampling strategy aimed originally at the investigation of the zooplankton distribution within the euphotic zone. Therefore, only early life stages of cephalopods that were distributed within the upper 290 m of the water column could be taken into account, and benthic and bathypelagic species are consequently missing in the faunal description.

Although the sampling in September 1998 has not been repeated and, thus, the findings of the present study can only be interpreted as a first snapshot of the cephalopod community at GMS, the information provided is quite comprehensive. In general, a typical oceanic subtropical cephalopod fauna was found. All species occurred within their known distributional range. No neritic species, *e. g.*, myopsid squids or some representatives of the family Ommastrephidae (*e. g.*, *Illex coindetii*, *Todaropsis eblanae*), which are abundant at the west African shelf and slope waters, were identified in the samples. A detailed comparison of the cephalopod fauna with other investigations was not possible as, to our knowledge, no information is available on the distribution of early life stages in the subtropical eastern North Atlantic. Kluchnik (1978) recorded a cephalopod community similar to our study in an area from 30° N to 37° S, east of the mid-Atlantic Ridge. However, the relative species composition was different because the sampling extended to south of the equator. The main differences were found within the Ommastrephidae, which was one of the dominating groups in the investigation of Kluchnik (1978) but less abundant in our study.

All specimens found in the zooplankton samples belonged to cephalopods known to remain pelagic during their whole life except one form of the family Octopodidae, which can be related to benthic adults, presumably of the species *Scaevurgus unicolor*. This octopod, which lives in the upper bathyal zone, is a typical inhabitant of seamounts (Nesis 1993a). Because GMS is widely isolated from other shallow topographic features and the water depth increases rapidly from 300 m at its top to about 5000 m at its flanks, it is very likely that the early life stage Octopodidae originated from an octopod stock inhabiting the seamount. The major component of the cephalopod fauna was represented by diurnal vertical migrators that may be advected by currents above the summit and descend to near the bottom during day (*e. g.*, *Pyroteuthis margaritifera*, *Abraliopsis pfefferi*, *Selenoteuthis scintillans*, *Chtenopteryx sicula*). The extensive diurnal vertical migratory behaviour of the adults is well known and was described by Clarke and Lu (1974) and Roper and Young (1975). According to Roper and Young (1975), early life stages of these species occur in near-surface waters, whereas the juvenile and adult forms live in deeper water layers. Nevertheless, the early life stages of some species investigated in our study already demonstrated significant diurnal vertical migrations (Pyroteuthidae) or showed at least a tendency for dispersing downwards during daytime (*e. g.*, Enoploteuthidae, *Selenoteuthis scintillans*).

The zooplankton sampling in the area of GMS revealed a combination of short-term temporal and small-scale spatial variability. During the cruise of RV Meteor the field work profited from favourable weather conditions and weak but constant winds. The assumptions about the flow field around GMS (Mohn and Beckmann 2002) and the distribution of passively advected and actively migrating organisms in a numerical model (Beckmann and Mohn 2002) were based on such constant weather conditions, because strong winds largely affect the direction and the velocity of near-surface currents. Thus, the hydrographic models very likely represented the real situation during the research cruise, and deviations from model predictions due to short-term shifts in circulation patterns were expected to be low. However, no clear indications were found for an influence of the seamount hydrography on cephalopod abundance. The relatively high species densities measured south-westward of the plateau may be related to weaker small-scale turbulence leeward of the seamount (Beckmann and Mohn 2002), but it could also be an effect of the time of sampling, as all hauls in this area were performed at dusk or during the night, favouring the catch of upward-migrating species. Nevertheless, a similar observation has been made in a study by Huskin *et al.* (2001). They found a general tendency of increasing zooplankton biomass and copepod abundance following a transect from east to west of GMS, but could also not relate this phenomenon to hydrography nor to increased primary production. During our study slightly enhanced phytoplankton biomass was measured above the summit of GMS, but not leeward of it (Kaufmann, pers. comm.). Phytoplankton biomass concentrations seemed to be only weakly increased and a direct response of higher trophic levels was unlikely. Furthermore, for measurable effects on secondary production, physical anomalies above topographic elevations have to be maintained for a few weeks (Genin and Boehlert 1985; Rogers 1994).

Specimens without extensive vertical migration behaviour (*e. g.*, early life stages of *Onychoteuthis banksii*) could be retained above the summit because the water mass above the seamount was virtually isolated, laterally and vertically (Beckmann and Mohn 2002). An influx of early life stages into this water body via ocean currents is, thus, hardly possible. An increased density of cephalopods above the summit could only be expected if the seamount was an area of high spawning activity, *viz.* cephalopod production. According to the generally low abundances of early life stages, especially above the plateau, this was obviously not the case at GMS, at least not during the sampling period. Therefore, we concluded that the distribution patterns of cephalopods were attributed to the interaction of currents, topography and vertical migration behaviour of zooplankton rather than to retention potential or enhanced primary and secondary production above the plateau. The comparison of the vertical distribution patterns of all cephalopod species between GMS and the surrounding open ocean indicated an influence of the seamount on their overall abundance. The higher abundance of cephalopods during the day above the summit seemed to be related to “trapping” of vertical migrators (*e. g.*, Pyroteuthidae) that are usually concentrated in the water layers below the summit depth during the day (Rogers 1994). At night higher abundances in the open ocean compared to the plateau area indicate that vertically migrating species became susceptible to our sampling, whereas above the plateau their numbers might have been reduced by predation by, *e. g.*, demersal fish species inhabiting the summit. Genin *et al.* (1994) and Hauray *et al.* (2000) hypothesised that higher predation pressure on zooplankton organisms in the seamount area might be responsible for daily “gap formation”. They as-

sumed that these gaps are transported downstream and, accordingly, a higher zooplankton patchiness can be found leeward of the seamount. Our observation from the comparison of cephalopod abundances above and adjacent to the plateau leads us to suppose that a similar mechanism exists at GMS. Unfortunately, gap formation and patchiness downstream of the seamount could not be investigated directly due to the restricted sampling grid. However, the potential trapping of vertically migrating zooplankton organisms could support high concentrations of predatory benthopelagic fishes, as has been reported from GMS (Uiblein *et al.* 1999) and other seamounts (Dower and Perry 2001; Uchida and Tagami 1984).

In contrast to the influence on species abundances, no “seamount-effect” was revealed for the species composition as shown by the MDS analysis. Differences between stations were not related to topographic or hydrographic features. Octopodid early life stages, which were presumably spawned above the summit or the slope of the seamount, were distributed throughout the investigated area, and occurred even at deep-water stations. Possible effects might also be masked by the selected station grid. According to Beckmann and Mohn (2002) the influence of GMS extends to about four times the area of the summit plain, which means that no stations were sampled outside the vicinity of the seamount. Dower and Mackas (1996) demonstrated a seamount effect on the mesozooplankton community that extended to about one seamount diameter into the surrounding oceanic waters, and even beyond this area the similarity between off- and above-seamount communities was relatively high. The high diversity of the cephalopod catches at GMS and the large variability among consecutive tows made it extremely difficult to detect any differences between station groups. Similar large variability has been reported from early life cephalopod assemblages in Hawaiian Island waters (Bower *et al.* 1999) and from tropical seamounts and nearby oceanic islands off the north-eastern coast of Brazil (Haimovici *et al.* 2002).

In order to answer the question whether seamounts have a positive effect on cephalopod assemblages, especially on their early life stages, additional sampling of the surrounding oceanic region would be required, and stations would need to be repeatedly sampled, covering the entire day-night cycle. So far, commercially valuable cephalopod stocks have only been reported from around the shallow Saya de Malha Bank (14.7 m average water depth) in the western Indian Ocean (Nesis 1993b). Whether seamounts that do not reach into the productive euphotic zone provide a similar suitable environment for cephalopod aggregations and serve as recruitment areas remains, however, still debatable.

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