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The influence of seamounts on mesopelagic fish communities*)

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Abstract

The effects of decreasing water depth on vertically migrating mesopelagic fish was investigated at two shallow topographic features in the NE Atlantic, the Atlantis Seamount and the Great Meteor Seamount. For this purpose the fish assemblage was sampled by means of stratified horizontal midwater tows at three bathymetrically defined stations: plateau (water depth < 500 m), slope (depth 500 to 1000 m) and oceanic realm (depth > 2300 m). The results show reduced mesopelagic fish densities, species numbers and diversity above the flanks of Atlantis Seamount and Great Meteor Seamount compared to the surrounding oceanic deep water. Multivariate statistical analysis supplied no evidence for the existence of a seamount-associated mesopelagic community at either of the two study areas. Mesopelagic fish assemblages sampled above the seamount slopes are best described as a "thinned-out oceanic community". A total lack of mesopelagic fish species was typical above the plateaus of both seamounts. Truncation of the vertical migration range by shallow bottom topography and enhanced predation by benthopelagic species are thought to be the main reasons for the observed gaps in mesopelagic fish abundance above the plateaus of both seamounts.

Kurzfassung

Einfluss von Seebergen auf mesopelagische Fischgemeinschaften

An zwei subtropischen Seebergen des Nordostatlantiks, der Atlantis-Bank und der Grossen Meteorbank, wurde der Einfluss abnehmender Wassertiefe auf die Verteilung und die Zusammensetzung der mesopelagischen Fischgemeinschaft untersucht. Zu diesem Zweck wurden stratifizierte Fänge mit einem pelagischen Trawl auf drei bathymetrisch definierten Stationen durchgeführt: a) über dem Seebergplateau bis 500 m Wassertiefe; b) am Abhang zwischen 500 und 1500 m Tiefe; c) im ozeanischen Bereich über Tiefen > 2300 m. Die Untersuchungen zeigten eine deutliche Abnahme der Artenzahl, Diversität und Dichte der mesopelagischen Fischgemeinschaft über den Abhängen beider Seeberge im Vergleich zu den ozeanischen Referenzstationen. Multivariate statistische Verfahren erbrachten keinen Nachweis für eine Seeberg spezifische mesopelagische Artengemeinschaft. Über den flachen Plateaus beider Seeberge fehlten mesopelagische Fische fast vollständig. Die physikalische Begrenzung des Lebensraums durch die abnehmende Wassertiefe, sowie der erhöhte Prädationsdruck durch benthopelagische Fische werden als Hauptgründe für den beobachteten Ausdünnungseffekt beider Seeberge auf die mesopelagische Fischgemeinschaft diskutiert.

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Introduction

Mesopelagic fish represent a major component of the oceanic micronekton community (Salvanes and Kristoffersen 2001). They inhabit the vast oceanic habitat with often gradually changing conditions, bounded by the continental slopes (Hopkins *et al.* 1981). One behavioural characteristic of the majority of mesopelagic fish species is their nocturnal vertical migration, from daytime depths below 500 m into the productive surface layers at night (Kinzer and Schulz 1985; Gartner *et al.* 1987). Mesopelagic fish species with gas-filled swim bladders are the most prominent records on echosounders and may appear as a layer (Salvanes and Kristoffersen 2001). Such sound-scattering layers move upward after sunset and downward before dawn (Mozgovoy and Bekker 1991). Seamounts are elevations of the seafloor and are known to alter the characteristics of the water masses surrounding them (Rogers 1994). The present paper deals with the interaction of seamounts with the prevailing current system and its effects on the spatial distribution of the vertically migrating fish community.

There are several species of mesopelagic fish of principally oceanic families (*e. g.* Sternoptychidae, Photichthydae, Myctophidae, Melamphaidae) that are known to occur in higher abundances at seamounts and slopes in comparison to deep oceanic waters. They are therefore termed as pseudoceanic (*sensu* Hulley 1981). Parin and Prut'ko (1985) reported on a myctophid species, *Diaphus suborbitalis*, living in strong association with a seamount in the western tropical Indian Ocean, and Boehlert *et al.* (1994) described aggregations of *Maurolicus muelleri* at Southeast Hancock Seamount in the central Pacific Ocean. In addition, there are reports of a distinct boundary community over the slope of Hawaii, consisting of mesopelagic fish, decapods and cephalopods (Reid *et al.* 1991; Benoit-Bird *et al.* 2001), that benefit from a higher food supply or a higher structural diversity in these habitats compared to the oceanic deep water.

On the other hand, numerous publications describe reduced abundances of vertically migrating organisms above shallow topographic features, such as mesopelagic fish larvae and euphausiids above Great Meteor Seamount (Nellen 1973; Weigmann 1974), and zooplankton above the summits of the eastern North Pacific seamounts (Genin *et al.* 1988; Genin *et al.* 1994; Haury *et al.* 2000).

A particular feature above seamounts has been described as “daily gap formation”, *i. e.* a lack of organisms during certain times of the day (Genin *et al.* 1994). Possible reasons for this phenomenon include interactions with predators, prevailing flow regime, and local topography. The mechanism of gap formation can be explained as follows: the animals that ascend into the epipelagic layers upstream of the shallow topographic feature at night are advected into the area just above the summit of the seamount. At dawn, their diurnal descent is blocked by the shallow bottom, where they are faced with heavy predation by resident predators (Rogers 1994).

One prerequisite for understanding the distribution patterns of biota associated with seamounts is a sound knowledge of the local circulation pattern. On seamounts a wide range of hydrographic features such as internal wave reflection, tidal amplification, eddy trapping, and bottom-intensified Taylor columns are observed (Roden 1987). Taylor columns are thought to occur when a steady current impinging on a seamount causes an uplift of isotherms. Under certain current, stratification and topographic conditions a closed streamlined anticyclonic vortex, or Taylor column, is expected to persist above the seamount (Roden 1987). It has been speculated that Taylor column formation in oligotrophic waters may enhance nutrient levels in epipelagic waters and cause an increased primary productivity, resulting in a transfer of organic carbon into higher trophic levels (Boehlert and Genin 1987; Rogers 1994). It is not known whether these closed circulation cells have a bearing on micronekton and their lateral advection from the surrounding deep water.

Shallow topographic features like seamounts are known to carry large stocks of benthopelagic fish (Ehrich 1977; Uiblein *et al.* 1999). The question whether these stocks are supported by autochthonously derived energy (*e. g.* enhanced primary production) or by an advected energy supply of zooplankton and micronekton remains under scientific consideration (Dower and Mackas 1996). Vertically migrating micronekton play a significant role in the food of demersal fishes living on these topographic features (Pereyra 1969; Fock *et al.* 2002a). Therefore, knowledge of the distribution patterns of mesopelagic fish around oceanic subsurface structures is a valuable requisite for the understanding of seamount ecosystems and the trophic interactions of these communities.

The present study is intended to address whether two classical table seamounts in the NE Atlantic harbour spatially associated specific mesopelagic fish assemblages. The influence of the Atlantis Seamount and the Great Meteor Seamount on density and diversity of the mesopelagic fish community is analysed with respect to the shoaling bottom topography and the prevailing hydrographic features.

Materials and methods

Sampling site

The Atlantis Seamount (34°09' N; 30°15' W) and Great Meteor Seamount (30°00' N; 28°30' W) are classical table seamounts (Figures 1 and 2). They are part of the Atlantis-Meteor Seamount complex located on the eastern flank of the Mid-Atlantic Ridge about 700 km south of the Azores. The Atlantis Seamount is characterised by a plateau area of approximately 410 km^2 at depths ranging from 250 to 400 m below the sea surface (Bednarz 1991; Figure 1a). The topography of the Atlantis Seamount is quite complex, and characterised by numerous underwater plateaus and pinnacles (Figure 1b).

The Great Meteor Seamount is clearly structured into plateau, slope (gradient > 13°, max. 50°), and basement (< 5° gradient) (Figure 2a). It is one of the largest isolated submarine features in the Atlantic Ocean, with a flat plateau area of approximately 2132 km^2 in depths of less than 330 m (Ulrich 1971).

To investigate the influence of decreasing water depth on the mesopelagic fish community, three bathymetric zones were sampled. They are defined as the plateau (depth < 500 m), the slope (500 to 1000 m depth) and the oceanic realm with depths > 2300 m (Figures 1b and 2b).

Hydrography

Oceanic data were recorded in 1998 with 52 conductivity temperature and density (CTD) profiles across three transects above the Great Meteor Seamount. Additionally, at the

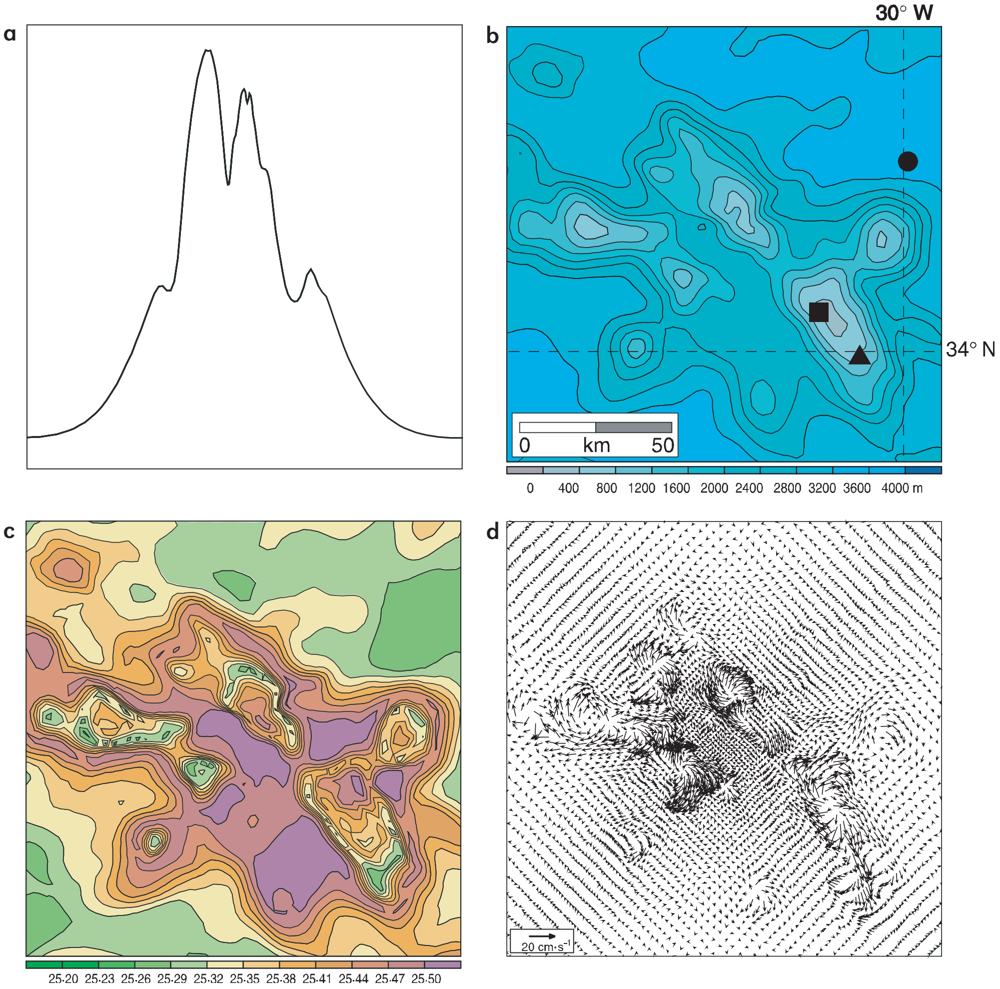

Figure 1: Topography and hydrography of the Atlantis Seamount complex.

(a) cross section (oriented southwest-northeast) of the topography (vertical scale × 100) through the center of the region; (b) depth contours and YFT stations, ● oceanic; ▲ slope; ■ plateau; (c) time-mean density [g/l] distribution at 50 m depth, indicating the large scale doming of isopycnals at the seamount complex; (d) time-mean (residual) velocity field at 50 m depth, indicating generally outward and anticyclonic (clockwise) flow around the individual peaks.

beginning of the field campaign, two Self Contained Acoustic Doppler Current Profilers (SC-ADCP) were placed at the northern and southern edges of the seamount to investigate tidal activity and flow regime as described by Mohn and Beckmann (2002). At the Atlantis Seamount, two CTD profiles were taken at each sampled station.

The flow regime in the mid-latitude NE Atlantic is characterised by the eastern recirculation branch of the wind-driven anticyclonic subtropical gyre. The Atlantis and Great Me-

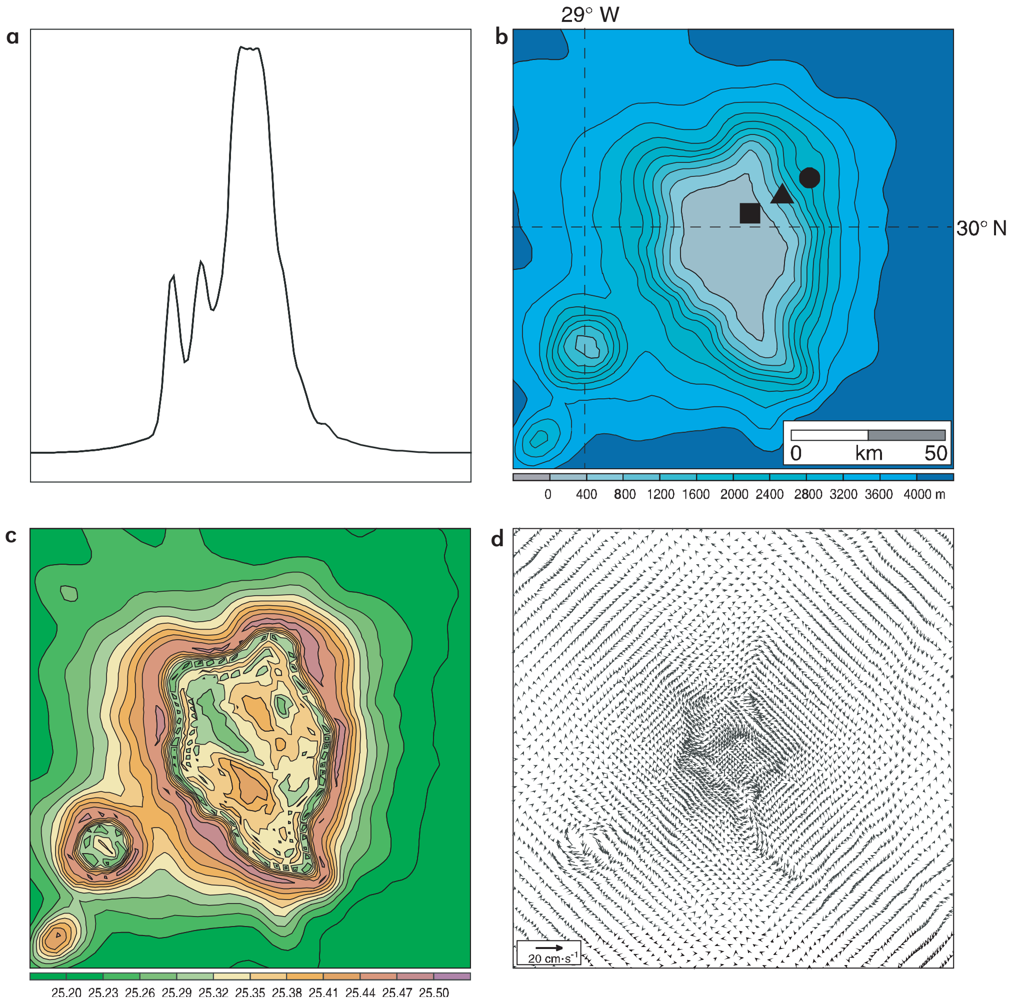

Figure 2: Topography and hydrography of the Great Meteor Seamount complex. The descriptions for parts a, b, c and d are as in Figure 1.

teor Seamounts are located in a zone of relatively weak south-westward mean currents and relatively strong semidiurnal tides.

A more detailed picture of circulation at these seamounts can be obtained from numerical models. The upper ocean circulation at Great Meteor Seamount was investigated by Mohn and Beckmann (2002), who combined analyses of the observational data with simulations from a numerical model. The model results can be used to obtain a consistent picture of the time-mean three-dimensional mass and flow fields. Accordingly, Figure 2c shows the density anomaly at 50 m depth at the Great Meteor Seamount. A very prominent feature in the near-surface layers is an uplift (“doming”) of isopycnals at the outer rim of the seamount roughly aligned with the 2000 m isobath. This feature is formed as the residual of the combined diurnal and semidiurnal tidal currents, and leads to a corresponding anticyclonic circulation around the seamount of typically 6 cm·s^{-1} (Figure 2d). For this study, the same model was also applied for the Atlantis Seamount.

A comparison of Figures 1d and 2d indicates that the hydrographic structure at the Atlantis Seamount is much more complex, and that prevailing currents are characterised by higher velocities (the anticyclonic recirculation features velocities up to 15 cm·s^{-1}) compared to the Great Meteor Seamount. Nevertheless, some similarities can also be found: there is a general doming of isopycnals around the main plateau, again roughly coinciding with the 2000 m depth contour (Figure 1c). Each individual summit, although much smaller, features a density anomaly structure similar to that observed at the Great Meteor Seamount.

The deep-ocean reference stations of both sampling areas are located in the upstream direction north-east of the plateaus. At the Atlantis Seamount, this station is located outside the flow regime of the submerged feature while at Great Meteor Seamount the deep-sea station is influenced by the anticyclonic recirculation cell. All sampling sites above the slope and on the shallow plateau area are located within the anticyclonic cell.

Sampling

The mesopelagic fish assemblage was studied on a cruise with RV "Meteor" in September 1998 to the Great Meteor Seamount and a cruise with RV "Heincke" in October 2000 to the Atlantis Seamount. The fishes were sampled with a non-closing pelagic Young Fish Trawl (YFT). The estimated effective mouth area of the YFT is 80 m^2, with a mesh size of 11 mm in the codend. The sampling depth and the vertical opening of the net was controlled by a Furuno probe. Additional depth and temperature data were obtained by a temperature-depth recorder (Minilog) fixed in the trawl. Tows were of approximately 30 min duration at night and 1 h in daytime at a towing speed of 3 to 3.5 knots to assure a mouth opening of about 80 m^2. The filtered volume of each tow was calculated by multiplying the trawled distance by the effective mouth opening of the YFT.

The sampled vertical depth horizons differed between study areas and with time of day (Table 1). At the Atlantis Seamount night samples were taken at six target depths: 25 m, 100 m, 250 m, 400 m, 600 m, and 800 m. Because of the well documented vertical migration of mesopelagic fish and their resulting daytime depth below epipelagic layers, daytime samples focused on depths below 100 m. Above the summit (plateau station), tows were restricted to the three upper depth horizons, *i. e.*, 25, 100, and 250 m. At the Great Meteor Seamount, the sampling effort was much lower than that at the Atlantis Seamount, with the maximum sample depth restricted to the upper 400 m (Table 1). Different sampling strategies were applied during the day and night at Great Meteor Seamount. During the day double oblique tows were performed down to 400 m depth at the oceanic station and close to the seafloor above the seamount plateau. During the night stratified tows were performed below and within the Deep Scattering Layer (DSL).

On board the vessels, the total catch was weighed and sorted by taxonomic groups. Immediately after retrieval, mesopelagic fishes were either fixed in 8 % formalin or deep frozen at –20 °C. In the laboratory, fishes were identified to species level.

Table 1: Sampling effort in terms of the number of tows per station at given sampling depths for: Atlantic Seamount (AS) and Great Meteor Seamount (GMS).

Area/Time	Station	Approximate sample depth [m]						Sum
		25	100	250	400	600	800	
AS day	Oceanic			1	1	1	1	4
	Slope			1	2	2	2	7
	Plateau		1	1				2
AS night	Oceanic	1	1	1	1	1	1	6
	Slope	2	2	3	1	2		10
	Plateau	1	2	3				6
GMS day*	Oceanic				2			2
	Slope				1			1
	Plateau			2				2
GMS night	Oceanic			1	1			2
	Slope		1	1				2
	Plateau		1	1				2

* Day tows at GMS have been performed as oblique tows; the indicated depth is the maximum sample depth.

Data and statistical analysis

Only mesopelagic species are considered in the present study according to the classification given by Whitehead *et al.* (1984). Epipelagic and benthopelagic species are excluded from data analysis together with fishes of the genus *Cyclothone*, as these were not quantitatively sampled by the YFT. The densities of mesopelagic fish were calculated as individuals per filtered volume (ind./10 000 m^3) in each sample.

Three univariate indices were applied to characterise the species assemblages at different stations and times of the day. The number of species (S) and Shannon's diversity index H' (Shannon and Weaver 1949) were calculated as a measure for species diversity. The latter was calculated as follows:

$$H' = -\sum_i p_i \ln p_i \tag{1}$$

in which

$$p_{\mathrm{i}} = \frac{N_i}{N}$$

N_{i} is the number of individuals of the i-th species in the sample, and N is the total number of individuals. The Pielou's evenness index J' was calculated to examine how evenly the individuals were distributed among species:

$$J' = \frac{H'}{\log S} \tag{2}$$

A non-parametric Kruskal-Wallis test was performed to test for statistical differences in mesopelagic fish densities between stations. In case of significance a Dunn's test was performed to test for differences between sample groups.

Community structure was investigated with multivariate statistical methods using the Primer-E5 Software package (Clarke and Warwick 2001). Samples containing less than three fish specimens were omitted from data analysis (two plateau and one slope sample at the Atlantis Seamount). To reduce the weighting of dominant species, the abundance values were square-root transformed prior to the computation of triangular similarity matrices based on Bray-Curtis similarities (Field *et al.* 1982). The results of the latter were classified by hierarchical agglomerative cluster analysis using the group average linking method and ordinated by using non-metric, multi-dimensional scaling techniques (MDS). The one way analysis of similarity, (ANOSIM) was employed to test for significant differences in species composition among the stations (Clarke and Warwick 1994).

The similarity percentage procedure, (SIMPER) of square–root transformed fish abundances was used to identify the most characteristic species of the different stations (Clarke and Warwick 1994). These are species with an even distribution, *i. e.*, species that show little variance within the chosen group of samples.

Results

Atlantis Seamount

The mesopelagic fish assemblage at the Atlantis Seamount is dominated by species of the family Myctophidae (Table 2). Twelve of the 20 ranking species were myctophids that could be classified as subtropical, tropical and widespread species according to the classification of Hulley (1984). The tropical myctophid species *Ceratoscopelus warmingii* was the most abundant species (35.9 % of all individuals), followed by *Notoscopelus resplendens* (8.0 %), and *Lobianchia dofleini* (7.8 %). Besides representatives of the Myctophidae, species of the mesopelagic fish families Sternoptychidae, Phosichthydae and Stomiidae occurred in significant numbers.

The analysis of mesopelagic fish densities revealed a strong time-of-day effect (Figure 3; Table 3). Mesopelagic fish densities were significantly lower in day samples than in night samples at comparable depth horizons at the oceanic reference station (Mann-Whitney U-test; $p < 0.05$). Although over the slope the average densities of night samples were four times higher than day samples, the difference was not statistically significant (Mann-Whitney U-test; $p > 0.05$). During the daytime, there was a noticeable lack of mesopelagic fish above the plateau.

To study the effect of decreasing water depth on the mesopelagic fish assemblage we focused on night samples, as the effect was expected to be more pronounced at night. Average mesopelagic fish density (individuals/10 000 m^3) decreased from 11.71 at the oceanic reference station to 4.41 over the slope, and reached a minimum value of 0.16 above the plateau. A Kruskal-Wallis test using pooled samples from different depth horizons indicated significant differences in median density among three stations ($p < 0.05$). However, the observed differences between stations were only significant between the oceanic and plateau samples ($p < 0.05$, Dunn's Test). The observed decline in mesopelagic fish densities above the slope and plateau of the Atlantis Seamount was associated with an apparent reduction in species number and diversity (Table 3). At the oceanic station, 70 mesopelagic fish species were identified, and this number decreased over the slope of the

Table 2: The most abundant species in the mesopelagic fish assemblage of the Atlantis Seamount and the Great Meteor Seamount and their zoogeographical affinity (ZA) (according to Hulley, 1984; Badcock 1984a, 1984b); N_{abs} total catch number; Rel. N = percentage of total catch according to the location; Rank = rank of the 20 most abundant species at each seamount. NT = north-temperate species; S = subtropical species; ST = subtropical-tropical species; T = tropical species; W = widespread species.

			Atlantis Seamount			Great Meteor Seamount		
Family	Species	ZA	N_{abs}	Rel. N [%]	Rank	N_{abs}	Rel. N [%]	Rank
Gempylidae	*Diplospinus multistriatus*	ST	1	0.03		36	4.60	7
Myctophidae	*Bolinichthys indicus*	S	38	0.99	17	25	3.19	11
	Ceratoscopelus maderensis	NT	38	0.99	18	0	0.00	
	Ceratoscopelus warmingii	T	1375	35.85	1	86	10.98	1
	Diaphus mollis	T	32	0.83		18	2.30	15
	Diogenichthys atlanticus	W	94	2.45	10	1	0.13	
	Hygophum hygomii	S	99	2.58	8	79	10.09	2
	Hygophum reinhardtii	T	61	1.59	11	28	3.58	10
	Lampadena chavesi	S	10	0.26		8	1.02	19
	Lampanctus cuprarius	S	8	0.21		24	3.07	12
	Lampanyctus ater	S	40	1.04	14	0	0.00	
	Lampanyctus festivus	S	4	0.10		24	3.07	13
	Lampanyctus pusillus	S	195	5.08	4	0	0.00	
	Lepidophanes gaussi	S	100	2.61	7	42	5.36	5
	Lepidophanes guentheri	T	6	0.16		12	1.53	17
	Lobianchia dofleini	W	299	7.80	3	78	9.96	3
	Lobianchia gemellari	T	40	1.04	15	8	1.02	20
	Notoscopelus resplendens	T	305	7.95	2	14	1.79	16
Paralepididae	*Lestidops affinis*	ST	0	0.00		53	6.77	4
	Sudis hyalina	W	0	0.00		29	3.70	9
Phosichthydae	*Vinciguerria nimbaria*	T	61	1.59	12	37	4.73	6
	Vinciguerria poweriae	S	35	0.91	20	11	1.40	18
Serrivomeridae	*Serrivomer beani*	W	39	1.02	16	0	0.00	
Sternoptychidae	*Argyropelecus aculeatus*	S	119	3.10	5	23	2.94	14
	Argyropelecus hemigymnus	W	55	1.43	13	0	0.00	
	Sternotyx diaphana	W	98	2.56	9	0	0.00	
	Valenciennellus tripunctulatus	ST	36	0.94	19	2	0.26	
Stomiidae	*Chauliodus danae*	S	113	2.95	6	30	3.83	8

seamount to 47. Above the plateau, just 10 mesopelagic fish species were recorded, represented by only 29 individuals. Shannon's diversity showed the same trend, declining from an average value of 2.43 in the oceanic samples, to 2.32 for slope samples, and 2.02 above the plateau.

A classification of night samples taken at the Atlantis Seamount showed a separation into two clusters at an arbitrary level of 40 % similarity (clusters I and II) (Figure 4). A third cluster is discernible at a level of 20 % similarity (cluster III). Haul A58 clustered at a very low similarity level due to the low species number. The first cluster (I) included all oceanic samples taken in six depth horizons, and one slope sample (A76). The second cluster (II)

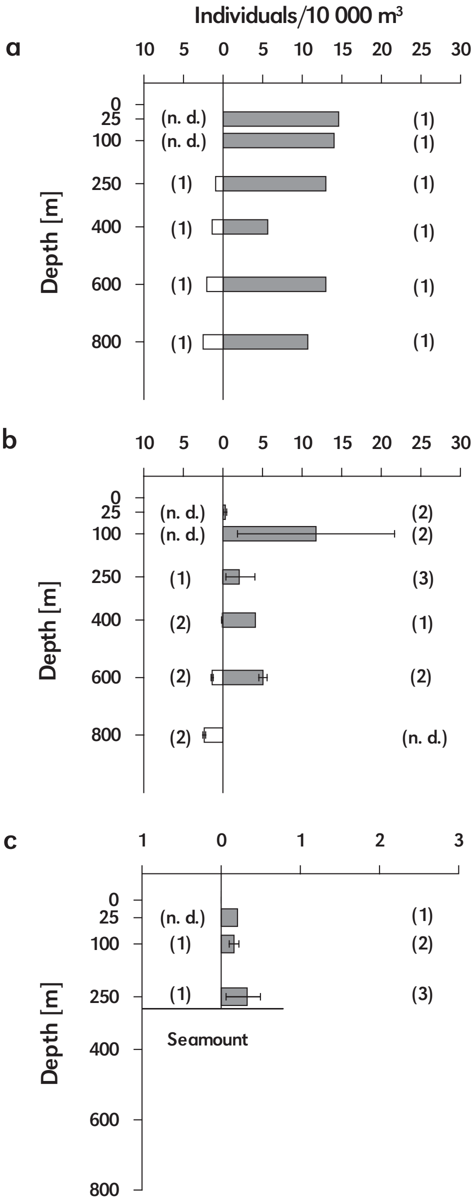

Figure 3: Vertical day/night distribution of mesopelagic fish at the Atlantis Seamount shown as average densities (individuals/10 000 m^3) at various sampling depths: a) oceanic station, b) slope station, c) plateau station – note that different scales have been used for samples taken above the plateau; open bars = day samples; shaded bars = night samples; number of samples in parentheses; n. d. = no data; error bars indicate minimum and maximum values.

was exclusively composed of slope samples taken in five various depth horizons. The third cluster (III) was composed of slope and plateau samples taken in the upper three depth horizons. Ordination of the same data showed no clearly defined clustering of samples, but rather a continuous multivariate pattern (Figure 5). While oceanic samples were strongly agglomerated, indicating a high concordance in species composition, slope samples were more scattered. Nevertheless, the slope samples were clearly separated from the oceanic samples with the exception of sample A76, which was spatially closely associated with the samples of the oceanic reference station. The four samples taken above the plateau were widely scattered over the MDS plot, indicating a low similarity in species composition among themselves.

ANOSIM, based on the R-statistic, was performed in order to test the a priori hypothesis of no differences in species composition among the three station types. The global test showed that stations differed significantly (global $R = 0.55$; $P < 0.001$). The pairwise tests showed significant differences for all three comparisons, whereby the differences were greatest between the oceanic and plateau samples ($R = 0.821$; $P < 0.005$). The samples of oceanic and slope stations showed a smaller R-value but were still significantly different ($R = 0.29$, $P < 0.025$).

To investigate whether the extent of vertical migration is related to the effects of decreasing water depth we concentrated on the di-

Table 3: Univariate indices of pooled densities of day and night samples at three stations (oceanic, slope, plateau) for the Atlantis Seamount and the Great Meteor Seamount.

	Oceanic		Slope		Plateau	
	Day	Night	Day	Night	Day	Night
Atlantis Seamount						
Number of individuals	316	1865	321	1244	-	29
Number of species	34	70	42	47	-	10
Density (N/10 000m^3)	1.72	11.71	1.05	4.41	-	0.16
Shannon's diversity (*H*')	2.97	2.43	3.06	2.32	-	2.02
Pielou's evenness (*J*')	0.84	0.57	0.82	0.60	-	0.88
Great Meteor Seamount						
Number of individuals	14	563	5	138	9	54
Number of species	5	48	3	19	2	10
Density (N/10 000 m^3)	0.15	5.06	0.11	2.31	0.11	0.7
Shannon's diversity (*H*')	1.24	3.06	1.05	2.23	0.34	1.55
Pielou's evenness (*J*')	0.91	0.84	0.96	0.86	0.99	0.81

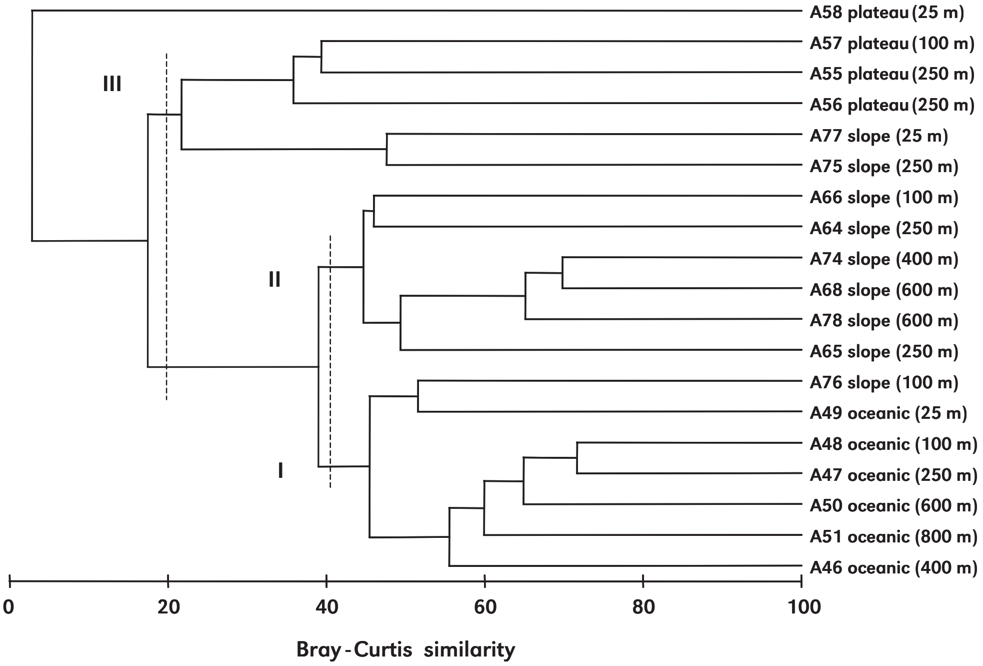

Figure 4: Dendrogram for hierarchical cluster analysis of 19 night samples according to the mesopelagic fish assemblage at the Atlantis Seamount; sample number, station, and sampling depth are indicated to designate different samples.

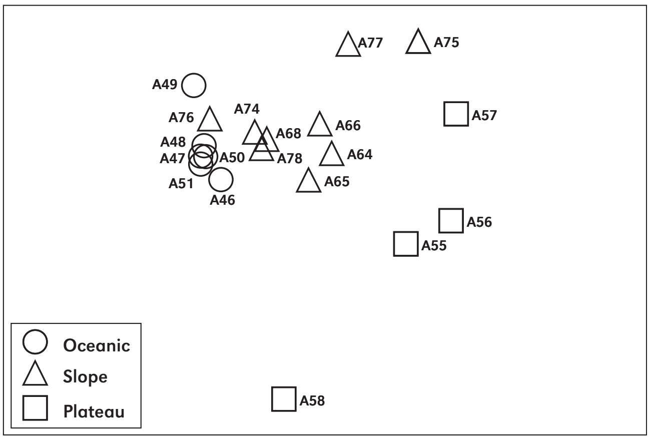

Figure 5: MDS ordination of 19 night samples according to the mesopelagic fish assemblage at the Atlantis Seamount; stress = 0.09.

urnal vertical distribution of two mesopelagic species, *Ceratoscopelus warmingii* and *Argyropelecus aculeatus*, which are characterised by different migration patterns (Figure 6). The myctophid *C. warmingii* showed high densities in night tows at the oceanic station and was completely absent in depth horizons 250 to 800 m sampled during the daytime, indicating strong vertical migrating behaviour. During the night, *C. warmingii* showed a heavy decline in density above the slope compared to the oceanic reference station and a complete absence above the plateau of Atlantis Seamount. The overall difference in median densities between stations was significant (Kruskal-Wallis Test, $P < 0.05$), however, only the pairwise comparison between the oceanic and plateau stations (Dunn's Test, $P < 0.05$) showed significant differences in density.

The sternoptychid *A. aculeatus* was identified as a weak migrator, showing only a small change in diurnal vertical distribution. At night, the density of *A. aculeatu*s was little affected above the slope of Atlantis Seamount compared to the oceanic reference station. *A. aculeatus* was also present, albeit in low densities, above the plateau. In agreement with these findings, there was no statistically significant difference in fish density among stations (Kruskal-Wallis Test, $P > 0.05$).

A similarity analysis (SIMPER) was performed to identify those species that are most characteristic of the different stations (Table 4). Samples taken over the slope and at the oceanic reference station had large numbers of characteristic species in common and differed mainly in the relative ranking of species. The three most representative species in slope samples were found among the top four species representative of oceanic samples. *Ceratoscopelus warmingii* was by far the most important species at oceanic and slope stations, contributing 26.7 and 27.4 %, respectively, to the overall similarity of stations. Above the plateau only three myctophids and one hatchet fish occurred in low densities.

Great Meteor Seamount

The mesopelagic fish assemblage at the Great Meteor Seamount was dominated by species of the family Myctophidae (Table 2). Thirteen of the 20 ranking mesopelagic fish

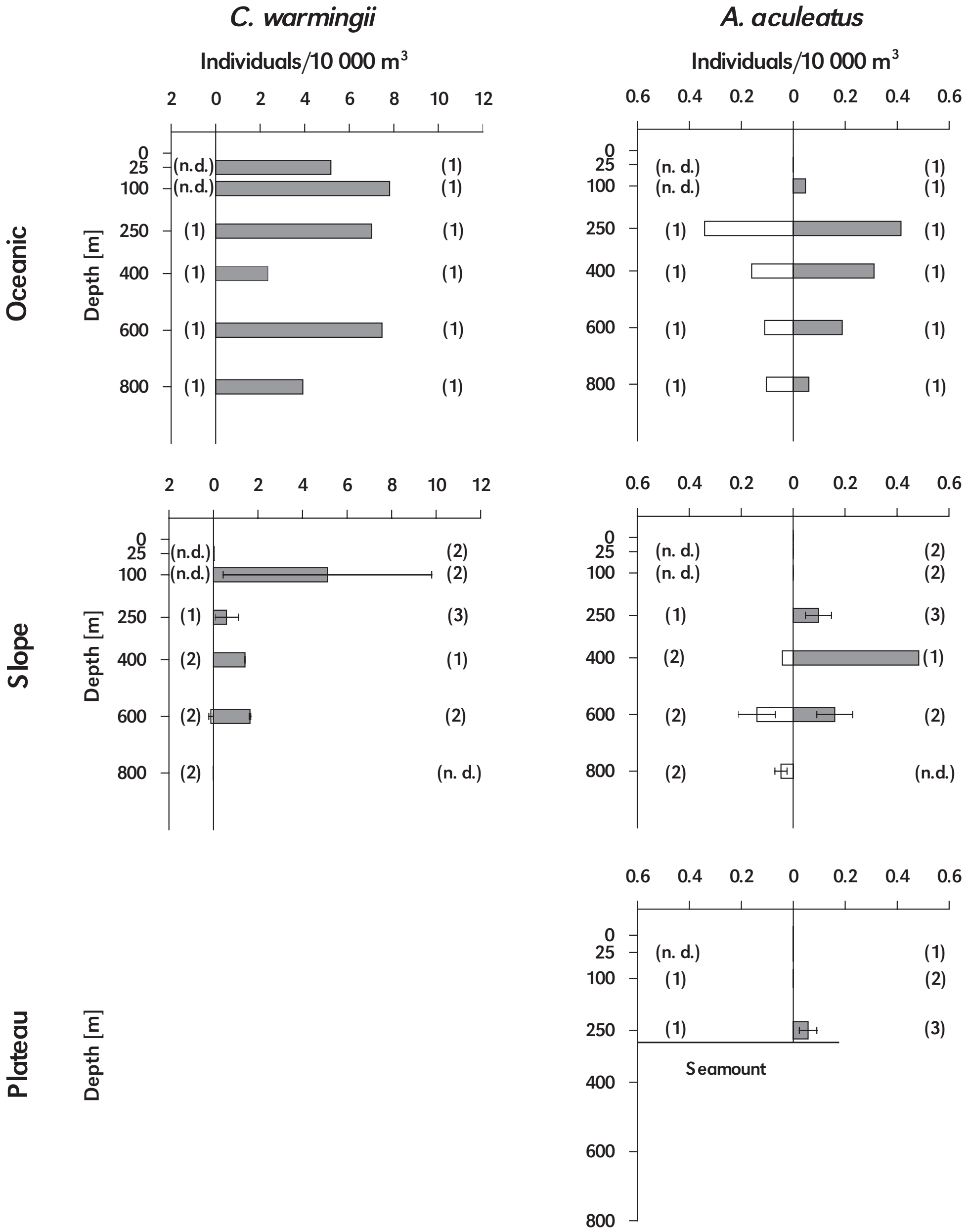

Figure 6: Vertical day/night distribution of *Ceratoscopelus warmingii* and *Argyropelecus aculeatus* at the Atlantis Seamount shown as average densities (individuals/10 000 m^3); open bars = day samples; shaded bars = night samples; number of samples in parenthesis; n. d. = no data; error bars indicate minimum and maximum values.

Table 4: Results of similarity percentage (SIMPER) analysis according to mesopelagic fish densities in night samples at the Atlantis Seamount and the Great Meteor Seamount; consolidating species of stations are ordered by decreasing contribution (Contrib. %) to the overall similarity and listed up to 90 % cumulative contribution; average density (Avg. Dens.) expressed as individuals/10 000 m^3.

Atlantis Seamount			**Great Meteor Seamount**		
Taxon	Avg. Dens.	Contrib. [%]	Taxon	Avg. Dens.	Contrib. [%]
Oceanic					
Ceratoscopelus warmingii	5.62	26.68	*Ceratoscopelus warmingii*	1.34	8.36
Notoscopelus resplendens	0.94	7.65	*Hygophum hygomii*	1.22	7.8
Lampanyctus pusillus	0.59	5.78	*Lobianchia dofleini*	1.35	7.45
Lobianchia dofleini	0.43	4.77	*Lepidophanes gaussi*	0.81	5.6
Lampanyctus ater	0.2	4.25	*Bolinichthys indicus*	0.49	4.91
Hygophum reinhardtii	0.31	4.17	*Hygophum reinhardtii*	0.55	4.77
Lepidophanes gaussi	0.55	3.98	*Chauliodus danae*	0.5	4.66
Hygophum benoiti	0.14	3.83	*Lampanyctus festivus*	0.49	4.36
Chauliodus danae	0.2	3.78	*Vinciguerria nimbaria*	0.43	4.13
Hygophum hygomii	0.25	3.76	*Argyropelecus aculeatus*	0.33	4.11
Lampanyctus photonotus	0.15	2.78	*Lestidiops affinis*	0.28	3.8
Argyropelecus aculeatus	0.17	2.61	*Diaphus mollis*	0.28	3.8
Notolychnus valdiviae	0.08	2.59	*Lepidophanes guentheri*	0.24	3.47
Photostomias guernei	0.08	2.25	*Notolychnus valdiviae*	0.14	2.39
Bolinichthys indicus	0.07	2.11	*Lobianchia gemellari*	0.17	2.39
Benthosema suborbitale	0.11	1.82	*Sudis hyalina*	0.1	2.2
Ceratoscopelus maderensis	0.18	1.45	*Vinciguerria poweriae*	0.13	2.2
Symbolophorus veranyi	0.07	1.17	*Lampadena chavesi*	0.15	2.2
Valenciennellus tripunctulatus	0.07	1.16	*Lestidiops jayakari*	0.1	2.2
Vinciguerria poweriae	0.14	1.14	*Gonostoma elongatum*	0.1	2.2
Vinciguerria nimbaria	0.06	1.14	*Hygophum taaningi*	0.12	2.2
Melamphaes simus	0.09	0.99	*Magrethia obtusirostra*	0.08	1.95
Lampanyctus festivus	0.02	0.87	*Symbolophorus rufinus*	0.08	1.95
			Taaningichthys minimus	0.1	1.95
Slope					
Ceratoscopelus warmingii	1.86	27.42	*Hygophum hygomii*	0.63	19.27
Lobianchia dofleini	0.63	20.14	*Vinciguerria nimbaria*	0.49	17.24
Notoscopelus resplendens	0.67	11.72	*Notoscopelus resplendens*	0.48	14.93
Vinciguerria nimbaria	0.09	9.07	*Lestidiops affinis*	0.88	13.63
Hygophum hygomii	0.19	7.53	*Sudis hyalina*	0.53	11.6
Diogenichthys atlanticus	0.32	3.93	*Diaphus mollis*	0.15	8.62
Hygophum reinhardtii	0.04	3.38	*Diplospinus multistriatus*	0.29	8.62
Argyropelecus aculeatus	0.11	3.14			
Lampanyctus pusillus	0.22	3.07			
Lobianchia gemellari	0.05	1.66			
Plateau					
Hygophum hygomii	0.06	58.1	*Diplospinus multistriatus*	0.53	34.9
Diaphus mollis	0.05	17.37	*Lestidiops affinis*	0.51	31.21
Lobianchia dofleini	0.04	14.45	*Sudis hyalina*	0.12	18.29
Argyropelecus aculeatus	0.03	10.08	*Diplophos taenia*	0.05	15.61

species were members of this family. Similar to the results from the Atlantis Seamount *C. warmingii* was the most numerous species (11.0 % of all individuals), followed by *Hygophum hygomii* (10.1 %) and *Lobianchia dofleini* (10.0 %).

The investigation of the mesopelagic fish community at the Great Meteor Seamount showed comparable patterns to those observed at the Atlantis Seamount. The species diversity and density of mesopelagic fish showed strong differences between night and day samples (Table 3). No conclusions can be drawn about vertical migration behaviour of mesopelagic fish at the Great Meteor Seamount, as different sampling strategies were performed for the day and night.

In accordance with the results at the Atlantis Seamount, a decline in mesopelagic fish density was observed in the night samples above the slope and plateau of the Great Meteor Seamount in comparison to the oceanic reference station (Table 3). At the deep oceanic station an average density of 5.06 (individuals/10 000 m^3) was recorded, decreasing to 2.31 above the slope and to 0.7 at the plateau station. Due to the small sample size, a test for statistical differences was not applied.

Similar to the fish density, species number and diversity were heavily affected by the shallow topography of this seamount, as seen in the night samples (Table 3). Values of Shannon's diversity index (H') declined from 3.06 in the oceanic samples, to 2.23 and 1.55 in the slope and plateau samples, respectively.

The classification of samples based on the Bray-Curtis similarity matrix of densities at the Great Meteor Seamount were in good agreement with the results obtained from the Atlantis Seamount (Figure 7). Three clusters (I to III) were discernible at an arbitrary Bray-Curtis similarity of 40 %. The first Cluster (I) comprised oceanic samples that fused on a high similarity level. Cluster II contained the two slope samples, and the third cluster (III) included the samples taken over the plateau of the Great Meteor Seamount. The results of the cluster analysis were further validated by the ordination of samples by MDS, which showed high separation between stations (Figure 8).

Again ANOSIM was performed to test the null hypothesis of no differences among stations. Although the global test and the pairwise comparison of stations indicated strong separation of stations (R = 1), the test results were not significant ($P > 0.05$) due to the small sample size.

Analysis of similarity percentage (SIMPER) performed on night samples identified *Ceratoscopelus warmingii* as the most representative species of the oceanic station (Table 4). However, the dominance of this myctophid was less conspicuous (average density 1.34 individuals/10 000 m^3) than at the Atlantis Seamount. At the slope station, *Ceratoscopelus warmingii* as the dominant species was replaced by *Hygophum hygomii*, which contributed 19.3 % to the overall similarity. It was evident that the fish family Paralepididae contributed the most to the species composition over the plateau station. At the latter station, the three most important species were paralepidids, and these accounted for nearly 85 % of overall similarity.

Discussion

The collection of mesopelagic fish species with non-closing pelagic trawls has advantages and disadvantages. Pelagic trawls with a relatively large mouth opening have a higher catch efficiency and can be towed with a higher speed (3 to 3.5 knots in our study) than scientific nets equipped with opening–closing devices such as Rectangular Midwater Trawl (RMT) and Isaacs-Kidds Midwater Trawl (IKMT), which usually have mouth openings of less than 10 m^2. Micronectonic species, which, like larger mesopelagic fish, small squids and larger decapods are strong swimmers, are not sampled adequately by "scientific nets" (Watanabe *et al.* 1999).

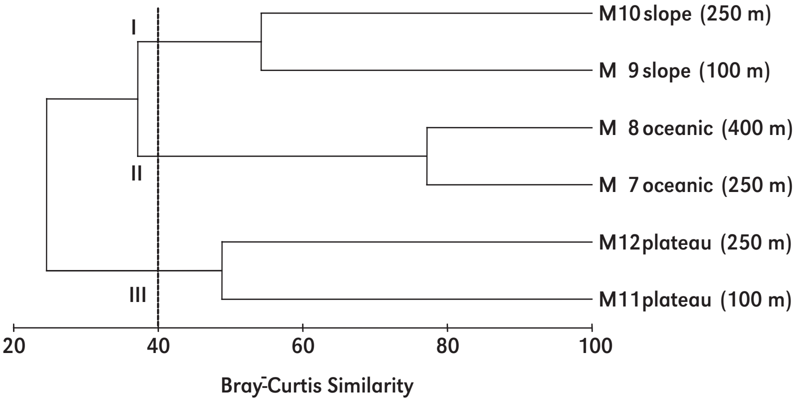

Figure 7: Dendrogram for hierarchical cluster analysis of 6 night samples according to the mesopelagic fish assemblage at the Great Meteor Seamount. Sample number, station, and sampling depth are indicated to designate different samples.

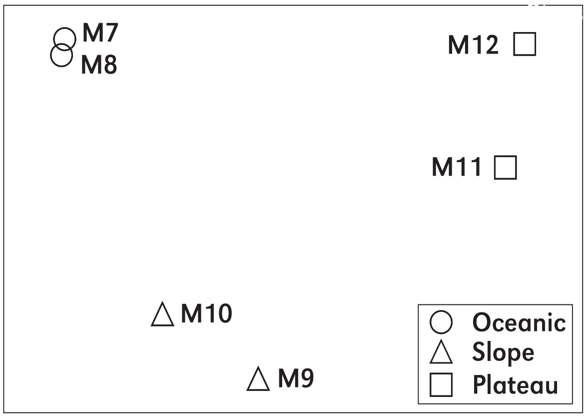

Figure 8: MDS ordination of 6 night samples according to the mesopelagic fish assemblage at the Great Meteor Seamount; stress = 0.00.

The YFT used in this study had a mesh size of 11 mm in the codend. The disadvantage of this net configuration is that individuals of less than 30 mm standard length are lost or escape and are therefore under-represented in the catch (Gartner *et al.* 1989). The use of non-closing sampling devices is problematical due to contamination of the catch by individuals sampled during casting and retrieval. The vertical net opening in our study was monitored by a probe that showed that the net collapsed during casting and retrieval. Therefore, we expect the degree of contamination by species resident in non-target depths to be negligible. Watanabe *et al.* (1999) have shown that the contamination of deeper tows can be reduced to less than 2 %, by using appropriate sampling procedures.

The species compositions of the mesopelagic fish assemblages at the Atlantis and Great Meteor Seamounts showed a high degree of similarity. Among the 20 most abundant mesopelagic fish species, the two seamounts had thirteen species in common. In general, a typical subtropical oceanic assemblage, dominated by the family Myctophidae, was present at both seamounts. The species composition was in good agreement with previous studies of mesopelagic fishes in the subtropical NE Atlantic (Backus *et al.* 1970; Kotthaus 1972; Krefft 1974). While the taxonomy and zoogeographic distribution of mesopelagic fish species in the NE Atlantic are well documented, relatively little is known about the influence of submerged features on the migratory mesopelagic fish assemblage.

Although multivariate statistical analysis indicated considerable changes in species composition in samples taken from different bathymetric depth zones at the Atlantis and Great Meteor Seamounts, analysis of similarity percentage (SIMPER) did not reveal a specific seamount-associated mesopelagic fish assemblage. These findings are in contrast to results of Parin and Prut'ko (1985) who described concentrations of pseudoceanic fish species close to Equator Seamount in the tropical Indian Ocean and of Boehlert and Genin (1987) who observed a similar phenomena at the mid-Pacific Southeast Hancock Seamount. One reason for the concentration of pseudoceanic species at shallow topographic features might be an increased food supply due to nutrient upwelling and a resulting enhanced primary production (Merrett 1986). During the study of Great Meteor Seamount in 1998, Mohn and Beckmann (2002) observed a doming of isotherms, and Kaufmann (pers. comm.) noticed a slight increase of primary production. Nevertheless, as generation times for most zooplankton are on a time scale of weeks/months, conditions of enhanced primary production have to persist for comparable time periods to have a significant effect on the zooplankton stock (Rogers 1994). A numerical model of the Great Meteor Seamount indicated a relatively high sensitivity of the flow system to storm events (Beckmann and Mohn 2002). Net samples taken in various locations at the Great Meteor Seamount showed no increased zooplankton density over the seamount compared to deep-water stations (Martin 2002). Accordingly, it is unlikely that mesopelagic fish would encounter a richer food supply in the vicinity of the Great Meteor Seamount as compared to the surrounding oceanic waters. This may explain the observed lack of pseudoceanic fish species at Great Meteor Seamount.

Instead of a specific seamount-associated fish community, we found a thinned-out oceanic community in night samples taken over the slopes of the Atlantis and Great Meteor Seamounts. Density, species number and diversity were markedly reduced above the steep flanks compared to the oceanic reference station. The abundance and species diversity were further reduced over the plateau. The observed patterns of mesopelagic fish distribution are in good agreement with the results of several studies on interaction between zooplankton and shallow topographic features. Nellen (1973) reported a lower abundance of vertically migrating mesopelagic fish larvae above the Great Meteor Seamount compared to the surrounding oceanic deep water. Weigmann (1974), over the Great Meteor Seamount, and Genin *et al.* (1988), over Nidever Bank in the North Pacific, both noted an almost complete lack of vertically migrating euphausiids. Our own data support what is well documented in the literature (Kinzer 1969; Kinzer and Schulz 1985): that the majority of subtropical mesopelagic fish species perform marked vertical migrations. During the day, the bulk of midwater fish reside at depths below 500 m, *i. e.*, beneath the summit depths of the seamounts investigated in this study. Therefore, the most plausible means for these mesopelagic fish to be transported above the slope and the shallow plateau are lateral advection and active horizontal migration during their nightly ascent. Active horizontal migration was documented in the mesopelagic fish community associated with the Hawaiian Islands (Benoit-Bird *et al.* 2001). The authors hypothesised that the migration enhances the available food supply by bringing the fish community closer to land-based nutrient inputs and productive shallower waters. At the Great Meteor and Atlantis Seamounts, the occurrence of active horizontal migration by mesopelagic fish in the direction of a trophic gradient is quite unlikely, as enhanced primary production and zooplankton biomass were not detected over the seamount summits. Therefore, lateral advection seems to be the best possible explanation for the presence of mesopelagic fish over the seamount plateaus. Mesopelagic fish that nocturnally ascend to epipelagic layers upstream of the seamount could be advected passively over the slope, as the general flow pattern indicated by the circulation model is a south-westwardly directed current. Therefore, the probability of sampling a water mass containing vertical migrators at slope locations is high.

The reasons for the strong decline of midwater fish density above the slopes and the plateaus of the seamounts could be manifold. The following three hypotheses for the observed gap formation of vertical migrating zooplankton and micronekton above shallow topographic features are frequently presented in the literature (Rogers 1994; Dower and Mackas 1996), and are discussed below with respect to the mesopelagic fish distribution at the Atlantis and Great Meteor Seamounts:

- Midwater fish laterally advected into the plateau areas of the seamounts are unable to complete their vertical migration cycle as water depth shallows, and will impinge on the bottom during their descent at dawn.
- Mesopelagic species that are passively advected above the plateau may be quickly eliminated by predators residing on the seamount.
- The rare occurrence of mesopelagic fish above the seamount may result from a behavioural response to the circulation patterns prevailing above the slope and the summit.

The first hypothesis is supported by our findings that the midwater fish assemblage at the oceanic reference stations of both seamounts were dominated by strong vertical migrators like *Ceratoscopelus warmingii*, but that this species shows a greatly reduced density at the seamount slope stations and an almost complete absence above the plateau area. Species with a less pronounced vertical migration, such as *Argyropelecus aculeatus*, seemed to be less affected by the shallower depth. This result is in good agreement with findings of Hopkins *et al.* (1981), who observed a strong decrease of mesopelagic fish species on a transect above the continental slope of West Florida. They found a significant relationship between the most landward occurrence of mesopelagic fish species and their vertical distribution range in the adjacent oceanic waters. The strongest decline of species number was observed between 275 and 400 m depth, the range that contains the summit depths of the Atlantis and Great Meteor seamounts. The same mechanism is also effective for vertically migrating zooplankton as shown by Genin *et al.* (1988). These authors observed that species with strong vertical migrations are less abundant above the Nidever Bank compared to an oceanic station, while the density of weak migrators was only marginally affected by the shallow bottom topography.

Evidence for the second mechanism comes from stomach content analyses of *Zenopsis conchifer* and *Antigonia capros* by Fock *et al.* (2002a). Both species are benthopelagic piscivores and were sampled in bottom trawls over the plateau of Great Meteor Seamount in 1998. It was shown that both predators feed on mesopelagic fish species, mainly myctophids, that are abundant in samples taken above the slope and in oceanic waters. Fock *et al.* (2002b) found specific resident benthopelagic species on the plateau of Great Meteor Seamount to be concentrated at the margins of the seamount summit, which they considered to be an effect of enhanced food supply represented by mesopelagic fish and crustaceans advected above the plateau. Such interactions between predators resident on isolated topographic features and organisms of the sound-scattering layer are well documented from the literature (Genin *et al.* 1988; Genin *et al.* 1994; Haury *et al.* 1995) and are part of the "sound-scattering layer interception hypothesis" as postulated by Isaacs and Schwartzlose (1965). Therefore, a great possibility exists that mesopelagic fish individuals swept above the seamount slope undergo a higher mortality than those in the surrounding deep water, either by impinging on the bottom (which would be accompanied by a high degree of disorientation), or due to their predation by piscivorous fish.

The third mechanism proposed for the lack of mesopelagic fish above seamounts is a kind of behavioural response to the prevailing flow regime, as suggested by Dower and Mackas (1996) for a zooplankton community at Cobb Seamount (Pacific Ocean). A study by Mackas *et al.* (1993) showed that copepod species seek specific flow regimes within the water column of the subarctic Pacific Ocean. Numerical models of the Great Meteor Seamount (Mohn and Beckmann 2002) and the Atlantis Seamount (this study) indicate that current fluctuations are increased above the edges of both seamounts. The summits and flanks of both features are dominated by relatively high-velocity anticyclonic flow systems (6 $\mathrm{cm \cdot s^{-1}}$ at Great Meteor Seamount and up to 15 $\mathrm{cm \cdot s^{-1}}$ at Atlantis Seamount). Although not much is known about the locomotive abilities of midwater fish, extensive horizontal migration is documented and a migratory speed of up to 25 $\mathrm{cm \cdot s^{-1}}$ is suggested (Benoit-Bird *et al.* 2001). Therefore, it is possible that midwater fish are able to avoid or escape these zones of anticyclonic circulation, assuming the existence of a navigatory orientation behaviour as proposed by Parin (1986) for the pseudoceanic species *Diaphus suborbitalis.*

We hypothesise that strong vertical migrators like *Ceratoscopelus warmingii* are more effective than weak migrators like *A. aculeatus* in avoiding, or seeking, specific water masses. This hypothesis is consistent with the occurrence of the latter species above the summit of the Atlantis Seamount. The questions of whether, and to what extent, micronekton responds to the flow patterns remain unsolved at this point, and will require future studies.

Conclusions

We can conclude that the Atlantis Seamount and the Great Meteor Seamount both impose strong effects on the composition of the mesopelagic fish community. Instead of a specific seamount-associated mesopelagic fish assemblage, we found a thinned-out oceanic community above the slopes of both seamounts. The large plateau areas seem to represent hostile habitats for the mesopelagic fish community. We propose that a combination of the following mechanisms are responsible for the observed distribution patterns: a) physical truncation of the vertical migratory range due to the shallow topography, b) enhanced predation effects, and c) active avoidance (*e. g.* horizontal migration) by strong migrators. The results of our study give support to the hypothesis that demersal stocks residing on seamounts may be supported by a flow-through energy supply (such as the mesopelagic fish advected over the seamount) instead of an autochthonous energy source generated by locally-enhanced primary production.

References

Backus, R. H.; Craddock J. E.; Haedrich R. L.; Shores D. L., 1970: The distribution of mesopelagic fishes in the equatorial and western north Atlantic Ocean. J. Mar. Res. 28: 179–201.

Badcock J., 1984a: Photichthyidae. In: Whitehead P. J. P.; Bauchot M. L.; Hureau J. C.; Nielsen J.; Tortonese E. (eds.): Fishes of the North-eastern Atlantic and the Mediterranean. Vol. I. Paris: UNESCO, p. 318–324.

Badcock J., 1984b: Sternoptychidae. In: Whitehead P. J. P.; Bauchot M. L.; Hureau J. C.; Nielsen J.; Tortonese E. (eds.): Fishes of the North-eastern Atlantic and the Mediterranean. Vol. I. Paris: UNESCO, p. 302–317.

Beckmann, A.; Mohn, C., 2002: The upper circulation at Great Meteor Seamount. Part II: Retention potential of the seamount induced circulation. Ocean Dynamics 52: 194–204.

Bednarz, U., 1991: Petrologie des Atlantis-Seamount-Komplexes. In: Wefer G.; Weigel W.; Pfannkuche O. (eds.): Eastern Atlantic '90 Expedition, (RV Meteor) Cruise No. 12, 13th March to 30th June 1990: Meteor-Ber. 91-1, p. 115–123.

Benoit-Bird, K. J.; Au, W. W. L.; Brainard, R. E.; Lammers, M. O., 2001: Diel horizontal migration of the Hawaiian mesopelagic boundary community observed acoustically. Mar. Ecol. Prog. Ser. 217: 1–14.

Boehlert, G. W.; Genin, A., 1987: A review of the effects of seamounts on biological processes. In: Keating, B. H.; Fryer, P.; Batiza, R.; Boehlert, G. W. (eds.): Seamounts, Islands and Atolls. Washington, D.C.: American Geophysical Union, p. 319–334.

Boehlert, G. W.; Wilson, C. D.; Mizuno, K., 1994: Populations of the sternoptychid fish *Maurolicus muelleri* on seamounts in the Central North Pacific. Pac. Sci. 48: 57–69.

Clarke, K. R.; Warwick, R. M., 1994: Change in marine communities: an approach to statistical analysis and interpretation. Natural Environmental Research Council, Plymouth

Clarke, K. R.; Warwick, R. M., 2001: Primer-E (5) computer program. Natural Environmental Research Council, Plymouth

Dower, J. F.; Mackas, D. L., 1996: "Seamount effects" in the zooplankton community near Cobb Seamount. Deep-Sea Res. I 43: 837–858.

Ehrich, E., 1977: Die Fischfauna der Großen Meteorbank. Meteor Forschungsergeb. (D Biol.) 25: 1–23.

Field, J. G.; Clarke, K. R.; Warwick, R. M., 1982: A practical strategy for analysing multispecies distribution patterns. Mar. Ecol. Prog. Ser. 8: 37–52.

Fock, H.; Matthiessen, B.; Zidowitz, H.; Westernhagen, H. von, 2002a: Diel and habitat-dependent resource utilisation by deep sea fishes at the Great Meteor seamount: niche overlap and support for the sound scattering layer interception hypothesis. Mar. Ecol. Prog. Ser. 244: 219–233.

Fock, H.; Uiblein, F.; Köster, F.; Westernhagen, H. von, 2002b: Biodiversity and species-environment relationships of the demersal fish assemblage at Great Meteor Seamount (subtropical NE Atlantic) sampled by different trawls. Mar. Biol. 141: 185–200.

Gartner, J. V., Jr.; Conley, W. J.; Hopkins, T. L., 1989: Escapement by fishes from midwater trawls: A case study using lanternfishes (Pisces: Myctophidae). Fish. Bull. 87: 213–222.

Gartner, J. V., Jr.; Hopkins, T. L.; Baird, R. C.; Milliken, D. M., 1987: The lanternfishes (Pisces: Myctophidae) of the eastern Gulf of Mexico. Fish. Bull. 85: 81–98.

Genin, A.; Greene, C.; Haury, L.; Wiebe, P.; Gal, G.; Kaartvedt, S.; Meir, E.; Fey, C.; Dawson, J., 1994: Zooplankton patch dynamics: Daily gap formation over abrupt topography. Deep-Sea Res. I 41: 941–951.

Genin, A.; Haury, L.; Greenblatt, P., 1988: Interactions of migrating zooplankton with shallow topography: Predation by rockfishes and intensification of patchiness. Deep-Sea Res. I 35: 151–175.

Haury, L.; Fey, C.; Gal, G.; Hobday, A.; Genin, A., 1995: Copepod carcasses in the ocean. 1. Over seamounts. Mar. Ecol. Prog. Ser. 123: 57–63.

Haury, L.; Fey, C.; Newland, C.; Genin, A., 2000: Zooplankton distribution around four eastern North Pacific seamounts. Prog. Oceanogr. 45: 69–105.

Hopkins, T. L.; Milliken, D. M.; Bell, L. M.; McMichael, E. J.; Heffernan, J. J.; Cano, R. V., 1981: The landward distribution of oceanic plankton and micronekton over the west Florida continental shelf as related to their vertical distribution. J. Plankton Res. 3: 645–658.

Hulley, P. A., 1981: Results of the research cruises of FRV "Walther Herwig" to South America LVIII. Family Myctophidae (Osteichthyes, Myctophiformes). Arch. FischWiss. 31: 1–300.

Hulley, P. A., 1984: Myctophidae. In: Whitehead P. J. P.; Bauchot M. L.; Hureau J. C.; Nielsen J.; Tortonese E. (eds.): Fishes of the North-eastern Atlantic and the Mediterranean. Vol. I. Paris: UNESCO, p. 429–483.

Isaacs, J. D.; Schwartzlose, R. A., 1965: Migrant sound scatterers: interaction with the seafloor. Science Wash. 150: 1810–1813.

Kinzer, J., 1969: On the quantitative distribution of zooplankton in deep scattering layers. Deep-Sea Res. I 16: 117–125.

Kinzer, J.; Schulz K., 1985: Vertical distribution and feeding patterns of midwater fish in the central Equatorial Atlantic. I. Myctophidae. Mar. Biol. 85: 313–322.

Kotthaus, A., 1972: Die meso- und bathypelagischen Fische der "Meteor"-Roßbreiten Expedition 1970 (2. und 3. Fahrtabschnitt). Meteor Forschungsergeb. (D Biol.) 11: 1–28.

Krefft, G., 1974: Investigations on midwater fish in the Atlantic Ocean. Ber. dt. wiss. Kommn. Meeresforsch. 23: 236–254.

Mackas, D. L.; Sefton, H.; Miller, C. B.; Raich, A., 1993: Vertical habitat partitioning by large calanoid copepods in the oceanic Subarctic Pacific during spring. Prog. Oceanogr. 32: 259–294.

Martin, B., 2002: Composition and distribution of zooplankton at Great Meteor Seamount, subtropical NE Atlantic. ICES Counc. Meet. Pap. M 27, 11 pp.

Merrett, N. R., 1986: Biogeography and the oceanic rim: A poorly known zone of ichthyofaunal interaction. UNESCO Techn. pap. mar. Sci. 49: 201–209.

Mohn, C.; Beckmann, A., 2002: The upper oceanic circulation at Great Meteor Seamount. Part I: Structure of density and flow Fields. Ocean Dynamics 52: 179–193.

Mozgovoy, V. A.; Bekker, V. E., 1991: Volume sound scattering and the composition of sound-scattering layers in the Canary Basin region. Oceanol. Acad. Sci. USSR. 31: 293–298.

Nellen, W., 1973: Untersuchungen zur Verteilung von Fischlarven und Plankton im Gebiet der Großen Meteorbank. Meteor Forschungsergeb. (D Biol.) 13: 47–69.

Parin, N. V., 1986: Distribution of mesobenthopelagic fishes in slope waters and around submarine rises. UNESCO Tech. Pap. Mar. Sci. 49: 226–229.

Parin, N. V.; Prut'ko, V. G., 1985: The Thalassial mesobenthopelagic icthyocene above Equator Seamount in the western tropical Indian Ocean. Oceanology 25: 781–783.

Pereyra, W. T., 1969: *Sebastodes flavidus*, a shelf rockfish feeding on mesopelagic fauna, with considerations of the ecological implications. J. Fish. Res. Bd. Can. 26: 2211–2215.

Reid, S. B.; Hirota, J.; Young, R. E.; Hallacher, L. E., 1991: Mesopelagic-boundary community in Hawaii: micronekton at the interface between neritic and oceanic ecosystems. Mar. Biol. 109: 427–440.

Roden, G. I., 1987: Effect of seamount and seamount chain on oceanic circulation and thermohaline structure. In: Keating B. H.; Fryer P.; Batiza R.; Boehlert G. W. (eds.): Seamounts, Islands and Atolls. Washington D. C.: American Geophysical Union, p. 335–354.

Rogers, A. D., 1994: The biology of seamounts. Adv. Mar. Biol. 30: 305–350.

Salvanes, A. G. V.; Kristoffersen, J. B., 2001: Mesopelagic Fishes. In: Steel J.; Thorpe S.; Turekian K. (eds.): Encyclopedia of Ocean Sciences. San Diego: Academic Press, p. 1711–1717.

Shannon, C. E.; Weaver, W., 1949: The Mathematical Theory of Communication. Chicago: University Illinois Press, p. 29–124.

Uiblein, F.; Geldmacher, A.; Koester, F.; Nellen, W.; Kraus, G., 1999: Species composition and depth distribution of fish species collected in the area of the Great Meteor Seamount, Eastern Central Atlantic, during cruise M42/3 with seventeen new records. Inf. Tec. Inst. Canar. Cienc. Mar. 5: 49–85.

Ulrich, J., 1971: Zur Topographie der Grossen Meteorbank. Meteor Forschungsergeb. (C Geol. Geophys.): 48–68.

Watanabe, H.; Moku, M.; Kawaguchi, K.; Ishimaru, K.; Ohno, A., 1999: Diel vertical migration of myctophid fishes (Family Myctophidae) in the transitional waters of the western North Pacific. Fish. Oceanogr. 8: 115–127.

Weigmann, R., 1974: Untersuchungen zum Vorkommen der Euphausiaceen (Crustacea) im Bereich der Großen Meteorbank. Meteor Forschungsergeb. (D Biol.) 17: 17–32.

Whitehead, P. J. P.; Bauchot, M. L.; Hureau, J.-C.; Nielsen J.; Tortonese, E., 1984: Fishes of the North-eastern Atlantic and the Mediterranean. Vol. I – III. Paris: UNESCO, 1473 pp.

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