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Biodiversity and species–environment relationships of the demersal fish assemblage at the Great Meteor Seamount (subtropical NE Atlantic), sampled by different trawls

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Abstract Quantitative data collected with different bottom trawls at the Great Meteor Seamount (subtropical NE Atlantic, 30°N; 28.5°W) in 1967, 1970 and 1998 are compared. Bootstrap estimates of total catch per unit effort increased from 6.96 and 10.8 ind. m⁻¹ h⁻¹ in 1967 and 1970, respectively, to 583.98 ind. m⁻¹ h⁻¹ in 1998. Gear effects and an effect of gear over time accounted for 47.1% and 20% of species variability. Further significant factors were time of day and habitat, while season was not significant. A total of 43 species was collected. Including supplementary species information, a grand total of 46 species was found associated with the Great Meteor Seamount. Diversity was higher in 1967 and 1970 (Shannon's diversity: $H' = 2.5$ and 1.6) than in 1998 ($H' = 0.9$). Species–environment relationships are discussed in terms of a sound-scattering layer–interception hypothesis, i.e. utilisation of prey from a diurnally moving sound-scattering layer for the benthopelagic community. This is probably augmented by concentration effects in a circular current around the seamount (Taylor-column). Long-term changes are discussed with respect to a decrease in biodiversity due to considerable increases in *Macroramphosus scolopax* and *Capros aper*. In 1998, the increase of abundance of *Trachurus picturatus* and the respective decreases for genuine benthic

species were likely to have been caused by a change of gear.

Introduction

The Great Meteor Seamount (GMR; 30°N; 28.5°W) is a large, isolated, flat-topped seamount in the central eastern Atlantic (Pratt 1963). It covers an area of 1,465 km², with a minimum depth of 275 m (Fig. 1A). All data on the GMR gathered prior to 1945 were lost (Pratt 1963). Since then, first ecological investigations on GMR were carried out in 1967 and continued in 1970 (e.g. Hesthagen 1970; Kotthaus 1972; Weikert 1972; Nellen 1973; Weigmann 1974). Demersal fishes were investigated quantitatively by Ehrlich (1977) and qualitatively by Maul (1976). Pelagic stocks were investigated by Kotthaus (1972). Recently, data on primary production and hydrography have further supplemented existing knowledge (Mourino et al. 2001). The status of fisheries at GMR is unknown; however, it has at least been subject to exploratory fishing (e.g. Shcherbachev et al. 1985).

GMR is assigned to the biogeochemical province of the Subtropical Eastern Gyre (Sathyendranath et al. 1995). In this oligotrophic province, primary production estimates are comparably low, ranging from 88 and 140 g C m⁻² year⁻¹ (after Yentsch 1990; Platt et al. 1995; Sathyendranath et al. 1995). The adjacent domain to the north, the North Atlantic Drift, has a higher annual production of approximately 170–240 g C m⁻² year⁻¹. For the North Atlantic Tropical Gyre to the south, production is slightly lower (approx. 80–120 g C m⁻² year⁻¹). The seasonal cycle is weak, and the water column is almost permanently stratified (Jickells et al. 1996). Chlorophyll distributions are characterised by a winter maximum and summer minima (Campbell and Aarup 1992; Mourino et al. 2001).

Despite impoverished nutritional conditions in the ambient oceanic regions, seamounts often maintain high

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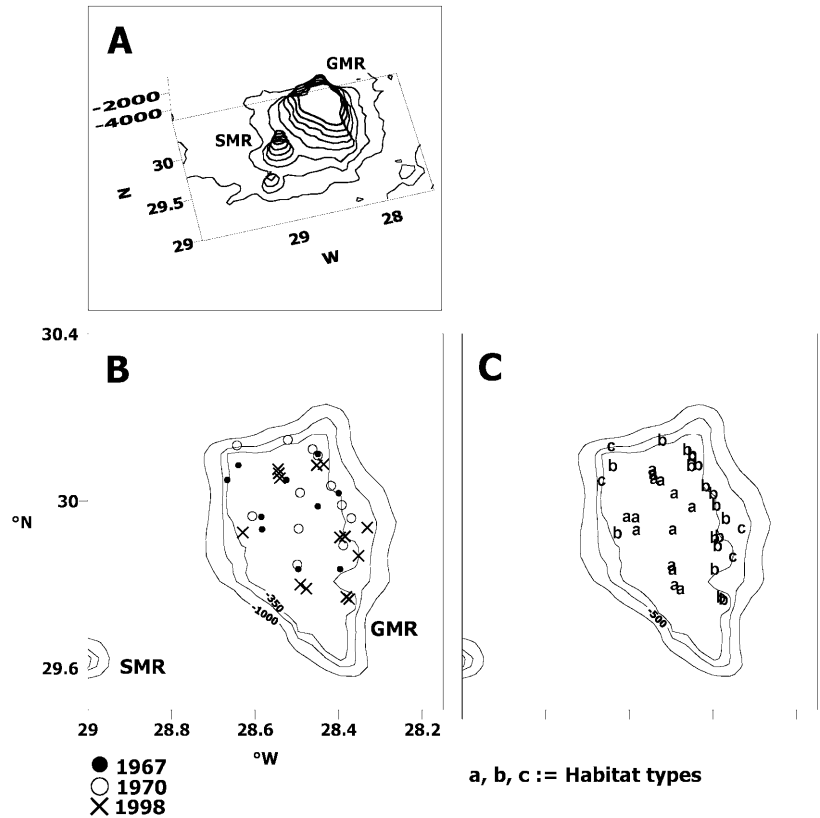
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Fig. 1A–C. Topography, trawling positions and habitats. **A** Extended topography from bird's eye view, depth axis inflated. **B** Detailed view of trawling positions in 1967, 1970 and 1998. **C** Distribution of sampled habitats according to classifications (see "Materials and methods"). In **B** and **C** depth contours at 350, 500 and 1,000 m (*GMR* Great Meteor Seamount; *SMR* Small Meteor Seamount; *a* plateau; *b* inner margin; *c* outer margin)



standing stocks of micronecton and demersal fishes (Boehlert and Genin 1987), in some areas even with economically important fisheries (Koslow et al. 1994; Rogers 1994). However, due to life history traits, with remote pelagic juvenile stages and probably complex recruitment mechanisms (e.g. Humphreys and Tagami 1986), seamount populations are often at the risk of overexploitation (Rogers 1994; Koslow et al. 2000). Recent theory on "seamount effects" suggests that interruption of ocean currents with subsequent formation of eddies and circular currents ("Taylor-column") as well as local upwelling are causative factors for increased local primary and secondary production. Planktonic larval retention and accumulation of production advected to the area are influenced by these currents. Further, seamounts interfere with zooplankton by disrupting the diurnal vertical migration (DVM; Hesthagen 1970; Genin et al. 1994; Haury et al. 2000). Evidence for seamount effects on zooplankton (Dower and Mackas 1996), primary production (Comeau et al. 1995) and larval retention (Mullineaux and Mills 1997) has previously been provided.

Community structure of the deep-sea fish fauna in the North Atlantic was originally mapped by Haedrich and Merrett (1988) and has been controversially debated by Haedrich and Merrett (1990) and Koslow (1993). In 1998, a German follow-up survey to GMR was conducted. The repeatedly conducted surveys at GMR in 1967, 1970 and 1998 provide a database for the first analyses of long-term changes of community structure

and biodiversity for mid-Atlantic seamount fish assemblages. Questions of community persistence and reliance on "seamount effects" are also addressed in the present paper.

In our analysis of species–environment relationships we want to: (1) identify major abiotic factors affecting community structure and (2) analyse biodiversity and community structure and their long-term changes.

Materials and methods

Fisheries

Sampling

Samples were obtained during two cruises of the former R.V. "Meteor" in May/July 1967 and February 1970 and one of the new R.V. "Meteor" in September 1998 (Fig. 1B). Gear type and sampling duration varied considerably between the cruises (Table 1). The nets applied were the Agassiz-trawl, a 6 m wide and 1 m high framed net (Thiel 1970), a commercial 90-ft otter-trawl (vertical opening about 1.7 m, Thiel 1970; FAO Fisheries Dept. 1978, p. 45) and an Engel bottom-trawl of approximately 170-ft size (3.5 m vertical opening, H. Engel, personal communication). Horizontal openings at a sampling speed of 3 knots were estimated as 6, 15 and 32 m, respectively. Codend mesh sizes were 15, 30 and ca. 15 mm, respectively. Sampling duration was usually < 1 h, except for one haul in 1967 which lasted 2 h. According to a time–depth sampling scheme in Haedrich and Merrett (1988), sampling durations can be assumed to be adequate. Descriptions of fauna and data were presented in Ehrich (1977) and Uiblein et al. (1999). Furthermore, catch data were provided for the 1998 cruise by one of the authors (F.K.).

Species acronyms are given in Table 5. Data have been archived in the seamounts online database (<http://seamounts.sdsc.edu/>).

Preparation of catch data

In a modified catch per unit effort (CPUE) approach all values were scaled to a 1 m net opening and 1 h sampling time [CPUE in $n(\text{individuals}) \text{ m}^{-1}(\text{horizontal net opening}) \text{ h}^{-1}(\text{trawling time})$]. This approach was chosen, since the 1967/1970 cruises swept areas; thus, abundance per square metre could not be assessed exactly due to the variability of towing speed. Log-transformed CPUE data were applied in the analysis of habitat, diurnal and seasonal variability. For the 1967/1970 cruises, only those samples were selected for further analysis, which: (1) had a total catch of more than ten individuals per haul and (2) were sampled correctly regarding sampling speed, net opening and other parameters indicated by Ehrich (1977).

For the long-term comparison of community structure and diversity, aggregate datasets were generated by means of bootstrap resampling. Pros and cons of bootstrapping, i.e. resampling from a given entity with replacement, have been widely discussed (e.g. Millar 1993; Smith 1997; Pelletier 1998; Stahel 1999). Generally, the robustness of estimates is increased by downweighting outliers when distributions are unknown. Bootstrap sample sizes varied between 200 and 300, depending on the size of the original sample.

Classification of abiotic data

Time of day (termed “daytime”), type of habitat, gear and season were classified for each station, viz. haul, by means of dummy coding (ter Braak and Smilauer 1998). For variance decomposition, daytime and season were further pooled into the category “time”, and gear and habitat into the category “environment”, respectively.

The “daytime” factor was employed to analyse possible relationships to DVM of potential prey organisms. For daytime, five subcategories were distinguished (see Table 1): “night”, “dawn”, “day”, “noon” and “dusk”. For each haul, the time of lowering the trawl was used for assignment, since in the older cruises the times when the breaks of the winches were arrested (i.e. time over ground) were not documented.

In order to account for effects associated with the plateau margin, i.e. marginal currents, upwelling as detected for the GMR by Meincke (1971) and Mourino et al. (2001), and interception with the sound-scattering layer, stations were arranged into three types of habitat (see Fig. 1C): “type a” for plateau with mean soundings ranging from 285 to 310 m, “type b” for the inner margin of the plateau with a mean catching depth from 302 to 365 m, and an outer margin “c” with soundings from 358 to 470 m. The marginal habitats, type b and c, are assumed to be directly affected by processes at the border of the plateau.

The factor “gear” was determined by the net types deployed (see Table 1).

Table 1. Dataset information [*AT* Agassiz-trawl; *KT* common 90-ft otter-trawl (“Kutter”-trawl); *BT* 170-ft Engel bottom-trawl]

	R.V. “Meteor”, built 1964, 72.8 m length		R.V. “Meteor”, built 1986, 97.5 m length, engine power 2×1,150 kW
	Cruise 1967	Cruise 1970	Cruise 1998
Season	Summer (May/Jul)	Winter (Feb)	Summer (Sep)
Sunrise–sunset (hours) ^a	0505–1855	0630–1746	0539–1758
Nautical twilight (hours) ^{a,b}	0405–1955	0538–1838	0447–1850
Time range (hours) for hauls ^c for:			
Dawn	0655–0730	0600	0523
Day	1420–1545	0922–1643	0809–1543
Noon	1158	1118–1135	1158–1251
Dusk	1720–1854		1704–1815
Night	0025–0215	2045–2145	2028–0157
Number of selected stations out of total number (<i>n/n</i>)	12/20	12/22	14/14
Number of stations during night-time (<i>n</i>)	4	2	4
Number of stations during day-time (<i>n</i>)	8	10	10
Gear type applied	9 AT, 3 KT	2 AT, 10 KT	14 BT
Catching depth range (m)	296–505	285–466	294–435
Speed over ground (knots)	2–3	2–3	2–3.5
Time at depth (min)	58–66	30–60	16–45
Corresponding reference stations in Ehrich (1977)	1, 55, 56, 60, 64, 71, 77, 79, 80, 82, 83, 84	3, 4, 11, 12, 14, 16, 17, 18, 19, 20, 21, 22	
Horizontal net opening (m)	AT = 6 KT = 15 ^d BT = 32		
Codend mesh size (stretched, mm)	AT = 15 KT = 30 BT = ca. 15 (knot–knot distance 10 mm)		
Ground rope	AT = fixed iron frame KT = not known BT = rubber discs 400 mm, with 160-mm spacers		

^aAccording to U.S. Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil/data/docs/RS_One-Year.html)

^bNautical twilight as defined by U.S. Naval Observatory begins in the morning and ends in the evening, when the centre of the sun is geometrically 12° below the horizon

^cStart of lowering trawl into water

^dNet opening assessed according to the 5/8-of-head-rope rule (see Haedrich and Merrett 1988, equivalent to 2/3-rule, see Rijnsdorp et al. 1996)

The factor “season” accounts for potential changes of production as suggested by Ehrich (1977) and Mourino et al. (2001) and weather conditions (Ehrich 1971). The latter are likely to affect catch efficiency. Two seasons were set: “summer” (1967 and 1998) and “winter” (1970).

Analysis of species–environment relationships

CANOCO (ter Braak and Smilauer 1998) provides opportunities to analyse nominal data (dummy-coded abiotic factors) together with numerical data (species) by means of direct unimodal or linear gradient analysis. Direct gradient analysis ordinated the species to canonical axes extracted from the abiotic factors instead of aligning both species and abiotic factors to ordination axes extracted from species variance (indirect gradient analysis, e.g. principal components analysis). In direct gradient analysis, unimodal methods [e.g. canonical detrended correspondence analysis (DCA)] can be applied in the presence of conspicuous gradients, with species following a Gaussian distribution along these gradients. In contrast, if distributions are not bell shaped, i.e. gradients are too short, linear methods [redundancy analysis (RDA)] are recommended.

DCA has frequently been used to analyse deep-sea fish assemblages (Gordon and Bergstad 1992; Gordon et al. 1996). A canonical DCA of the whole set of abiotic factors (unpartialled) and the top 20 species for between-cruise comparisons revealed short gradients with lengths of 2.3 and 1.1 standard deviations for the first two canonical environmental axes, whereas values > 4 were required for successful application of unimodal models (for details see ter Braak and Wiertz 1994; ter Braak and Smilauer 1998, p. 123). Thus, as a linear method RDA, was carried out with covariables, in order to analyse effects for each group of abiotic factors independently (partial RDA). For species, covariances were applied (no post-adjustment of scores, scaling mode “–2” in CANOCO), in order to preserve the individual contributions to overall variance. In biplots (two types of ordinated data in the same *x,y*-graph), the relationships between objects (species, samples, or abiotic factors) can be evaluated in three ways. Firstly, the length of an arrow from the origin (point 0,0) to the respective object indicates its contribution to overall variance for that particular set-up of variables and covariables. This is expressed as an example for scores *c_i* of abiotic factor *i* by means of species scores *b_j* of species *j* for a particular ordination axis:

$$c_i = \sum_j cov_{ij} b_j / \sum_j b_j^2$$

where *cov_{ij}* denotes the covariance between the abiotic factor and the respective species scores. Secondly, qualitative relationships are indicated by the angle between two objects (species, factors), since the arrows indicate the direction of increase. Thirdly, a ranking of relationships can be obtained by projection of one object on the other. This system of plotting is used, for example, in Fig. 2 for *Anthias anthias* (ANA) and *Macroramphosus scolopax* (MAC) projected on the factor “day”. The increase of ANA is less related to daytime (i.e. wider angle) than for MAC, although the factor “day” provides sufficient variance to explain ANA (i.e. “day” is longer than ANA), but not for MAC. MAC has a better rank on “day” than ANA (higher position of its projection on the extrapolated “day” arrow).

Significance of species–environment relationships was tested for the complete ordination by means of permutation tests, in order to avoid overinterpretation of the ordinations. For individual species–environment relationships, *t*-plots were evaluated (not shown). In CANOCO the vector in a *t*-plot is scaled to a *t*-value of 2. The corresponding table gives a *t*_{0.05(2), 24} = 2.065, so that with 24 degrees of freedom (number of samples – number of abiotic factors – 1) a two-tailed significance level of *P* < 0.05 can be attributed to those relationships for which the species point can be projected onto the environmental variable without extrapolation of the latter. The contribution of each environmental factor to overall variance was analysed by means of variance decomposition (Borcard et al. 1992).

In multi-factorial analysis of variance (ANOVA), groups of observations are considered and thus balanced designs are recommended (Zar 1996, p. 236). In contrast, linear regression techniques such as RDA and general linear methods (GLM) can cope with unbalanced designs, since each observation is considered individually as part of the data, viz. the calculation matrix (SAS 1994; SPSS 1999). Actually, it appears that the GMR design matrix is not balanced. For instance, the Engel bottom-trawl was only deployed in 1998, and no 90-ft otter-trawl was deployed in habitat c. Generally, habitat c and the morning time were underrepresented according to the number of hauls within these categories. This limits the capabilities of the statistical tests (permutation test, *t*-test) to indicate significant preferences in relation to these underrepresented categories. Notwithstanding the applicability of ordinations with reasonable design matrices, viz. coding for the analysis of spatio-temporal changes (ter Braak and Wiertz 1994), the unbalanced sampling-design matrix at GMR inhibits the proper analysis of long-term changes. The dummy coding for a likely change between 1967/1970 and 1998, which is to be anticipated, cannot be discerned from the dummy coding for the 170-ft Engel bottom-trawl in 1998.

Diversity analysis and community structure

Frequency as a measure of regularity of distribution was classified according to Ehrich (1977). Frequency was calculated as the number of samples in which the species occurred in relation to the total number of samples. This index is equivalent to what Merrett et al. (1991) termed “species fidelity”. Frequency was divided into three classes : 100–75% occurrence during a cruise, < 75–50% occurrence and < 50% occurrence. Species belonging to the latter class are regarded as accessory or accidental species. Further community indices and species distributions were

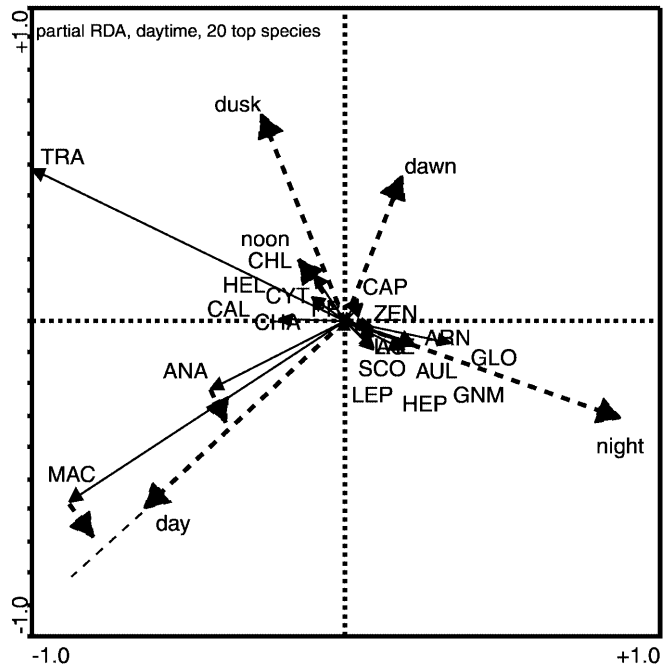


Fig. 2. Partial redundancy analysis (RDA) plot for factor “day-time” for the top 20 species. Contributed variance is indicated by the length of the arrows for a given object (species, abiotic factor). The relationship between two objects is indicated by the angle between their corresponding arrows and the relative importance, i.e. rank is given by the projection of one object on the other. *Antigonia capros* is hidden but related to “night”. Acronyms given in Table 5 (solid vectors species; broken vectors environmental factors)

calculated with BioDiversityPro software (ver. 11.99, McAleece et al., available at <http://www.nrmc.demon.co.uk/bdpro/index.htm>). Rarefaction analysis, cumulative abundance plots, and plots of species numbers and of estimated species numbers were chosen. Rarefaction is a method for the analysis of diversity of samples of different sizes. Abundance plots indicate the dominance of a species by means of its relative share to the overall number of specimens. Relative to the number of samples taken, species plots analyse the number of species caught as well as the estimated maximum number of species, i.e. the jack-knife estimate, which would have been obtained under more intensive sampling (for calculation see Fock 2000).

Results

Summary statistics

For 1967 and 1970 each, 12 hauls were analysed, compared to 14 in 1998. In 1967 and 1970 trawling was carried out with small-sized gear for an average time of 1 h, whereas in 1998 large-sized gear was applied for an average time of 30 min. Fishing success differed considerably between the years: whereas in 1967 and 1970 a total of 1,597 and 2,305 individuals were collected, respectively, the catch rose to 116,464 specimens in 1998 [numbers differ slightly from Uiblein et al. (1999) due to a revised database]. This increase is mirrored by a corresponding increase in CPUE values: in 1967 and 1970 only 6.96 and 10.8 ind. m⁻¹ h⁻¹ were caught, respectively, compared to 583.98 ind. m⁻¹ h⁻¹ in 1998 (bootstrap estimates). The total number of taxonomic units was nearly the same in the summer cruises of 1967 (36) and 1998 (33, since *Macroramphosus gracilis* is not counted separately, see Tables 2, 8), but was considerably rarer during the winter cruise in 1970 (26). The numerically dominant species were *Macroramphosus scolopax*, *Capros aper*, *Trachurus picturatus* and *Anthias anthias* (Table 2).

Species–environment relationships

The analysis considers four groups of abiotic factors and the 20 top species available for between-cruise comparison. Gear effects explained 43.4% of community variability after taking into account the covariables daytime, season and habitat (Table 3). Gear effects were highly significant ($P=0.005$). However, it must be noted that net effects are confounded by temporal changes between 1967/1970 and 1998, since these were not distinguishable from the coding for BT in 1998; BT was used exclusively in 1998. Daytime and habitat significantly contributed another 10.8% to total variability, whereas season only caused minute variability and proved to be an insignificant effect (0.2%, $P=0.96$). In total, 74.3% of community variability can be explained by the four groups of abiotic factors.

The decomposition reveals a considerable combined effect of time and environment in terms of shared variance, accounting for 20% of total variability (Table 4).

Shared variance could be due to a temporal structure within the selected environmental factors or due to a factor that has not been considered yet (Borcard et al. 1992). Because of the dominance of gear effects, the shared variance could be understood as an interaction between gear effects and time, i.e. daytime; however, this is not well understood. Hence, together with the amount of unexplained variance, 45.7% of total variability (20% + 25.7%) requires more detailed investigation.

With regard to daytime, the least important of the three significant factor groups, with 2.4% of explained variance, two groups of differently reacting species can be discerned (Fig. 2). Nine species were related to night, among which were *Arnoglossus rueppelli*, *Antigonia capros* and *Heptranchias perlo*; 11 species were related to daytime, among which *Trachurus picturatus*, *Macroramphosus scolopax* and *Anthias anthias* were major contributors to overall variance. Specifications such as “dawn”, “dusk” and “noon” did not explain much of the variance of the species and were not significantly linked to any of the species. Although numerically dominant, *Capros aper* delivered no respective share to overall variance. Significant relationships were mostly found in relation to the factor night, either positive or negative (Table 5). The species negatively related to night were all comparably large (mean fresh weight from 0.16 to 0.4 kg), whereas one of the smallest species found over the GMR, the Argentine *Glossanodon leioglossus*, was positively related to night.

Habitat, accounting for 7.2% of total species variability, showed the most diverse response of species. Species were affiliated with all three categories (Fig. 3), and 15 relationships were significant (Table 5). Four species were linked to the plateau habitat type a, *Heptranchias perlo*, *Macroramphosus scolopax*, *Phycis phycis* and *Chaunax pictus*. A total of 16 species were associated to marginal habitats, with 11 significant relationships, for which double negative countings of “not a” and “not b” were considered to indicate a preference for habitat type c. Further preference for marginal habitats is also evident for less abundant species (Table 6).

Although quantitatively dominant, ordination of gear effects produced a less diverse response pattern for species; 14 species were barely related to gear effects (Fig. 4). However, in terms of significance, seven species were significantly linked to the factor “BT”, indicating relevance also for rare species. The benthic *Arnoglossus rueppelli* was linked to the Agassiz-trawl; *Antigonia capros* was weakly linked to the application of the 90-ft otter-trawl.

Composition and diversity indices

Based on the analysis of species–environment relationships, datasets were agglomerated in such a way that the major effects gear and gear over time were retained. Thus, bootstrap estimates were calculated for each of the cruises, suspending effects of daytime and habitat. For

Table 2. Bootstrap CPUE (*b-CPUE*) estimates and ordered frequency (*freq*, i.e. percentage occurrence in all samples) values for the three cruises (1967, 1970, 1998). Species with *freq* > 75% are euconstant, species with *freq* = 50–75% are constant, Shannon diversity *H'* calculated to base *e* comparable to Koslow et al. (1994)

1967				1970				1998			
Species	<i>b-CPUE</i>	<i>freq</i>	Species	<i>b-CPUE</i>	<i>freq</i>	Species	<i>b-CPUE</i>	<i>freq</i>	Species	<i>b-CPUE</i>	<i>freq</i>
<i>Macroramphosus scolopax</i> ^a	1.913	100	<i>Macroramphosus scolopax</i> ^a	5.861	100	<i>Macroramphosus scolopax</i> ^a	369.742	100	<i>Macroramphosus scolopax</i> ^a	369.742	100
<i>Anthias anthias</i>	1.125	83	<i>Anthias anthias</i>	1.832	100	<i>Capros aper</i>	179.333	100	<i>Capros aper</i>	179.333	100
<i>Arnoglossus rueppelli</i>	0.549	67	<i>Antigonita capros</i>	1.071	83	<i>Zenopsis conchifer</i>	0.527	100	<i>Zenopsis conchifer</i>	0.527	100
<i>Capros aper</i>	0.430	67	<i>Capros aper</i>	0.721	83	<i>Aulopus filamentosus</i>	1.611	93	<i>Aulopus filamentosus</i>	1.611	93
<i>Aulopus filamentosus</i>	0.226	67	<i>Phycis phycis</i>	0.188	75	<i>Trachurus picturatus</i>	18.215	86	<i>Trachurus picturatus</i>	18.215	86
<i>Phycis phycis</i>	0.159	67	<i>Aulopus filamentosus</i>	0.130	75	<i>Antigonita capros</i>	0.557	86	<i>Antigonita capros</i>	0.557	86
<i>Antigonita capros</i>	0.871	58	<i>Arnoglossus rueppelli</i>	0.125	75	<i>Anthias anthias</i>	1.398	79	<i>Anthias anthias</i>	1.398	79
<i>Callanthias ruber</i>	0.155	58	<i>Synchiropus phaeon</i>	0.117	67	<i>Heptanchias perlo</i>	0.368	79	<i>Heptanchias perlo</i>	0.368	79
<i>Zenopsis conchifer</i>	0.200	33	<i>Laemonema yarrellii</i>	0.118	50	<i>Callanthias ruber</i>	1.442	71	<i>Callanthias ruber</i>	1.442	71
<i>Gnathophis mystax</i>	0.123	33	<i>Callanthias ruber</i>	0.112	50	<i>Lepidopus caudatus</i>	0.452	71	<i>Lepidopus caudatus</i>	0.452	71
CALY ^b	0.046	33	<i>Polymixia nobilis</i>	0.198	33	<i>Macroramphosus gracilis</i> ^a	3.905	57	<i>Macroramphosus gracilis</i> ^a	3.905	57
<i>Trachurus picturatus</i>	0.155	25	<i>Raja maderensis</i>	0.023	33	<i>Arnoglossus rueppelli</i>	0.270	57	<i>Arnoglossus rueppelli</i>	0.270	57
<i>Lepidopus caudatus</i>	0.074	25	<i>Scorpaena loppet</i>	0.060	25	<i>Gnathophis mystax</i>	0.271	43	<i>Gnathophis mystax</i>	0.271	43
<i>Synchiropus phaeon</i>	0.070	25	<i>Helicolenus d. dactylopterus</i>	0.039	25	<i>Phycis phycis</i>	0.069	43	<i>Phycis phycis</i>	0.069	43
<i>Chlorophthalmus agassizii</i>	0.061	25	<i>Glossanodon leioglossus</i>	0.027	25	<i>Synchiropus phaeon</i>	0.038	43	<i>Synchiropus phaeon</i>	0.038	43
<i>Helicolenus d. dactylopterus</i>	0.046	25	<i>Chamaux pictus</i>	0.021	25	<i>Scomber japonicus</i>	1.557	36	<i>Scomber japonicus</i>	1.557	36
MACR ^c	0.115	17	<i>Lepidopus caudatus</i>	0.021	25	<i>Helicolenus d. dactylopterus</i>	0.263	36	<i>Helicolenus d. dactylopterus</i>	0.263	36
<i>Scorpaena loppet</i>	0.109	17	<i>Zenopsis conchifer</i>	0.019	25	<i>Laemonema yarrellii</i>	0.108	36	<i>Laemonema yarrellii</i>	0.108	36
<i>Echiodon dentatus</i>	0.091	17	<i>Cyttopsis rosea</i>	0.047	17	<i>Chamaux pictus</i>	0.064	29	<i>Chamaux pictus</i>	0.064	29
<i>Protogrammus sousai</i>	0.048	17	<i>Gadella maraldi</i>	0.013	17	<i>Scorpaena loppet</i>	0.064	29	<i>Scorpaena loppet</i>	0.064	29
<i>Chlopsis bicolor</i>	0.046	17	<i>Trachurus picturatus</i>	0.018	8	<i>Glossanodon leioglossus</i>	0.992	21	<i>Glossanodon leioglossus</i>	0.992	21
<i>Gnathophis codoniphorus</i>	0.032	17	<i>Chlorophthalmus agassizii</i>	0.014	8	<i>Gadella maraldi</i>	0.046	21	<i>Gadella maraldi</i>	0.046	21
<i>Pontinus kuhlii</i> ^d	0.029	17	<i>Gnathophis mystax</i>	0.014	8	<i>Polymixia nobilis</i>	0.055	14	<i>Polymixia nobilis</i>	0.055	14
<i>Laemonema yarrellii</i>	0.025	17	<i>Hymenocephalus gracilis</i>	0.006	8	<i>Hymenocephalus gracilis</i>	0.035	14	<i>Hymenocephalus gracilis</i>	0.035	14
<i>Raja maderensis</i>	0.022	17	<i>Heptanchias perlo</i>	0.003	8	<i>Argyropelecus aculeatus</i>	0.020	14	<i>Argyropelecus aculeatus</i>	0.020	14
<i>Chamaux pictus</i>	0.009	17	<i>Physiculus dabwigki</i>	0.003	8	<i>Chlorophthalmus agassizii</i>	1.984	7	<i>Chlorophthalmus agassizii</i>	1.984	7
<i>Glossanodon leioglossus</i>	0.088	8			<i>Setarches guentheri</i>	0.431	7	<i>Setarches guentheri</i>	0.431	7	
<i>Polymetme corythaeo</i>	0.083	8			<i>Cyttopsis rosea</i>	0.106	7	<i>Cyttopsis rosea</i>	0.106	7	
<i>Centrodraco acanthopoma</i>	0.023	8			<i>Echiodon dentatus</i>	0.017	7	<i>Echiodon dentatus</i>	0.017	7	
<i>Hymenocephalus gracilis</i>	0.018	8			<i>Physiculus dabwigki</i>	0.011	7	<i>Physiculus dabwigki</i>	0.011	7	
<i>Gadella maraldi</i>	0.017	8			<i>Pontinus kuhlii</i>	0.009	7	<i>Pontinus kuhlii</i>	0.009	7	
<i>Cyttopsis rosea</i>	0.004	8			<i>Dipturus oxyrinchus</i>	0.008	7	<i>Dipturus oxyrinchus</i>	0.008	7	
<i>Polymixia nobilis</i>	0.004	8			<i>Torpedo nobilitiana</i>	0.008	7	<i>Torpedo nobilitiana</i>	0.008	7	
Shannon diversity <i>H'</i>	2.54				<i>Grammicolepis brachiusculus</i>	0.008	7	<i>Grammicolepis brachiusculus</i>	0.008	7	
Evenness	0.73					0.94			0.94		
						0.27			0.27		

^a*M. gracilis* was described but not distinguished from *M. scolopax* in the earlier datasets

^bContains unprocessed *Synchiropus phaeon* and *Centrodraco acanthopoma* (Ehrich 1974), and is therefore not treated as a taxonomic unit

^cContains unprocessed *Malacocephalus laevis* (Ehrich 1974), and is therefore treated as taxonomic unit

^dEhrich (1971) questions the determination of *P. kuhlii* in 1967, reference material is lacking

Table 3. Variance components for partial redundancy analysis (RDA) and RDA without covariables (i.e. not adjusted) for the Great Meteor Seamount fish assemblage, 1967–1998. Analysis carried out for the top 20 species present in all three datasets. Abiotic variables explained in “Materials and methods”

	Abiotic variables	Type of analysis	Covariables	Canonical eigenvalue (i.e. explained variance)	Significance test of canonical axes to explain biotic variability (<i>P</i> -value)
{1}	Habitat	Partial RDA	Daytime, gear, season	0.038	0.043
{2}	Gear	Partial RDA	Daytime, habitat, season	0.434	0.005
{3}	Daytime	Partial RDA	Gear, habitat, season	0.07	0.024
{4}	Season	Partial RDA	Gear, habitat, daytime	0.002	0.96
{5}	Time	Partial RDA	Habitat, gear	0.072	0.067
{6}	Environment	Not adjusted	–	0.671	0.0005
{7}	Environment	Partial RDA	Time	0.471	0.0005
{8}	Env + time	Not adjusted	–	0.743	0.005

Table 4. Decomposition of variance for redundancy analysis for variables in Table 3. Numbers {1} to {8} refer to Table 3

	Variance components	Calculation	Amount
{a}	Unexplained	$1 - \{\text{env} + \text{time}\} = 1 - \{8\}$	0.257
{b}	Shared between environmental and temporal factors	$\{\text{environment}\} - \{\text{adjusted environment}\} = \{6\} - \{7\}$	0.2
{c}	Pure environmental	$\{\text{adjusted environment}\} = \{7\}$	0.471
{d}	Pure time	$\{\text{adjusted time}\} = \{5\}$	0.072
	Total	$\{a + b + c + d\}$	1.00

Table 5. Significant species–environment relationships. Abiotic variables explained in “Materials and methods”. Double negative relationships must be regarded as non-significant preferences for a third category. Supplementary information on weight and acronyms also given. Bottom-trawl (*BT*) not only comprises gear effects for this trawl, but also a possible temporal change between 1967/1970 and 1998. Two species have no significant relationships (** $P < 0.05$, otherwise $P < 0.1$) (*AT* Agassiz-trawl)

Species	Acronym	Mean fresh weight in 1998 (kg)	Daytime		Habitat		Gear	
			Positive	Negative	Positive	Negative	Positive	Negative
<i>Anthias anthias</i>	ANA	0.031	Day		Type b**			
<i>Antigonia capros</i>	AC	0.273						BT** AT**
<i>Arnoglossus rueppelli</i>	ARN	0.010	Night**		Type b**			AT**
<i>Aulopus filamentosus</i>	AUL	0.175	Night**		Type a**			BT**
<i>Callanthias ruber</i>	CAL	0.031					Type a** Type b**	
<i>Capros aper</i>	CAP	0.025			Type b**			BT**
<i>Chaunax pictus</i>	CHA	0.207		Night**	Type a**			BT**
<i>Chlorophthalmus agassizii</i>	CHL	0.014	–	–	–			–
<i>Cyttopsis rosea</i>	CYT	0.020					Type a** Type b**	
<i>Glossanodon leioglossus</i>	GLO	0.006	Night**		Type b**			
<i>Gnathophis mystax</i>	GNM	0.044	Night**		Type b**			BT**
<i>Helicolenus d. dactylopterus</i>	HEL	0.340		Night**			Type a** Type b**	
<i>Heptranchias perlo</i>	HEP	1.291			Type a**			
<i>Laemonema yarrellii</i>	LAE	0.033					Type a**	
<i>Lepidopus caudatus</i>	LEP	0.055			Type b**			BT**
<i>Macroramphosus scolopax</i>	MAC	0.013	Day		Type a**			
<i>Phycis phycis</i>	PP	0.408		Night**				BT**
<i>Scorpaena loppei</i>	SCO	0.020	Night					
<i>Trachurus picturatus</i>	TRA	0.168		Night**			Type a**	BT**
<i>Zenopsis conchifer</i>	ZEN	1.066	–	–	–		–	–

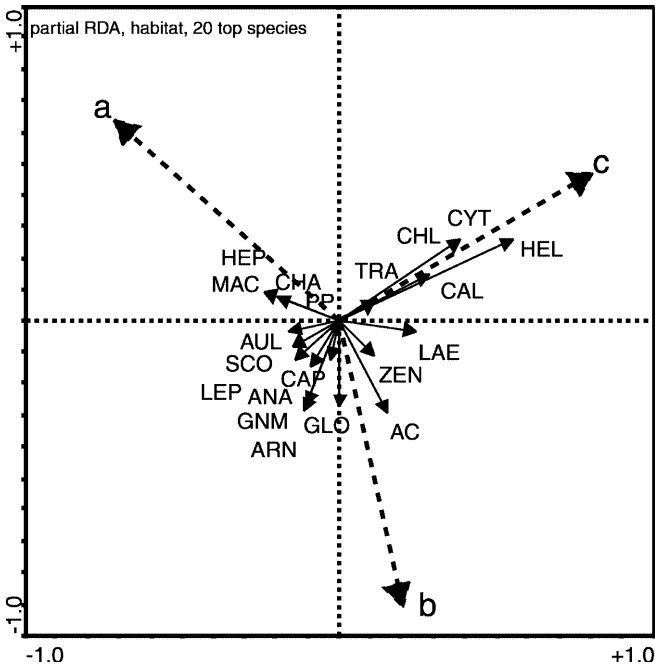


Fig. 3. Partial RDA plot for factor “habitat” for the top 20 species. For interpretation of RDA see Fig. 2; acronyms, see Table 5; for locations of habitats see Fig. 1 (*a* plateau; *b* inner margin; *c* outer margin)

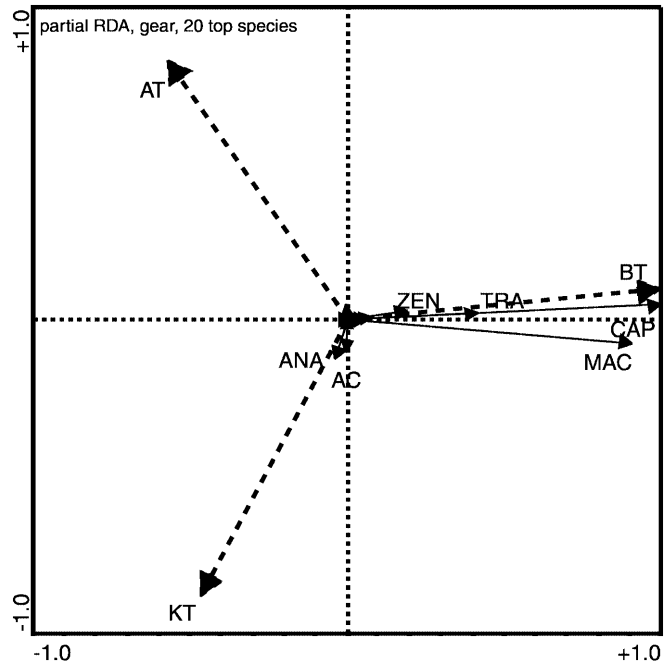


Fig. 4. Partial RDA plot for factor “gear” for the top 20 species. For interpretation of RDA see Fig. 2; acronyms, see Table 5; 14 species orientated around origin (0,0) and are hidden (ARN, AUL, CAL, CHA, CHL, CYT, GLO, GNM, HEL, HEP, LAE, LEP, PP, SCO) [AT Agassiz-trawl; KT common 90-ft otter-trawl (“Kutter”-trawl); BT 170-ft Engel bottom-trawl]

1967 and 1970, means were calculated from 200, in 1998, from a sample size of 300 resampled values. The 1967 dataset was mainly characterised by the Agassiz-trawl, the 1970 dataset, by the 90-ft otter-trawl, and the 1998 dataset, by the Engel-trawl. The effect of the bootstrapping is exemplified in Fig. 5. The bootstrap estimate and the raw mean are equal for highly frequent species (*Macroramphosus scolopax*, *Capros aper*, *Zenopsis conchifer*), whereas for rare species the bootstrap estimate is always smaller than the raw mean (e.g. *Cyttopsis rosea*), since outliers are downweighted.

On the order level, the preponderance of Zeiformes and Syngnathiformes is evident (Table 7). The share of Perciformes in total CPUE decreased from 21.7% in 1967/1970 to 3.9% in 1998. In terms of abundance, Gadiformes, a typically shelf-dwelling species group, contributed only 3.29% in 1967/2000 and 0.05% in 1998.

Table 6. Sampling habitats for rare species in 1967, 1970 and 1998 (no preference sampling in habitats a, b and c without recognisable pattern)

Plateau, type a	Marginal habitats, types b and c	No preference
<i>Raja maderensis</i>	<i>Torpedo nobiliana</i>	<i>Scomber japonicus</i>
<i>Chlopsis bicolor</i>	<i>Dipturus oxyrinchus</i>	<i>Hymenocephalus gracilis</i>
	<i>Setarches guentheri</i>	<i>Polymixia nobilis</i>
	<i>Gadella maraldi</i>	<i>Physiculus dalwigki</i>
	unidentified Macrouridae	<i>Synchiropus phaeton</i>
	<i>Polymetme corythaelo</i>	
	<i>Gnathophis codoniphorus</i>	

The number of species with high frequency increased from 1967 to 1998 (Table 2), presumably reflecting the increased gear size from 1967 (mainly Agassiz-trawl) over 1970 (mainly 90-ft otter-trawl) to 1998 (Engel bottom-trawl). The highly abundant and very common species, characteristic of the community during all cruises [snipefish (*Macroramphosus scolopax*), seabass (*Anthias anthias*), boarfishes (*Capros aper* and *Antigonia capros*), flatfish (*Arnoglossus rueppelli*) and aulopid (*Aulopus filamentosus*)] maintained their high position according to frequency, indicating consistent community composition. *M. scolopax* was the numerically dominant species during all three cruises, reaching extremely high bootstrap CPUE (b-CPUE) values of 369.7 ind. m⁻¹ h⁻¹ in 1998. Also in 1998, *C. aper* reached extraordinarily high abundances of 179.3 ind. m⁻¹ h⁻¹. This marks an increase in abundance by two orders of magnitude from 1967/1970 to 1998. This trend was similar to values for *Trachurus picturatus*, which increased from between 0.018 and 0.155 ind. m⁻¹ h⁻¹ in 1967/1970 to 18.2 ind. m⁻¹ h⁻¹ in 1998.

Among the less abundant species, a decrease was recognised for *Phycis phycis*, which was very common in 1967 and 1970, but was rather rare in 1998. Opposite trends were found for *Lepidopus caudatus*, *Zenopsis conchifer* and the shark *Heptanchias perlo*, all of which were very frequent in 1998, but relatively rare during the early cruises.

Changes in species composition between the cruises were related to rare species (Table 8). Isolated catches

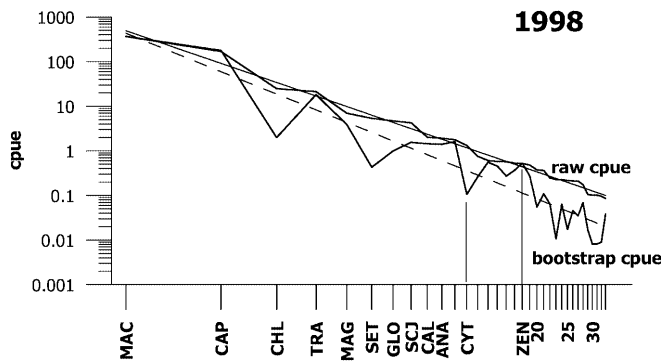


Fig. 5. Effect of bootstrapping on CPUE values for 1998. Species ranked by raw CPUE values. Species indicated by acronyms. *Trend lines* indicate the generally lower bootstrap CPUE values (CPUE in ind. m⁻¹ h⁻¹, on a logarithmic scale) (MAC, *Macroramphosus scolopax*; CAP, *Capros aper*; CHL, *Chlorophthalmus agassizii*; TRA, *Trachurus picturatus*; MAG, *Macroramphosus gracilis*; SET, *Setarches guentheri*; GLO, *Glossanodon leioglossus*; SCJ, *Scomber japonicus*; CAL, *Callanthias ruber*; ANA, *Anthias anthias*; CYT, *Cyttopsis rosea*; ZEN, *Zenopsis conchifer*)

during the earlier cruises were recorded for *Centrodraco acanthopoma*, *Protogrammus sousai*, *Raja maderensis*, *Gnathopis codoniphorus* and *Chlopsis bicolor*. In contrast, the rays *Dipturus oxyrinchus* and *Torpedo nobiliana* were only recorded during the 1998 cruise.

The analysis of community structure reveals reduced biodiversity (H') in 1998 compared to 1967 and 1970 (Table 2). This is mirrored by the rarefaction analysis and the abundance plot. The species density per unit CPUE is indicated by the rarefaction plot (Fig. 6A). Up to 7 units CPUE sampled, species density was similar for the cruises of 1970 and 1998 and only slightly lower in 1967. With more units sampled, the number of species in 1970 was higher, indicating higher species diversity. In 1998, even at 20 units CPUE sampled, the species density of 1970 was not reached. In the abundance plot (Fig. 6B), the 1967 and 1970 samples showed a similar

gradual increase of proportional abundance per species, i.e. slope, for ranks 1–8. In contrast, in the 1998 sample, only two species contributed almost 100% of total abundance, marked by a steep slope at the beginning and no increase in cumulative abundance for ranks > 2. Absolute differences in sampled CPUE and proportion of first species between 1967 and 1970 are likely to be attributable to the size of gear.

Species distributions showed no difference between the 1967 and the 1998 surveys, although very different nets were applied (Fig. 6C, D). Furthermore, under addition of the species only qualitatively recorded for 1967 (four species, Table 8) and supposing that they were captured during additional hauls, a perfect concordance can be reached between the 2 years. The winter samples of 1970 had, on average, lower species numbers per haul. The jack-knife estimates of 43 species for 1967 (39 + 4) and of 41 for 1998 are in good agreement with the total of 43 species from all German surveys, which included 40 species from the pooled surveys in 1967, 1970 and 1998 plus *Pollichthys mauii*, *Bellotia apoda* and *Agyripnus atlanticus* (see Table 8). Including Russian findings, a grand total of 46 species is obtained for the demersal community associated with the GMR.

Discussion

Species–environment relationships

Bulk portions of variance of species–environment relationships were due to unexplained variance, shared variance of time and gear, and gear effects. The application of a large trawl in 1998 compared to 1967 and 1970 exerted considerable influence on the catch data. Notwithstanding, further significant effects were due to daytime and habitat. Due to the dominance of gear effects, partial analysis was required to resolve the effects for other environmental factors. No seasonal effects were

Table 7. Taxonomic composition and percentage catch per order. Abundance values based on bootstrap CPUE estimates (*b-CPUE*, in ind. m⁻¹ h⁻¹). Examples of genera in *parentheses*

Order (genera)	b-CPUE		Percentage of total b-CPUE	
	1967/1970	1998	1967/1970	1998
Anguilliformes (<i>Chlopsis</i> , <i>Gnathopis</i>)	0.14	0.271	1.5	0.1
Aulopiformes (<i>Aulopus</i> , <i>Chlorophthalmus</i>)	0.23	3.6	2.6	0.6
Gadiformes (<i>Phycis</i> , <i>Physiculus</i> , <i>Gadella</i>)	0.29	0.27	3.3	0.05
Hexanchiformes (<i>Heptranchias</i>)	0.002	0.368	0.02	0.06
Lophiiformes (<i>Chaunax</i>)	0.017	0.064	0.19	0.01
Ophidiiformes (<i>Echiodon</i>)	0.051	0.017	0.6	0.00
Osmeriformes (<i>Glossanodon</i>)	0.091	0.992	1.02	0.17
Perciformes (<i>Anthias</i> , <i>Callanthias</i> , <i>Lepidopus</i> , <i>Trachurus</i>)	1.93	23.1	21.7	3.96
Pleuronectiformes (<i>Arnoglossus</i>)	0.339	0.270	3.8	0.05
Polymixiiformes (<i>Polymixia</i>)	0.112	0.055	1.3	0.01
Rajiformes (<i>Raja</i>)	0.022	0.008	0.25	0.0
Scorpaeniformes (<i>Pontinus</i> , <i>Setarches</i> , <i>Scorpaena</i>)	0.13	0.77	1.5	0.13
Stomiiformes (<i>Polymetme</i>)	0.086	0.017	0.96	0.0
Syngnathiformes (<i>Macroramphosus</i>)	3.823	373.65	42.9	63.98
Torpediniformes (<i>Torpedo</i>)		0.008		0.0
Zeiformes (<i>Antigonia</i> , <i>Capros</i> , <i>Zenopsis</i> , <i>Cyttopsis</i>)	1.63	180.52	18.3	30.91

Table 8. Changes in species composition during German Great Meteor Seamount cruises, including species with single-catch records and supplementary species information. Mesopelagics except for the genera *Agyropelecus* and *Pollichthys* omitted

Quantitatively recorded in 1967/1970 by Ehrich (1977)	Recorded in 1998 (Uiblein et al. 1999)	Russian observations until 1982 (Shcherbachev et al. 1985)
<i>(Pollichthys maui^a)</i> <i>(Argyripnus atlanticus^a)</i>	<i>Grammicolepis brachiusculus</i> <i>Scomber japonicus</i> <i>Torpedo nobiliana</i>	<i>Grammicolepis brachiusculus</i> <i>Scomber japonicus</i>
<i>(Setarches guentheri^b)</i>	<i>Setarches guentheri</i> <i>Argyropelecus aculeatus</i> <i>Dipturus oxyrinchus</i>	<i>Setarches guentheri</i>
<i>Centrodraco acanthopoma</i> <i>Chlopsis bicolor</i> <i>Gnathophis codoniphorus</i> <i>Polymetme corythaelo</i> <i>Protogrammus sousai</i> <i>Raja maderensis</i>		<i>Polymetme corythaelo</i>
		<i>Promethichthys prometheus</i> <i>Zeus faber</i> <i>Coryphaenoides</i> sp. (probably <i>Nezumia aequalis</i>)
<i>(Bellottia apoda^b)</i>		

^aQualitatively listed by Ehrich (1971)
^bQualitatively listed by Maul (1976) for GMR

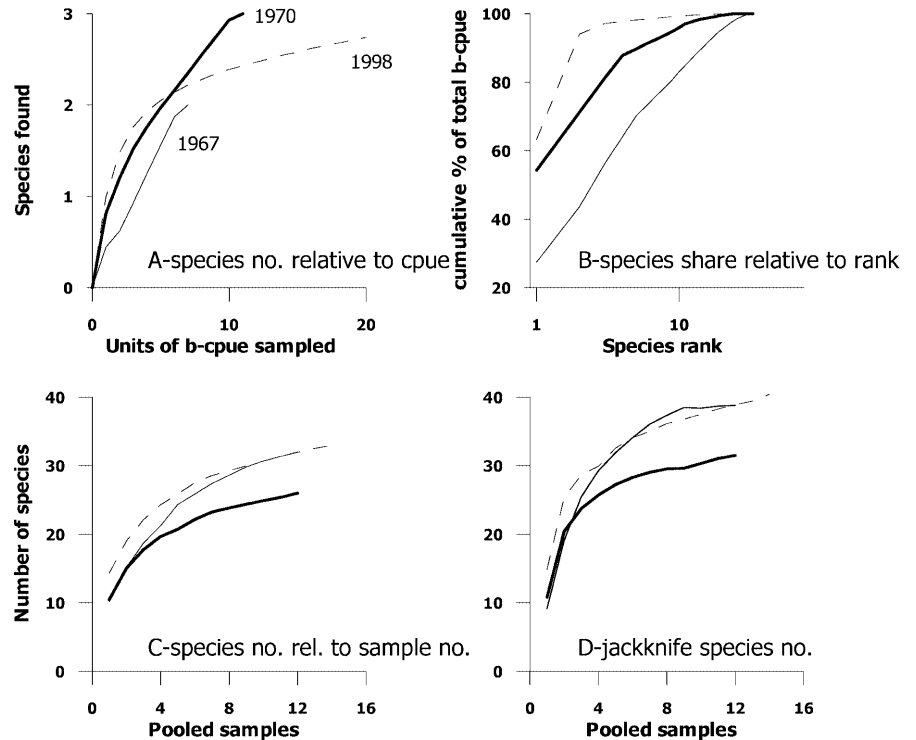
found, similar to findings from deep-sea fishes from Rockall Trough (Gordon and Bergstad 1992) and subtropical fish assemblages (Watson et al. 1990; Lee and Hwang 1995).

In line with theory on “seamount effects”, the species–environment relationships are accounted with a trophic hypothesis, in order to explain observed variation. Firstly, we consider enhancement of primary production by means of upwelling in the region influenced by the Taylor-column to be the driving force; this would explain the preference of marginal habitats for many fish

species fairly well, but not the pronounced diurnal patterns. The failure to find persistently increased levels of primary production at GMR (Mourino et al. 2001) further weakens the primary-production hypothesis.

In contrast, the sound-scattering layer (SSL)-interception hypothesis (Isaacs and Schwartzlose 1965; Rogers 1994) accounts for both the diurnal and spatial patterns in explaining the sustained fish populations at GMR. Regarding daytime and habitat factors, two different groups of species were found for each: night-correlated and day-correlated species and species with

Fig. 6. Biodiversity charts of Great Meteor Seamount demersal fish assemblages for the years 1967, 1970 and 1998: **A** rarefaction plot, **B** abundance plot, **C** species number relative to number of hauls, **D** jack-knife estimation of species numbers. Bootstrap CPUE is in ind. m⁻¹ h⁻¹. *Macroramphosus gracilis* was excluded from analysis in 1998, since this species was not separately recorded in 1967 and 1970. Jack-knife is an estimation method to predict how many species would have been discovered had the sampling been more intensive. C and D represent means of 50 replicate runs; A–D based on quantitative hauls only



preferences either for plateau or marginal habitats (Table 5). For the eastern subtropical Atlantic, the sound-scattering layers undertake diurnal migrations from ca. 600–900 m to the surface (Kinzer 1969; Mozgovoy and Bekker 1991). This more-or-less covers the depth range of plateau, marginal and even upper slope habitats at GMR. Furthermore, the SSL consists of different layers inhabited by different groups of crustacean plankton at depths < 600 m (Kinzer 1969) and mesopelagic fishes, such as myctophids, down to 900 m (Mozgovoy and Bekker 1991). Under the SSL-interception hypothesis, those predators that prey upon components from the upper SSL (preferably pelagic crustaceans) follow the SSL to the surface during night and descend during the day, with a significant positive relationship to the factor day (in line with patterns for *Anthias anthias*, *Macroramphosus scolopax*, *Helicolenus d. dactylopterus*, *Phycis phycis* and *Trachurus picturatus*). Descending prey, in terms of planktivorous fishes, might also enhance the activity of fish predators in plateau habitats (*Chaunax pictus* and *Hepranchias perlo*). For seamount fishes interception probability with a diurnally moving SSL is likely to be highest in marginal habitats, especially if deeper reaches, i.e. slope habitats, are also utilised and a circular current concentrates or locks part of the stock from the SSL in a ring around the guyot. Thus, marginal habitat types b and c should be significantly preferred (in line with patterns for *Callanthias ruber*, *Capros aper*, *Cyttopsis rosea*, *Laemonema yarellii* and *Lepidopus caudatus*). Those species feeding on prey from the lower SSL descend during the day to the mid-reaches of the seamount slope and ascend at night to the depth level of the plateau and its margins. Species positively linked to marginal habitats and the factor night (*Gnathophis mystax*, *Glossanodon leioglossus* and *Arnoglossus rueppelli*) would fit into this scheme. In total, preferences for marginal habitats add up to 11:4 in terms of significance, 16:4 for the top 20 species in terms of tendency and findings for rare species (Table 6) even rise to 23:6. Direct proof for the diurnal component of the SSL-interception hypothesis has been given for zooplankton (Genin et al. 1994; Haury et al. 2000). For fishes, the alfonsino *Beryx splendens* serves as an example for the SSL hypothesis, by following its prey during diurnal migration (Vinnichenko 1997). Further observations from the Angolan shelf for *Trachurus* spp. caught by pelagic trawls (Misund et al. 1999) complement observations for *T. picturatus* over the GMR (see Table 5), in line with the SSL hypothesis. However, diurnal patterns for *Scorpaena loppei* and *Aulopus filamentosus* remain unexplained by the SSL hypothesis. Here, along with feeding aspects, light, viz. predator avoidance and competition, as well as specific activity patterns must be considered (e.g. Sissenwine and Bowman 1978).

Further morphological and ecological findings support the conclusions concerning differentiated habitat utilisation, as suggested by the SSL-interception hypothesis. Among the dominant species with preferences for marginal habitats were species with a deep-bodied

habitus (i.e. small length to body-depth ratio) presumably ideal for manoeuvring in regions with higher current velocities, e.g. the area influenced by the Taylor-column (*Capros aper*, *Cyttopsis rosea*, and insignificantly *Antigonia capros*, *Zenopsis conchifer*). In contrast, the more delicate *Macroramphosus scolopax* preferred the plateau side of GMR. The pelagic descendant *Trachurus picturatus* was related to habitat type c, the outer margin, whereas the bottom-burrowing *Chlopsis bicolor* and the lie-in-wait predator *Chaunax pictus* were related to the plateau.

Community composition

Concerning the dominant species, the composition of the fish assemblage in terms of rank order of species was consistent between 1967 and 1998 (Table 2), providing evidence for the structure of a specific and stable subtropical demersal fish community on GMR. An inspection of seamount faunas (Wilson and Kaufmann 1987; Parin et al. 1997) supports the concept of seamount zonal communities, since seamounts with similar community structure to GMR can be found in the subtropical areas both in the Pacific and in the Atlantic domain. This is in line with the analysis of Koslow (1993), who identified zonal fish communities for different types of regional habitats.

The GMR fish community is characterised by deep-bodied species of the Zeiformes and the Syngnathiformes (see Table 7). In contrast, Pleuronectiformes and Gadiformes contributed an extremely low share to overall catch, although these groups dominate in temperate areas at the same depths (Farina et al. 1997; Labropoulou and Papaconstantinou 2000) and on the shallower shelf of the NE Atlantic (Rogers et al. 1999). Hakes and Macrouridae, both typical targets of shelf and slope fisheries (Koslow et al. 2000), are caught in ample amounts along the African coast at 20–30°N (Maul 1976; Merrett and Domanski 1985), in the Mediterranean (Labropoulou and Papaconstantinou 2000) and off the Canary Islands (Uiblein et al. 1996), but are missing or rare on GMR. Furthermore, at GMR the most abundant gadiform, *Phycis phycis*, declined in abundance from 1967/1970 to 1998. During eight hauls in June–July 1982 on the GMR, only one specimen of *P. phycis* was caught (Shcherbachev et al. 1985).

The total number of species/taxonomic units (see notes on MACR in Table 2) in 1967 was slightly higher than in 1998 (36 vs. 32, summarised from Tables 2 and 8, not including *Macroramphosus gracilis*). The jack-knife numbers of species (Fig. 6) from bottom-trawls were the same for 1967 and 1998. The reduced number of species in 1970 was probably due to net selectivity of the 90-ft otter-trawl, which was widely used in 1970, with its larger codend mesh size. The observed changes in species composition can be attributed to those species that were recorded only in 1967/1970, and those species that were only recorded in 1998. Supplementary records

from Shcherbachev et al. (1985) allow an evaluation of the differences between 1967/1970 and 1998 (Table 8). New records of species in 1998 are likely to be linked to improved catchability (gear effects), for example for the rays *Dipturus oxyrinchus* and *Torpedo nobiliana*. According to Stevens et al. (2000) a downward trend for *D. oxyrinchus* has been noted for the NE Atlantic. *Grammicolepis brachiusculus*, seemingly, is a deep-water invader of the GMR, and was found both in 1998 as well as in Russian samples. In 1998, it was caught at a marginal station of the GMR plateau. *Scomber japonicus* and *Setarches guentheri* were both found in 1998 and in Russian samples, but were not quantitatively recorded in 1967/1970, probably due to low population density. From the species first recorded in 1998, taking into account the Russian results (Shcherbachev et al. 1985), none appeared to be dominant in such a way to regard it as an invader of the GMR community. Furthermore, the high degree of similarity between the jack-knife estimates of species numbers (41 vs. 43) and total species number (46, respectively) indicates that differences in species lists are probably attributable to sampling effort rather than to species turnover. Negligible turnover has also been suggested for the NE Atlantic shelf (Greenstreet et al. 1999). Species numbers found in comparable habitats, i.e. 47 species for the 500 m depth zone of the Rockall Trough (Gordon and Bergstad 1992) and 39 species at 400 m depth off the Californian shelf (Percy et al. 1982), suggest that the GMR community is species saturated.

Long-term changes

In view of the quantitative changes from 1967/1970 to 1998, long-term changes of community structure in terms of diversity and dominance must be considered. Gear together with an, in the RDA inseparable, effect of time and gear accounted for 67.1% of explained variance. Valuable approaches have been developed to uncover fishery trends despite the obstacles to long-term comparisons and inter-area calibrations created by changes in gear over time. One approach is based on changes in diversity (Rijnsdorp et al. 1996). Another way is to select particular population declines and increases that are unlikely to have been caused by changes in gear (e.g. decline of elasmobranchs, see Rijnsdorp et al. 1996; Zwanenburg 2000). With restrictions concerning specific reactions of particular species, changes in gear can be expected to systematically affect the yield. Larger nets should catch: (1) higher numbers of specimens (Sissenwine and Bowman 1978; Percy et al. 1982; Gordon and Duncan 1985; Ehrich 1991), (2) higher numbers of species due to increased numbers of specimens (Koslow 1993) or improved catchability (Merrett and Domanski 1985) and (3) higher numbers of larger specimens (Bethke et al. 1999). Changes in mesh sizes also affect catches, i.e. smaller meshes should increase selectivity (Wileman et al. 1996). Further variability

must be attributed to changes in ground ropes, application of chains, warps, engine power, etc.

No general decline for elasmobranchs or larger species has been recorded for the GMR. In contrast, from 1967 to 1998, numbers of the larger species *Heptanchias perlo* and *Zenopsis conchifer* increased, but not so for *Antigonia capros* and *Phycis phycis*. Furthermore, abundances increased considerably for *Macroramphosus* spp. and *Capros aper*, by a factor of approximately 50–100. In the following, we discuss both approaches with respect to long-term change, i.e. changes in diversity and particular declines and increases of abundances.

With regards to diversity, despite the application of larger nets and the larger number of specimens caught in 1998, the number of species did not increase from 1967 to 1998 (see Fig. 6; Table 2). On the contrary, a decrease in diversity was indicated in all aspects of the analysis (H' , rarefaction analysis and abundance plots) from 1967/1970 to 1998. In numbers, diversity decreased from 2.5 in 1968 to 0.9 in 1998. This was partly due to changes in abundance for the numerically dominant species. Excluding *Capros aper*, *Macroramphosus* spp. and *Trachurus picturatus* from the analysis, fairly similar diversity values of 2.6 (1967), 1.9 (1970) and 2.6 (1998) were obtained. Koslow et al. (1994, their Fig. 2F) calculated cumulative diversity values for mid-slope demersal fishes in southern Australia as ranging between $H' = 1.8$ and 1.95 for 1–20 aggregated samples (same log-base chosen), which are comparable to the values for 1967 and 1970. Hence, the low value for 1998 must be regarded as a decrease in diversity due to an enormous increase in three species. Similar decreases in diversity have been documented in the literature. For instance, Rijnsdorp et al. (1996) generated an exact copy of our Fig. 6B, indicating a comparable loss of diversity and one-sided increase of dominance within North Sea benthic fish assemblages. Again, the decrease could be attributed to massive increases of a few species (herring, sprat).

Linking the major change to only three particular species implies that the other species effected rather neutral changes, mostly related to variations in gear. Thus, a second approach was used to address this issue: the declines and increases of abundance were investigated. Abundance changes were derived from CPUE ratios between the early cruises and the 1998 cruise. Three categories were employed: decrease from 1967/1970 to 1998 (ratio < 1), moderate increase (ratio = 1–8) and considerable increase (ratio > 8). Moderate increase is assumed to be linked to the net size of the 170-ft trawl. Changes were compared with available vertical habitat information (Table 9). It appears that: (1) no off-bottom/off-bottom pelagic species decreased from 1967/1970 to 1998; (2) no benthic species increased from 1967/1970 to 1998; and (3) the group with moderate increases is balanced, with equal shares of benthic and off-bottom/off-bottom pelagic representatives and corresponding fairly well to the group hidden in Fig. 4. This diagonal arrangement of species in the table indicates a possible effect attributed to a change in gear. Therefore, changing from Agassiz- and 90-ft

Table 9. Separation of groups based on between-year differences and vertical habitat classification. Group separation based on comparison of values in Table 2. Individual weight (in kg wet weight) in *parentheses*. Differences between years based on bootstrap estimates for each species significant at $P < 0.001$ except

where indicated (*n.s.* not significant; $**P < 0.01$; the middle column was not analysed). Vertical habitat categories derived from Parin et al. (1997). Species classified according to Parin et al. (1997, their Table 9) and the database (FishBase 1999). Weight data obtained from the 1998 cruise

Habitat	I. Species with considerably increased abundance in 1998	II. Species with moderate increase in abundance in 1998, attributed to net effects	III. Species with increased abundance in 1967/1970
Benthic		<i>Chaunax pictus</i> (0.207) <i>Heliocolenus d. dactylopterus</i> (0.343)	<i>Arnoglossus ruepelli</i> ^{n.s.} (0.010) <i>Echiodon dentatus</i> ** (0.008) <i>Pontinus kuhlii</i> ^{n.s.} (0.026) Rajiformes ^a <i>Scorpaena loppel</i> ^{n.s.} (0.020) <i>Synchiropus phaeton</i> (0.052) <i>Anthias anthias</i> ^{n.s.} (0.031) <i>Antigonia capros</i> (0.273) <i>Phycis phycis</i> (0.408) <i>Polymixia nobilis</i> ^{n.s.} (0.231)
Near-bottom	<i>Capros aper</i> (0.025) <i>Chlorophthalmus agassizii</i> (0.014) <i>Heptanchias perlo</i> (1.29) <i>Macroramphosus scolopax</i> (0.013)	<i>Callanthias ruber</i> (0.031) <i>Gadella maraldi</i> (0.041) <i>Gnathophis mystax</i> (0.044) <i>Physiculus dalwigki</i> (0.057)	
Off-bottom		<i>Aulopus filamentosus</i> (0.175) <i>Glossanodon leioglossus</i> (0.006) <i>Hymenocephalus gracilis</i> (0.001) <i>Laemonema yarellii</i> (0.033.) <i>Lepidopus caudatus</i> (0.055)	
Off-bottom pelagic	<i>Trachurus picturatus</i> (0.168)	<i>Cyttopsis rosea</i> (0.020) <i>Zenopsis conchifer</i> (1.066)	

^aFor rajiformes: *Raja maderensis* (1967/1970) compared to *Dipturus oxyrinchus* (1998)

otter-trawl to the 170-ft Engel bottom-trawl is likely to have affected all of group II, but also the off-bottom pelagic species *Trachurus picturatus* and the antipodal group of genuine benthic species. This indicates increased catchability of pelagic species due to the higher vertical opening of the 170-ft trawl. In turn, reduced ground contact due to the rubber armament of the ground rope in 1998 could have caused reduced catchability of benthic species compared to samplings in 1967/1970. Good ground contact can at least be anticipated for the Agassiz-trawl. Apart from the diagonal arrangement, two groups remain to be considered, both of near-bottom habitat preference. Similar to the analysis of diversity, an increase was observed for *Capros aper* and *Macroramphosus scolopax*, as well as for *Heptanchias perlo* and *Chlorophthalmus agassizii*. Although increased considerably, in terms of frequency, the latter species were still rare in 1998 (Table 2). The second group comprises *Anthias anthias*, *Antigonia capros*, *Phycis phycis* and *Polymixia nobilis*. Based on diet composition (Ehrich 1971, 1974; Macpherson 1979; Clark 1984; Gomes et al. 1998; authors' unpublished results), the assessment of probable dietary overlaps provides a trophic explanation for the observed shifts in abundances. Assuming that morphologically similar young *A. capros* and *C. aper* compete strongly, dietary overlaps must be anticipated for *H. perlo* versus *P. phycis* and *M. scolopax*/*C. aper* versus *A. anthias*/*A. capros*/*P. nobilis*. The mode of ovoviviparous reproduction is likely to bestow an advantage on *H. perlo* over *P. phycis* in the efficient use of its prey, i.e. *M. scolopax*, *C. aper* and benthic-pelagic remnants. Analysing the second group, with a largely planktonic diet, in terms of r-K strategies, the small-sized *M. scolopax* and *C. aper*

probably are more successful and/or opportunistic in utilising ephemeral resources than the larger species, which were more abundant in 1967/1970. Spatially delimited grounds, such as seamounts, should be highly susceptible to short-term effects, released through fluctuations of weather and currents. Strong competition for food, in terms of intra-specific competition, was indicated for orange roughly over Australian seamounts (Koslow 1997).

To summarise, for all aspects of spatio-temporal variation of the benthic-pelagic fish community, a trophic hypothesis was applied, which in the case of long-term changes became a trophic community hypothesis, anticipating interactions not only between fish populations and prey, but also within the fish community. Such a trophic hypothesis is reasonable, since Merrett (1987) suggested that changes in productivity patterns can determine changes in fish community structure. It is fairly safe to assume shifts in productivity analogous to the observed differences in fish assemblages between 1967/1970 and 1998, as well as between the GMR and continental shelves. Thus, as a consequence the compositional and spatio-temporal structure of the GMR community would be an adaptation to certain productivity constraints on diurnal as well as decadal terms. This warrants further investigation.

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