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**Structure and diversity patterns of deep-sea pelagic fish assemblages
in relation to the Mid-Atlantic Ridge (45°N to 50°N)**

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Abstract

Pelagic fishes from depths of 250 m to 3200 m from 45 °N to 50 °N were sampled during a cruise over the Mid-Atlantic Ridge and adjacent waters in 1982. Cluster analysis revealed 6 assemblages, which were connected to ridge habitats, the continental shelf edge and oceanic habitats. Spatial boundaries for the clusters were set by frontal systems, of which the Southern Subarctic Front and the Mid-Atlantic Front determined the northern and western boundaries. Over the ridge, Melamphaidae, Serrivomeridae, Stomiidae and Centrolophidae increased in abundance. The abyssopelagic assemblages were characterised by the gonostomatid *Gonostoma bathyphilum*. The myctophid *Benthosema glaciale* indicated the transition from temperate to subarctic waters. The gadid *Micromesistius poutassou* and the alepocephalid *Xenodermichthys copei* were discussed as characteristic species for the shelf edge assemblage. The increase of gelatinous plankton feeders over the ridge, in particular for the centroplophid *Schedophilus medusophagus*, was discussed with respect to a probable increase of gelatinous plankton abundance in the area considered.

Introduction

Pelagic fish communities of the eastern North Atlantic are still poorly understood. Hitherto, in the eastern North Atlantic pioneering investigations have been carried out either with respect to local process studies (Badcock and Merrett 1976; Roe, Angel et al. 1984; Roe and Badcock 1984) or species distributions (e.g. Krefft 1974; Krefft 1976; Hulley 1981). With similar intentions the Gulf Stream and Sargasso Sea environments have been investigated in the western North Atlantic (Backus, Craddock et al. 1970; Jahn and Backus 1976; Backus and Craddock 1982; Boyd, Wiebe et al. 1986; Conte, Bishop et al. 1986). East of the Mid-Atlantic Ridge (MAR) at about 20°W,

detailed oceanographic investigations have been carried out within the framework of the Atlantic Meridional Transect program from 47 °N to the south (references in Aiken and Bale 2000; Maranon, Holligan et al. 2000; and Woold-Walker, Kingston et al. 2001). Also east of MAR, considerable effort has been undertaken to study the continental shelf edge fish assemblages at Rockall Trough and Porcupine Bank with regard to pelagic and benthopelagic fishes (Gordon and Duncan 1985; Merrett, Badcock et al. 1986; Merrett, Gordon et al. 1991; Gordon and Bergstad 1992; Hulley 1992; Hillgruber and Kloppmann 2000) and interactions between them (Mauchline and Gordon 1983; Mauchline and Gordon 1984; Mauchline and Gordon 1991).

Up to present, no studies have considered pelagic fish assemblages in relation to the Mid-Atlantic Ridge at 45 °N to 50 °N and its complex hydrography, withstanding the investigations on bottom fishes in that area (Vinnichenko, Gorchinskij et al. 1994; Vinnichenko 1998; Hareide and Garnes 2001). Recognising that the MAR in the Southern Ocean constitutes an ecosystem boundary also for meso- and epipelagic assemblages (John and Zelck 1998), marked effects must also be expected for the North Atlantic. We present data on the distributions of meso-, bathy- and abyssopelagic fish assemblages and their relationships to environmental factors.

Materials and methods

Sampling

Samples were taken during the FRV "Walther Herwig" cruise 52 in 1982 (see Table 1, and Post 1987, p. 57-61). The purpose of the cruise was to study the bathy- and benthopelagic fishes of the Mid-Atlantic-Ridge north of the Azores. The U-shaped course comprised a southern and a northern parallel of latitude, and a transverse section along the Mid-Atlantic Ridge (Fig. 1). Deep stations were trawled during daytime, while shallow stations were trawled at dawn (Table 1).

32 hauls were deployed with a MT 1600 net (1600 meshes pelagic trawl). The net spanned 20 m vertically and 30 m horizontally. Except for one station (St. 331) an inlet was fixed to the codend with 10 mm stretched mesh size (Post 1987, p. 6). The configuration used is likely to at least underestimate abundances of specimens < 30 mm (Gartner, Conley et al. 1989). Two 8 m² Süberkrüb doors were applied. During retrieval, the net was hauled very speedily in order to avoid contamination of deep hauls with specimens from shallower depths (Krefft 1976). With appropriate handling of winch and ship speed, retrieval contamination in non-closing devices can be reduced to < 2 % of total catch (e.g. Watanabe, Moku et al. 1999).

Community analysis

Following Jahn and Backus (1976), analysis was carried out excluding *Cyclothone* spp. (Gonostomatidae). *Cyclothone* spp. was either very rare or abundant in untreatable numbers (see Table 4). Further, species with single findings were excluded from the data set. As a first step, diversity measures were calculated from untransformed data. We employed Hill's indices N0 and N2 (Hill 1973; Magurran 1988), which have been frequently applied to analyses of long-term and large-scale changes in fish assemblages (see Greenstreet, Spence et al. 1999; Rogers, Maxwell et al. 1999). Hill (1973) developed a series of indices, which gradually differ in their indicative value for diversity. The general form is

$$N_a = (p_1^a + p_2^a + \dots + p_n^a)^{1/(1-a)},$$

with a=0,1,2,..., and p_i denotes the proportion of abundance for each species.

For a=0, N0 is the total number of species. N0 was estimated as the rarefied number of species in a sample of 250 specimens (ES250), which was the smallest sample size, avoiding sample size bias in the assessment of species numbers (e.g. Gordon 1986; Caley and Schluter 1997; Fock 2000; Gotelli and Colwell 2001). For a=1, N1 is the reciprocal Shannon-Wiener index H',

however we employed it in its more familiar form $H'_{10} = -\sum p_i \log_{10} p_i$ to enable easy comparisons with other studies. For $a=2$, N_2 is the reciprocal of Simpson's index. N_0 is a very accurate estimate of diversity with an emphasis on rare species, whereas N_2 focuses on the more abundant species (Hill 1973). Relationships between diversity measures and environmental factors were analysed by means of partial correlations.

For multivariate analysis, abundances were scaled to a trawling time of 1 hour and then root-root transformed. Fairly equivalent results were obtained for standardised data and thus are not explicitly considered. Only in one case, standardisation to relative abundances, i.e. percentages for compositional analysis (see Haedrich and Merret 1990; Greenstreet, Spence et al. 1999) yielded results different from the analysis of root-root transformed abundances. This will be discussed. Scaling to one hour accounts for quantitative aspects of community structure.

The PRIMER software package was employed for analysis (Clarke and Gorley 2001). For each data set, group average cluster analysis on Bray-Curtis similarities was conducted. Clusters were arbitrarily defined at levels of 50 – 60 % similarity. SIMPER was applied to identify characteristic species, non-parametric ANOSIM to evaluate the significance of the chosen level of partitioning. SIMPER takes two steps. Firstly it analyses contributions to similarity with a focus on evenly distributed species, i.e. species that have little variance within the chosen group and thus consolidate the cluster. The six top ranking species were tabulated. These are referred to as consolidating species for the respective cluster. Secondly, differences are considered with a focus on species which perform stable differences between groups. These are referred to as discriminating species for this cluster. However, differences may be small. Species were tabulated until 25 % cumulative dissimilarity was reached. For the ANOSIM of all clusters, a Bonferroni-corrected significance level α'' for multiple comparisons was applied (Sokal and Rohlf 1995) :

$$\alpha'' = \alpha / k ,$$

where k is the number of cluster-cluster comparisons.

Principal components analysis was carried out with CANOCO [ter Braak, 1998 #898].

Environmental data

In order to assess specific conditions for the year 1982, together with shipborne salinity and temperature data (Table 1), COADS and Reynolds sea surface temperature (SST) time series data were deployed. These were provided by the NOAA Climate Diagnostics Centre (NOAA-CIRES 2000) from their web site at <http://www.cdc.noaa.gov/>. Further satellite images facilitate a retrospective estimate of the distribution of chlorophyll and thus primary production in the Atlantic Ocean in 1982. Images were obtained from <http://seawifs.gsfc.nasa.gov/SEAWIFS/> from the Nimbus 7 – Coastal Zone Colour Scanner archive (CZCS).

Results

Hydrographical conditions with respect to the 1982 survey

Two different chlorophyll distribution patterns in terms of a deep chlorophyll maximum linked to the Mid-Atlantic Front and a silicate-linked region of high surface production at the northern parallel are anticipated. These are reflected in the climatological average spring chlorophyll distribution image 1978-1986 (Fig. 5 B).

Shipborne measurements during the cruise (Table 1), however with unknown accuracy, and the inspection of CZCS satellite images (Figure 5 A) indicate to the position of fronts and transition zones in the respective area. The coldest and most fresh surface water masses were met at the western and north-western stations of the cruise, stations 375 to 377 and 387 to 393 (Table 1). In

turn, the warmest and most saline waters were found in the south-eastern stations. Abrupt changes in water mass properties, i.e. decrease in SST for about 1°C from 14.9 °C (St. 369) to 13.45 °C (St. 375) and a further decrease from 13.36 °C (St. 384) to 12.4 °C (St. 387) indicate the transitions between the central part of the transverse and its southern and northern tail (f1 and f3 in Fig. 1). A further transition zone appeared between stations 378 and 381, where SST increased sharply from 13.16 °C to 14.56°C (f2 in Fig. 1). From station 390 to station 399, water of uniform temperature (13.2 to 13.3 °C) can be distinguished from the continental shelf break with warmer waters, most likely to be affected from the shelf edge current (f5 in Fig. 1). Satellite images substantiate the interpretation and position of the transition zones. f1 is indicated by a band of light chlorophyll opposed to the Mid-Atlantic Front (MAF, Fig. 5 A). The front f2 presumably is a derivative of the frontal system f4, which represents the uniform water body at the stations 390 to 399. The image indicates that f4 is connected with the Rockall Bank, whereas the neighbouring transition zone f5 is linked to the shelf edge. The transition zone f3 was aligned to the Southern Sub-Polar Front (SSAF). A comparison between a multi-year average (Fig. 5 B) and the situation in spring 1982 (Fig. 5 A) reveals, that the major frontal systems MAF and SSAF maintained their position in spring in all years, that they were shifted south- and south-eastwards in spring relative to their average annual positions (see Fig. 1) and that chlorophyll concentrations in 1982 were elevated within all transition zones.

A comparison of SST and salinity measurements during the cruise (Table 1) with property-property plots for potential temperature vs. salinity at 35 °W (Paillet, Arhan et al. 1998) and from 35 °W to 42 °W (Caniaux, Prieur et al. 2001) indicates the prevalence of freshened cold water of subarctic origin in the whole area of investigation in 1982. This is in line with the evidence of elevated levels of chlorophyll, since a negative relationship between chlorophyll and T0 is obtained for the area of investigation (see. Fig. 3 B). The distribution of approximate SST

anomalies as derived from COADS-data for June 1982 minus WOA98-data further substantiates the hypothesis of a massive subarctic water inflow (Fig. 2 A). A track with negative SST anomalies extends from the Northwest in southeasterly direction. The track of the negative anomalies is congruent with the main path of LSW as it enters the eastern basin (Paillet, Arhan et al. 1998). The congruence to shipborne measurements is better for COADS-data than for WOA98-data, which shows that the COADS-data sufficiently indicate modifications of the surface regime at that time (Fig. 3 A).

These findings indicate a cold inflow into the Mid-Atlantic in 1982 likely to be of subarctic origin.

Structure of the fish assemblages

The analysis of community structure for root-root transformed abundance data and standardised reference data (not shown) revealed, that despite some differences a general structure was common to both analyses: Specific assemblages were associated to the extended southern tail of the transverse (cluster B) and the northern parallel abutting on the continental shelf (cluster E). The shallowmost hauls at stations 378 and 381 were always outstanding (cluster C). In all analyses assemblages were related to the central part of the transverse, i.e. the Mid-Atlantic ridge proper (e.g. Fig 6 : cluster F). The analysis of root-root transformed data resembled the hydrographic structure of fronts f1 and f3, respectively (Fig. 4 , Fig. 5 A).

Six clusters were selected (Fig 6 , Tables 2 and 3). The analysis of similarity (ANOSIM) between clusters revealed a significant separation with $p < 0.015$ for the whole ensemble. In binary comparisons, significant separation ($p < 0.05$) was found for all pairs of clusters except for combinations A and E, A and C, and C and E, as indicated in Table 3.

Cluster A. This deep-bathypelagic cluster was confined to the zone of influence of Mediterranean Overflow Water (Fig. 3 D) on the easternmost section of the southern parallel. The gonostomatid *Gonostoma bathyphilum* was the prominent consolidating species. In relation to cluster F, which had the same average sampling depth as cluster A, comparably lower abundances for consolidating species *G. bathyphilum* (140.33 n h⁻¹ trawling) as well as for *Lampanyctus crocodilus* (7.33 n h⁻¹ trawling) were found. The average standardised number of species was high (ES250= 44.3), but due to dominance of *G. bathyphilum* diversity measures H'₁₀ and N2 were relatively low.

As a bathypelagic cluster, cluster B occupied the southern tail of the transverse and part of the southern parallel. In all analyses, the northern boundary was set by front f1 for this assemblage. It was dominated by myctophids (e.g. *Electrona risso*, *Diaphus rafinesquii*) and sternoptychids (*Argyropelecus olfersi*) as consolidating species (Tab. 2). Main discriminating species were *Benthosema glaciale* to clusters to the North and *Gonostoma bathyphilum* with respect to deep-bathypelagic clusters A and F (Table 3). A further important discriminating species was *Diaphus raffinesquii* in relation to cluster A. This cluster combined first ranks in terms of diversity (e.g. ES250=46.4) with a comparably low score in abundance (926 n h⁻¹ trawling).

Cluster C. This cluster joined the two shallowmost stations. With 505.71 n h⁻¹ trawling, *Diaphus rafinesquii* contributed 43.42 % of total abundance. This was the strongest dominance for one species in any one assemblage in this study. In total, consolidating myctophids contributed 61.05 % of total abundance. Compared to the neighbouring cluster F (Tables 2 and 3), *Benthosema glaciale* was less abundant in cluster C (71.29 to 195.68 n h⁻¹ trawling), whereas *D. rafinesquii* was more abundant (505.71 to 52.89 n h⁻¹ trawling). Discrimination was mainly achieved through species absent from the species-poor shallow assemblage. Correspondingly, diversity measures were low (e.g. ES250=19).

Cluster D. This cluster assembled hauls from different daytimes. Depending on daytime, mean sampling depth at dawn was 480 m (shallow assemblage) and 904 m (deep assemblage) during daytime. Cluster D was confined to the northern parallel and one station on the northern tail of the transverse. It represented stations of highest abundance during dawn and daytime with relatively low values for the diversity measures ES250, H'_{10} and N2. Predominant species was *B. glaciale* with 631.14 n h⁻¹ trawling, followed by *M. muelleri* with 389.43 n h⁻¹ trawling. Further, stomiids were characterised by high abundance in this cluster (*C. sloani* 248.29, *S. boa ferox* 309.43 n h⁻¹ trawling). This cluster was related to the frontal system f4 (Fig. 5 A) and thus related to the silicate rich region. Its western boundary coincides with f3 (Fig 1).

Cluster E. This mesopelagic assemblage was strictly associated with shallow hauls at the easternmost end of the northern parallel (Fig. 4). This assemblage was affiliated to the frontal system f5 at the continental shelf (Fig. 5 A). The consolidating sternoptychids and myctophids accounted for 55.7 % of total abundance (Tab. 2). With respect to the neighbouring clusters D and F, blue whiting *M. potassou* was an important discriminant species (Tab. 3). The centrolophid *Schedophilus medusophagus*, which was abundant in D and F, was missing in cluster E.

Cluster F. North of the front f1, this cluster covered wide parts of the transverse and parts of the northern parallel and represented 11 from 32 stations. This cluster combined features from mesopelagic as well as from abyssopelagic hauls. Thus, next to stomiids *Benthoosema glaciale* as a northern and *Gonostoma bathyphilum* as a deep component contributed to cluster characteristics. *B. glaciale*, *G. bathyphilum* and also *Schedophilus medusophagus* were important discriminating species. Within this cluster, *S. medusophagus* had a high average abundance of 143.38 n h⁻¹ trawling compared to cluster A with a similar average depth and an average abundance of 0.67 for this species. Further species important in terms of consolidation and

discrimination were *Scopelogadus beanii* and *Serrivomer beanii* with an average abundance of 102.15 and 63.48 n h⁻¹ trawling, respectively.

Comparisons between clusters

Excluding the occasionally large numbers of *Cyclothone* spp., the percentage by abundance on family level for analysis 2-clusters (Table 4 A) resembles the dominance patterns described on species level (Table 2) especially since in some families one species was predominating (e.g. *Nansenia* sp. – Microstomatidae, *Gonostoma bathyphilum* – Gonostomatidae). Although each assemblage consisted of hauls from different bathymetric zones, four types of dominance patterns can be discerned. The first type considers deep living assemblages (Table 4, A.1). Gonostomatids excluding *Cyclothone* spp. were leading in cluster A which consisted of bathy- and abyssopelagic stations, and further contributed a considerable share to cluster F. The second type (Table 4, A.2) considers the bathy- and mesopelagic environment. Here, myctophids and sternoptychids were predominating in meso- and bathypelagic clusters B, C, D, E. Whereas predominance for myctophids was most strongest in the assemblages C and E, sternoptychids had their highest share in the northern assemblages D and E. *Cyclothone* spp. in large numbers was also confined to northern and ridge assemblages D and F (Table 4, B), indicating a preference for deep mesopelagic and bathypelagic habitats for this genus, since no records were made for shallow assemblages C and E. This is in line with findings from Roe and Badcock (1984), indicating that only juveniles of 16 to 22 mm standard length assemble in the upper mesopelagic zone which are unlikely to be caught by the net deployed in this study. The third type of dominance pattern (Table 4, A.3) indicates a northern ridge component. Microstomatids and stomiids are concerned, abundantly present in clusters D and F over the ridge and the northern parallel. However, the abundance for the microstomatid *Nansenia* spp. was very variable in these

assemblages so that it did not achieve a consolidating status (see Table 2). The fourth type (Table 4, A.4) considers taxa related to assemblages of the deep and the ridge with a southern component. The southern component is proven by high relative abundances for cluster B. This concerns in the first line centrolophids. The centrolophid *Schedophilus medusophagus* was an important discriminating species for cluster F. Further taxa with this dominance scheme were melamphoids, serrivomerids, and eurypharyngids. Contrasting the case for centrolophids, the latter taxa were nearly absent in the upper mesopelagic zone represented by cluster C, but well present in clusters F and B (ridge and deep), and in cluster A (deep). In both analyses, *Scopelogadus beanii* (Melamphaidae) and *Serrivomer beanii* (Serrivomeridae) increased in abundance over MAR habitats. This was especially the case for cluster F. The increase of dominance for taxa of the fourth type over MAR with regard to the increased abundance data given in Table 2 is likely to affect the ecological function of this assemblage and must be regarded as adaptation to specific features of the MAR environment.

Discussion

Deep hauls from non-closing devices suffer from contamination with shallower living specimens. However, due to careful retrieval of nets contamination is likely to be of minor importance for consolidating species, since these deliver major contributions to cluster characteristics. Hence, contamination should be evident among the discriminating species. Especially species with minute abundances like *Diaphus rafinesquii* and *Bolinichthys supralateralis* in cluster A compared to cluster B (same latitude but a difference of 1000 m in mean catching depth, Tab. 3) with 0.33 n h⁻¹ trawling are candidates for indicating contamination with shallow living species in the deep hauls of cluster A. In turn, species with zero abundances and abundant species are

reasonable candidates for serious discrimination. Further, contamination is of minor importance in terms of discrimination as far as latitudinal gradients are considered. For instance, *Benthoosema glaciale* is a good discriminator between clusters A and F, although its abundance is minute in cluster A (1.00 n h⁻¹ trawling, likewise 5.5 n h⁻¹ trawling in cluster B) compared to F (195.68 n h⁻¹ trawling), and thus probably subjected to contamination. However, the quintessence of the comparison is reliable, i.e. that of a southern limit for *B. glaciale* with respect to cluster F.

As mentioned before, two types of analyses with fairly comparable results were conducted, i.e. an analysis with standardised data and an analysis with root-root transformed data. The only major difference between the analyses concerned the affiliation of the abyssopelagic samples. For standardised data, one abyssopelagic assemblage was obtained with a mean sampling depth of 2872 m comprising deep hauls from cluster A and cluster F as well. The cluster was evenly distributed on the parallels and the transverse. This cluster comprised the highest standardised number of species (ES250=41.8) and the lowest numbers of standardised specimens (1129 per hour trawling). *Gonostoma bathyphilum* was the prominent consolidating species with a share of 36.14 % of abundance and 51.7 % of overall similarity. Thus, the analysis of standardised data showed that one abyssopelagic assemblage was present in the whole investigation area. In the analysis of root-root transformed data, this cluster split up in a remaining cluster A with low abundance, and a high abundance assemblage joined under cluster F. In turn, composition on family level for both clusters A and F appeared to be very similar (Table 4). Krefft (1976) suggested that abyssopelagic communities should be widespread, probably on oceanic scale, which refers to the distribution of this cluster in the analysis of standardised data. The analysis of root-root transformed data then either revealed the influence of the Mediterranean Sea Outflow water with its low oxygen saturation and thus presumably lowered fish abundance, or in turn showed that over the ridge and the northern parallel due to specific processes abundance

increased considerably. Below, we will discuss a probable decrease for *G. bathyphilum* in relation to the lowered oxygen content. In turn, Kinzer et al. (1993) showed that pelagic fishes frequented the oxygen minimum zone in the Arabian Sea during their diel vertical migration. Compared to the Arabian Sea (< 0.2 ml/l), the oxygen concentration in the deep NE Atlantic (> 4 ml/l) still is moderate (according to WOA98 data at 1000 m), so that we suggest that the general increase of abundance over the ridge associated with cluster F reflects ridge specific processes.

Relationships between MAR environments, continental slopes and fish assemblages

The distribution of assemblages fairly followed the distribution of characteristics of the oceanic surface layer as indicated by SST and surface chlorophyll (Fig.1, Fig. 5). Thus, the correspondence between WOA98 data, shipborne measurements and the distribution of fish assemblages facilitates interpretation of community structure with respect to environmental factors. The analysis was capable of resolving the frontal systems f1, f3, f4 and f5.

Since the relationships to water mass characteristics hold for meso- as well as for bathy- and partly also for abyssopelagic assemblages, it is not likely that the fronts are confined to the sea surface alone, but also reflect deep water processes and that these processes were persistent. With respect to MAF and SSAF, frontal systems are to some extent determined by topography, so that anomalous topography may 'precondition' up- and downwelling (DiBatista, Maida et al. 2002). Actually, recent current measurements revealed a set of cyclonic / anticyclonic mesoscale eddies associated with MAF and a cyclonic eddy associated with SSAF (Fig. 2 in Lavender, Davis et al. 2000). However, it is unknown whether these eddies are stable. On the northern hemisphere, anticyclonic eddies cause downwelling, whereas cyclonic eddies induce upwelling. Thus, it is likely that upwelling was associated with the frontal systems in 1982 and downwelling with the central basin (i.e. PAP in Fig. 1). As a corollary of the link between topography and frontal

systems, there is a logical chain between topography, frontal systems and pelagic fish fauna. The multi-year composite satellite image (Fig. 5 B) indicates that surface features of these frontal systems were persistent with time. The temporal and spatial stability of current systems observed in the eastern North Atlantic (> 100 days and 80-160 km, see Losee, Richter et al. 1989; LeTraon 1991) is a necessary requisite for assemblages of all bathymetric zones to align themselves to surface features. West of MAR, spatio-temporal scales are much shorter (much variability within 2-3 km, see Losee, Richter et al. 1989). Particle flux from the surface down to 3200 m in the comparably stable Sargasso Sea takes about 30 days (Deuser 1986), so that actually the time scales in the eastern North Atlantic allow for a coupling between surface features and abyssopelagic assemblages.

Three assemblages fall into the category of being topography influenced, i.e. clusters D, E and F. Assemblage D found its western limit in f3 and was mainly associated with f4, a homogeneous silicate rich water body with an influence of the upwelled Antarctic Intermediate Water. As for the Rockall Trough (Hulley 1992), *Notoscopelus kroeyeri* was the dominant species there, more abundant in cluster D than in cluster E (Table 5). A link between cluster D and the Rockall Bank area was established via the frontal system f4 which presumably was originated in the Rockall area (Fig. 5 A). State of the art of hydrography endorses the statement that cluster D was related to the Rockall Trough fauna since a southward current is indicated at Rockall Bank, i.e. the western trough side, whereas the eastern side is characterised by the northward shelf edge current (see f5) (Fig. 8 in Mauchline 1986).

Assemblage E was linked to the shelf edge (Fig. 4). This hypothesis is supported by the presence of the gadid *Micromesistius poutassou* (Table 5), a mesopelagic dweller over depths of 400 to 3000 m and benthopelagic at depths < 400 m (after Gordon 1986; Svetovidov 1986; Merrett, Gordon et al. 1991). According to Gerber (1993), the area of the continental shelf from 45 °N to

55°N represented by cluster E is the characteristic distribution area for juvenile blue whittings. Fish lengths of 68 to 138 mm caught during the Walther Herwig cruise 52 indicate juvenile specimens and support this finding. Consolidating myctophids for cluster E (*L. crocodilus*, *Lobianchia gemmellarii*, *B. glaciale*) and *Myctophum punctatum*, which was a discriminating species with respect to the southern cluster B, were the same as for mesopelagic slope habitats in the Rockall Trough down to 400 m (Hulley 1992). A comparison with the spring assemblage from stations fished by Roe and Badcock (1984, crossed circle in Fig. 1) shows that the same type of habitat was addressed as for cluster E, i.e. habitats in conjunction with the continental slope comparable to stations 400 to 403 in this study. *Benthosema glaciale* was the predominant myctophid there (Roe and Badcock 1984). This southward shift for this species was linked to springtime hydrography in the respective area which was characterised by a southward shift of a thermohaline front associated with the North Atlantic Current and the eastern subtropical gyre, which moves to the North in summer (Roe, Angel et al. 1984). Further characteristics were the typical dominance of myctophids and sternoptychids (see Table 6), partly consisting of the same species as in cluster E. Another feature in common with Roe and Badcock (1984) was the high abundance of the alepocephalid *Xenodermichthys copei* in both assemblages. Due to its reproduction biology with the positioning of benthic eggs, *X. copei* is associated to continental slopes (Markle and Quero 1986).

The analysis revealed a certain assemblage concentrated over the ridge, i.e. cluster F. This cluster was characterised by an increase of abundance for Melamphaidae, Serrivomeridae, Eurypharyngidae and Stomiidae. In the first line, this group was characteristic for bathy- and abyssopelagic faunas as verified for cluster A. Over the ridge, the depth extension for this group was elevated to 700 m in cluster B and 900 m in F. In particular, Centrolophidae increased over MAR (clusters C and F, Table 4). Melamphaidae are to some degree feeding on gelatinous

plankton (Gartner and Musick 1989), which is the same as for Centrolophidae, i.e. *Schedophilus medusophagus* (Macpherson and Roel 1987). In turn, Serrivomeridae are facultatively and Stomiidae obligatorily piscivorous. This indicates a considerable shift in prey utilisation in the abysso-, bathy- and the mesopelagic fish fauna associated with the ridge and highlights changes in community composition and function with respect to micronekton and especially to gelatinous plankton. According to Williams and Koslow (1997), gelatinous plankton accounted for 60 % of total pelagic biomass in the shelf area off Tasmania. Angel and Baker (1982) showed, that below 2500 m medusae and siphonophores constituted a major and considerable component of the zooplankton in the NE Atlantic. Over the ridge, due to upwelling of deep-water populations or as a response to increased production, gelatinous plankton abundance may increase. Own unpublished data (Fock & Pusch, unpubl.) support this, indicating that the gelatinous plankton-micronekton fish biomass ratio in mesopelagic trawls was higher for North Atlantic mid-latitude seamount habitats (on average > 1 with a range of 0.02 to 79) than for oceanic habitats (on average < 1 with a range of 0.12 to 1.0). Correspondingly, Biggs et al. (1981) found an increase of gelatinous plankton in the NE Atlantic from 18 °W to 36 °W associated with ridge habitats.

A further modification of food web structure appears with respect to interactions with benthopelagic predators in cluster F. *Serrivomer beanii* (Serrivomeridae) and *Scopelogadus beanii* (Melamphaidae) are subjected to predation by roundfish (rattail: Haedrich and Henderson 1974; cod : Casas and Paz 1996). The former suggested that larger rattails leave the bottom habitats and advance their prey in the water column. During the cruise, the only four specimens of *Coryphaenoides rupestris* were caught on stations 381 to 388 over the ridge, supporting the view that over MAR their presence was correlated with some of their prey items, i.e. *Chauliodus* sp. (Stomiidae) and *Serrivomer beanii*. Similarly, Parin and Prutko (1985) found an increase of pelagic predators associated with an increase of prey over a Pacific seamount.

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Figures Captions

Figure 1:

Trawling stations, topography and location of fronts. Frontal systems as indicated by the literature: Position of Azores Front (AF) after Gould (1985), Mid-Atlantic Front (MAF) and Southern Sub-Polar Front (SSAF) after Caniaux et al. (2001). Fronts as indicated by shipborne measures of surface salinity and temperature in 1982 denominated f1,..., f5 and schematically shown by bold lines. The crossed circle indicates a reference station from Roe et al. (1984). Station labels arranged in offset order to preserve readability.

PAP – Porcupine-Abyssal Plain, IAP – Ibero-Abyssal Plain, NB – Newfoundland Basin, mar – Mid-Atlantic Ridge, abr – Azores-Biscay Rise. Depth contours at 3000 m and 4000 m.

Figure 2:

Approximate spatial distribution of SST anomalies in June 1982 with (A) negative, and (B) positive anomalies [in °C]. Anomalies calculated after $COADS_{June82}$ minus $WOA98_{June}$.

Fig. 3:

Temperature-temperature and temperature-chlorophyll plots: (A) Observed, i.e. shipborne measurements versus output data from WOA98, COADS and Reynolds data models, (B) relationship between temperature T50 and chlorophyll at different depths in the investigation area based on WOA98 data. The apparent relationship between T50 and Chl0 in figure B was applied to derive corrected chlorophyll estimates for shipborne T0 values. Parameter digits indicate water depth, Chl – chlorophyll, T – water temperature.

Fig. 4 : Distributions of clusters representing fish assemblages. For convenience stations partly written in juxtaposition and separated by comma. Fairly homogenous groups emphasised by differential shading.

Fig. 5 : CZCS-remote sensing images of chlorophyll distributions in the North Atlantic: (A) spring 1982 (April-May-June), (B) climatological spring image 1978 to 1986. In A, tentative frontal positions in 1982 indicated by lines and numbers f1 to f5. In B, frontal positions from A superimposed on composite image 1978-1986 in order to display similarity between frontal distribution patterns in A and B. MAF – Mid-Atlantic Front. f1 to f5 – frontal zones as defined in the text. Vertical lines at 15 °W and 30 °W, horizontal line at 50 °N. Chlorophyll colour scale from deep violet ($< 0.1 \text{ mg Chl / m}^3$) to red (about 10 mg / m^3).

Table 1 : Station data for the RV 'Walther Herwig' cruise 52, June 5-20, 1982, shipborne oceanographical measurements and cluster affiliation.

‡ Dawn (M) from beginning of nautical twilight to sunrise + 1 h, D – day, meteorological data from the U.S. Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil/data/docs/RS_OneYear.html). * Shipborne measurements, not recorded at all stations, # values duplicated due to nearly same position. † - ref. to Fig. 4.

Station	Bottom depth [m]	Catching depth [m]	Position North [°]	Position [°]	East Start haul [Winch arrested]	of End of [Start heaving]	haul Daytime of classification‡	Surface temperature* [°C]	Surface salinity* [ppt]	Affiliation to clusters †
WH331	4100	1800	45.21	346.58	15:45	16:45	D	14.82	35.6	A
WH335	3600	2250	45.17	344.375	7:20	8:20	D	14.31	35.62	A
WH336	4700	3200	45.06	343.87	13:30	14:30	D			A
WH343	4500	3200	44.25	340.24	7:00	8:00	D	14.38	35.71	B
WH344	4000	1100	44.20	339.91	13:07	13:37	D			B
WH345	4100	800	44.14	339.74	15:15	15:45	D			B
WH359	3100	1230	43.36	333.99	8:40	9:10	D	14.69	35.79	B
WH360	3000	2600	43.23	333.74	13:25	13:55	D	14.7	35.79	B
WH369	2400	700	43.62	331.43	14:45	15:15	D	14.9	35.87	B
WH370	2200	1550	43.71	331.55	16:45	17:25	D			B
WH375	2500	900	45.39	332.175	8:50	9:20	D	13.45	35.67	F
WH377	3400	3200	45.67	332.20	11:50	12:21	D			F
WH378	2550	250	46.49	332.74	5:25	5:55	M	13.16	35.61	C
WH380	3200	2800	47.06	332.67	15:40	16:10	D			F
WH381	3500	250	47.42	332.65	5:15	5:50	M	14.56	35.65	C
WH383	1875	1370	47.89	332.83	15:40	16:20	D	14.56	35.65	F
WH384	3350	3200	48.16	332.20	7:15	7:45	D	13.36	35.59	F
WH385	2000	1000	48.595	332.35	15:10	15:40	D			F
WH387	4300	3200	49.80	331.26	7:25	7:55	D	12.4	35.33	F
WH388	3100	900	49.955	331.16	15:10	15:40	D			D
WH390	3800	500	49.81	333.48	5:20	5:50	M	13.2	35.4	D
WH391	4200	3200	49.83	333.57	8:30	9:00	D	13.2	35.46	F
WH392	4200	1000	49.80	334.11	14:10	14:40	D	13.2#	35.46#	D
WH393	4050	460	49.78	336.52	4:30	4:45	M	13.2	35.35	D
WH394	4125	3200	49.81	336.70	7:25	7:55	D	13.2#	35.35#	F
WH396	4100	870	49.70	337.03	13:10	13:25	D			D
WH397	3500	3200	49.93	339.655	7:20	7:40	D	13.3	35.48	F
WH399	4400	800	49.99	339.90	13:10	13:25	D			D
WH400	4800	480	49.83	343.055	4:30	4:45	M	13.9	35.45	E
WH401	4800	3200	49.87	343.16	7:20	7:50	D	13.9#	35.45#	F
WH402	4750	950	49.94	343.53	13:10	13:25	D			D
WH403	3850	500	49.78	346.13	3:30	3:45	M	14.5	35.36	E

Table 2 : Cluster statistics and six top ranking consolidating species for each cluster.

For distribution of clusters see Fig. 4 C. Ordered measures for clusters indicate average / minimum / maximum value, respectively. Ordered measures for consolidating species indicate average abundance per 1 hour trawling and percentage by similarity contributed by the species (in brackets).

Cluster	A	B	C	D	D	E	F
Bottom depth (m)	4133 / 3600 / 4700	3328 / 2200 / 4500	3025 / 2550 / 3500	4110 / 3100 / 4750	3925 / 3800 / 4050	4325 / 3850 / 4800	3386 / 1875 / 4800
Catching depth (m)	2416 / 1800 / 3200	1597 / 700 / 3200	250 / 250 / 250	904 / 800 / 1000	480 / 460 / 500	490 / 480 / 500	2588 / 900 / 3200
Time of day	DAY	DAY	DAWN	DAY	DAWN	DAWN	DAY
Species caught S (n haul ⁻¹)	47.7 / 39 / 53	59.6 / 44 / 78	23 / 20 / 26	52 / 46 / 61	50 / 48 / 52	41 / 37 / 45	64.4 / 48 / 72
Individuals caught (n haul ⁻¹)	294.7 / 274 / 315	530 / 324 / 739	649 / 347 / 951	1082.2 / 399 / 2641	1783 / 918 / 2648	396 / 335 / 457	1154 / 636 / 2203
Individuals caught (n h ⁻¹ trawling)	294.7 / 274 / 315	926 / 592 / 1478	1248 / 594 / 1902	2698 / 1596 / 5282	4484 / 3672 / 5296	1584 / 1340 / 1828	2323 / 1242 / 4406
Estimated S (ES250)	44.3 / 34.9 / 49.1	46.4 / 36.2 / 54.5	19.0 / 18.2 / 19.9	35.3 / 29.8 / 40.5	28.1 / 27.3 / 28.9	34.8 / 34.4 / 35.3	38.4 / 27.7 / 46.5
H ₁₀ [']	1.07 / 0.76 / 1.23	1.39 / 1.19 / 1.54	0.89 / 0.81 / 0.98	1.17 / 1.10 / 1.27	1.10 / 1.06 / 1.14	1.23 / 1.21 / 1.25	1.22 / 0.95 / 1.43
N2	5.01 / 2.28 / 6.97	14.56 / 5.90 / 21.29	4.57 / 3.61 / 5.52	8.32 / 6.86 / 11.00	7.46 / 6.07 / 8.83	10.47 / 9.75 / 11.19	9.49 / 4.11 / 15.65
Consolidating species	<i>Gonostoma bathyphilum</i> 140.33 (9.29 %) <i>Poromitra crassiceps</i> 12.33 (5.13 %) <i>Argyropelecus olfersi</i> 9.33 (4.48 %) <i>Eurypharynx pelecانoides</i> 6.33 (4.47 %) <i>Electrona risso</i> 6.0 (4.31 %) <i>Lampanyctus crocodilus</i> 7.33 (3.85 %)	<i>Electrona risso</i> 85.4 (5.12 %) <i>Diaphus rafinesquii</i> 59.93 (4.18 %) <i>Lobianchia gemellarii</i> 49.00 (4.09 %) <i>Argyropelecus olfersi</i> 23.29 (3.78 %) <i>Lampanyctus crocodilus</i> 23.86 (3.71 %) <i>Diaphus holti</i> 39.64 (3.45 %) <i>Ceratoscopelus maderensis</i> 54.57 (3.20 %)	<i>Diaphus rafinesquii</i> 505.71 (13.72 %) □ <i>Chauliodus sloani</i> 71.71 (9.08 %) □ <i>Benthosema glaciale</i> 71.29 (7.93 %) □ <i>Symbolophorus veranyi</i> 67.29 (7.93 %) □ <i>Diaphus holti</i> 96.86 (7.48 %) □	<i>Benthosema glaciale</i> 631.1 (6.05 %) <i>Stomias boia ferox</i> 309.43 (5.84 %) <i>Chauliodus sloani</i> 248.29 (4.98 %) <i>Electrona risso</i> 214.57 (4.14 %) <i>Lampanyctus crocodilus</i> 104.29 (4.14 %) <i>Mauroliscus muelleri</i> 385.43 (4.06 %)		<i>Lampanyctus crocodilus</i> 314.0 (7.34 %) <i>Lobianchia gemellarii</i> 222.0 (6.70 %) <i>Argyropelecus hemigymnus</i> 92.0 (5.45 %) <i>Argyropelecus olfersi</i> 84.0 (5.38 %) <i>Nansenia</i> sp. 96.0 (5.17 %)	<i>Stomias boia ferox</i> 165.43 (4.21 %) <i>Gonostoma bathyphilum</i> 390.63 (3.92 %) <i>Scopelogadus beanii</i> 102.15 (3.71 %) <i>Benthosema glaciale</i> 195.68 (3.46 %) <i>Lampanyctus crocodilus</i> 68.44 (3.41 %) <i>Chauliodus sloani</i> 170.05 (3.28 %) <i>Serrivomer beanii</i> 63.48 (3.27 %)

Table 3 : Discriminating species for between-cluster differences. Only cluster pairs with significant differences according to ANOSIM considered. For each species, average abundance in first cluster (rows) and second cluster (columns) and contribution to overall dissimilarity is listed. Abundance in specimens per hour trawling.

First cluster ↓	Second cluster→					C	D	E	F																
	B																								
	species / 1 st abund. / 2 nd abund. / % dissim.					species / 1 st abund. / 2 nd abund. / % dissim.	species / 1 st abund. / 2 nd abund. / % dissim.	species / 1 st abund. / 2 nd abund. / % dissim.	species / 1 st abund. / 2 nd abund. / % dissim.																
A	Diaphus rafinesquii	0.33	59.93	2.48		n.s.	Benthosema glaciale	1.00	631.14	3.97	n.s.	Benthosema glaciale	1.00	195.68	2.72										
	Sternopyx diaphana	0	20.43	2.16			Mauroliscus muelleri	0	385.43	3.43			Scopelogadus beanii	1.00	102.15	2.28									
	Symbolophorus veranyi	0	29.29	2.13			Gonostoma bathyphilum	140.33	2.29	2.92			Stomias boaferox	5.33	165.43	2.25									
	Gonostoma denudatum	0	10.64	1.91			Stomias boaferox	5.33	309.43	2.81			Chauliodus sloani	7.33	170.05	2.07									
	Diaphus metapoclampus	0	12.71	1.88			Notoscopelus kroeyeri	0	117.71	2.67			Diaphus rafinesquii	0.33	52.89	2.03									
	Gonostoma bathyphilum	140.33	88.36	1.67			Chauliodus sloani	7.33	248.29	2.37			Schedophilus medusophagus	0.67	143.38	1.89									
	Hygophum benoitii	0	12.00	1.63			Symbolophorus veranyi	0	99.43	2.31			Lampanyctus macdonaldi	0.67	52.09	1.86									
	Electrona risso	6.00	85.43	1.57			Nansenia sp.	2.67	277.71	2.02			Symbolophorus veranyi	0	15.12	1.73									
	Ceratoscopelus maderensis	1.33	54.57	1.56			Diaphus rafinesquii	0.33	68.57	1.96			Nansenia sp.	2.67	218.41	1.69									
	Diaphus holti	3.33	39.64	1.50			Sagamichthys schnakenbecki	0	19.14	1.85			Bathylagus sp1	0.67	25.84	1.60									
	Poromitra crassiceps	12.33	5.57	1.49									Gonostoma bathyphilum	140.3	390.63	1.47									
	Chauliodus sloani	7.33	42.50	1.43									Lampadena speculigera	0	6.26	1.39									
	Bolinichthys supralateralis	0.33	5.79	1.28									Sagamichthys schnakenbecki	0	9.50	1.38									
	Poromitra capito	3.33	21.50	1.24									Serrivomer beanii	5.0	63.48	1.25									
	Scopelogadus beanii	1.00	19.50	1.14																					
B						Lampanyctus crocodilus	23.86	0	2.57		Mauroliscus muelleri	0	385.43	3.32		Gonostoma bathyphilum	88.36	390.63	2.17						
							88.36	0	2.52		Benthosema glaciale	5.50	631.14	3.20		Benthosema glaciale	5.50	195.68	2.0						
						Gonostoma bathyphilum																			
						Diaphus rafinesquii	59.93	505.71	2.34		Stomias boaferox	7.36	309.43	2.47		Gonostoma bathyphilum	88.36	0	2.11	Lampanyctus macdonaldi	0	52.09	2.00		
						Diaphus metapoclampus	12.71	0	2.06		Notoscopelus kroeyeri	2.57	117.71	2.07		Lampanyctus crocodilus	23.86	314	1.98	Stomias boaferox	7.36	165.43	1.91		
						Schedophilus medusophagus	11.43	104.86	2.05		Nansenia sp.	2.71	277.71	2.06		Myctophum punctatum	1.43	36	1.94	Poromitra crassiceps	5.57	51.68	1.68		
						Benthosema glaciale	5.50	71.29	1.94		Myctophum punctatum	1.43	49.14	2.04		Serrivomer beanii	29.36	0	1.94	Nansenia sp.	2.71	218.41	1.67		
						Serrivomer beanii	29.36	0.86	1.82		Lampanyctus macdonaldi	0	47.71	1.85		Micromesistius poutassou	0	14	1.87	Scopelogadus beanii	19.50	102.15	1.65		
						Bolinichthys supralateralis	5.79	0	1.78		Gonostoma bathyphilum	88.4	2.29	1.84		Diaphus metapoclampus	12.71	0	1.72	Borostomias antarcticus	0.14	17.86	1.60		
						Eurypharynx pelecanoides	16.07	0	1.72		Gonostoma denudatum	10.6	0	1.60		Sagamichthys schnakenbecki	1.86	30	1.67	Schedophilus medusophagus	11.43	143.38	1.53		
						Lestidiops similis	0	43.00	1.65		Sternopyx diaphana	20.4	0.86	1.50		Protomyctophum arcticum	0.00	6	1.51	Bathylagus sp1	1.50	25.84	1.45		
						Sternopyx diaphana	20.43	0.86	1.64		Chauliodus sloani	42.5	248.29	1.44		Hygophum benoitii	12.00	0	1.49	Chauliodus sloani	42.50	170.05	1.38		
						Poromitra capito	21.50	1.0	1.62		Bolinichthys supralateralis	5.79	0	1.35		Bolinichthys supralateralis	5.79	0	1.48	Hygophum benoitii	12.00	0.18	1.34		
						Opisthoproctus soleatus	6.07	0	1.56		Poromitra capito	21.5	9.71	1.32		Ceratoscopelus maderensis	54.57	8	1.46	Maulisia microlepis	1.29	22.41	1.33		
											Sagamichthys schnakenbecki	1.86	19.14	1.28		Eurypharynx pelecanoides	16.07	0	1.45	Myctophum punctatum	1.43	8.94	1.21		
C																	Bolinichthys supralateralis	5.79	0.90	1.20	Eurypharynx pelecanoides	16.07	42.95	1.10	
D																									
E																									

Table 4 : Percentage by abundance on family level for MAR fish assemblages. Part A without *Cyclothone* spp., part B also considering *Cyclothone* spp. relative to data from part A. Groups A.1 to A.4 consider characteristic taxa for each cluster. A.5 represents miscellaneous taxa. For details see text.

* Abundances are estimates.

Cluster	A	B	C	D	E	F
A. Relative abundances excluding <i>Cyclothone</i> spp.						
1.						
Gonostomatidae	47.81	11.27	0.32	0.18	0.38	17.77
2.						
Myctophidae	11.36	45.36	66.16	47.30	60.33	24.45
Sternoptychidae	4.16	7.59	9.90	14.38	12.47	3.71
3.						
Stomiidae	8.66	11.97	7.89	18.62	8.31	17.23
Microstomatidae	0.90	0.29	1.76	8.65	6.05	9.41
4.						
Centrolophidae	0.22	1.54	8.40	0.68	0.00	6.15
Melamphaidae	6.19	6.55	0.08	1.60	1.39	7.25
Serrivomeridae	2.14	3.52	0.07	1.32		2.77
Eurypharyngidae	2.14	1.73		0.02		1.85
5.						
Alepocephalidae	1.91	0.75		0.05	1.89	0.30
Bathylagidae	3.04	0.47		1.11	1.64	1.35
Chiasmodontidae	1.46	0.61		0.24	0.38	0.63
Derichthyidae	0.22	0.08		0.18	0.63	0.23
Nemichthyidae	0.34	0.59		0.36		0.19
Oneirodidae	0.56	0.54		0.04		0.38
Opisthoproctidae	0.56	0.75		0.05	0.76	0.10
Paralepididae	1.35	1.37	3.61	1.08	0.76	1.18
Percichthyidae	0.11	0.12		0.24	0.13	0.25
Platyroctidae	3.37	1.43	0.08	2.78	2.27	3.09
Trachipteridae	0.90	0.44	0.61	0.21	0.25	0.26
B. Relative abundance of <i>Cyclothone</i> spp. relative to data from A :						
<i>Cyclothone</i> spp.*	10.02	3.25		47.09		79.36

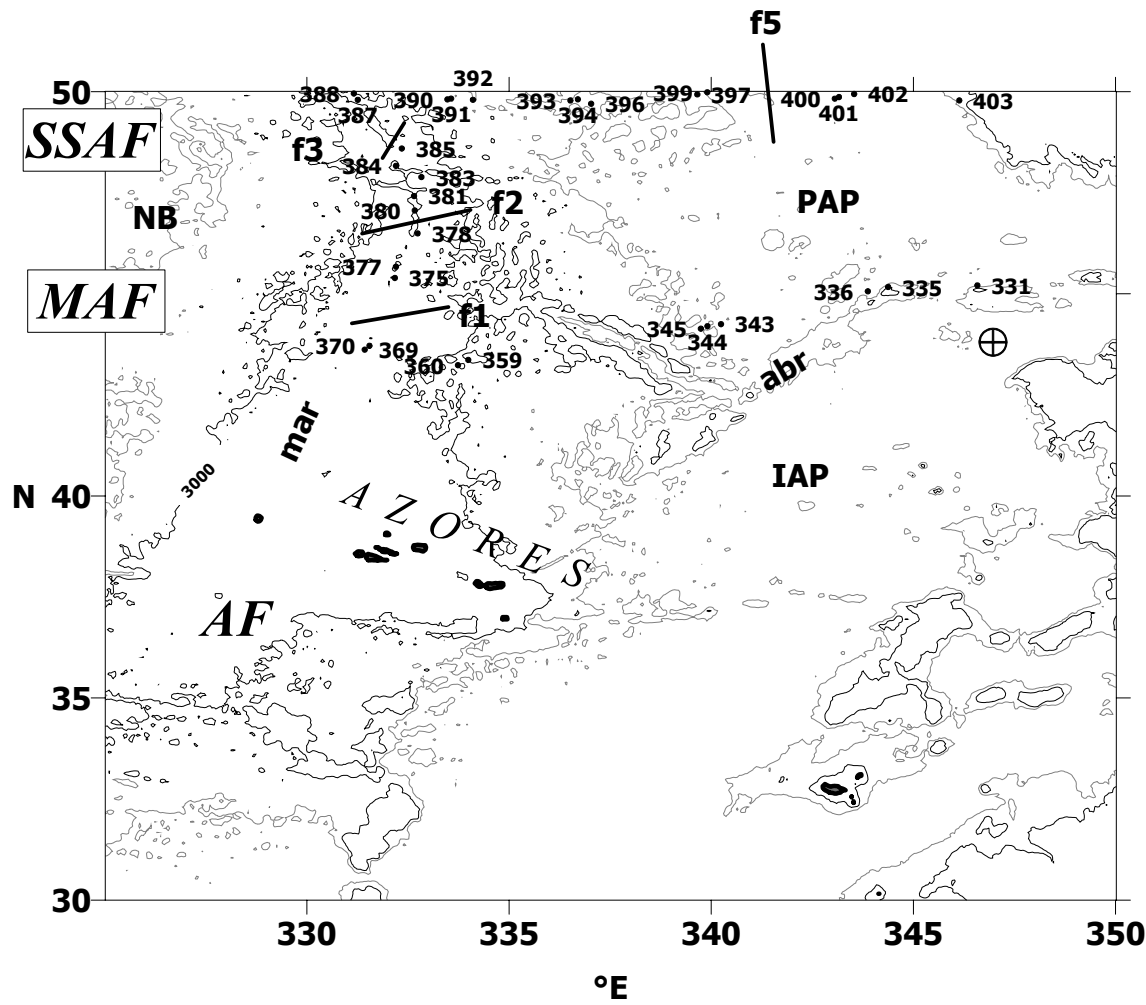


FIGURE 1

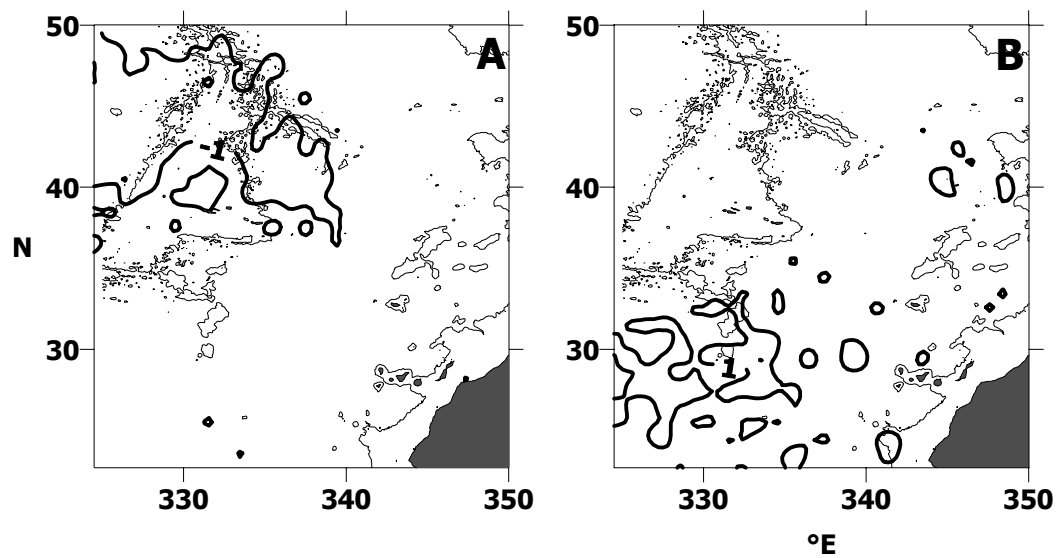


FIGURE 2

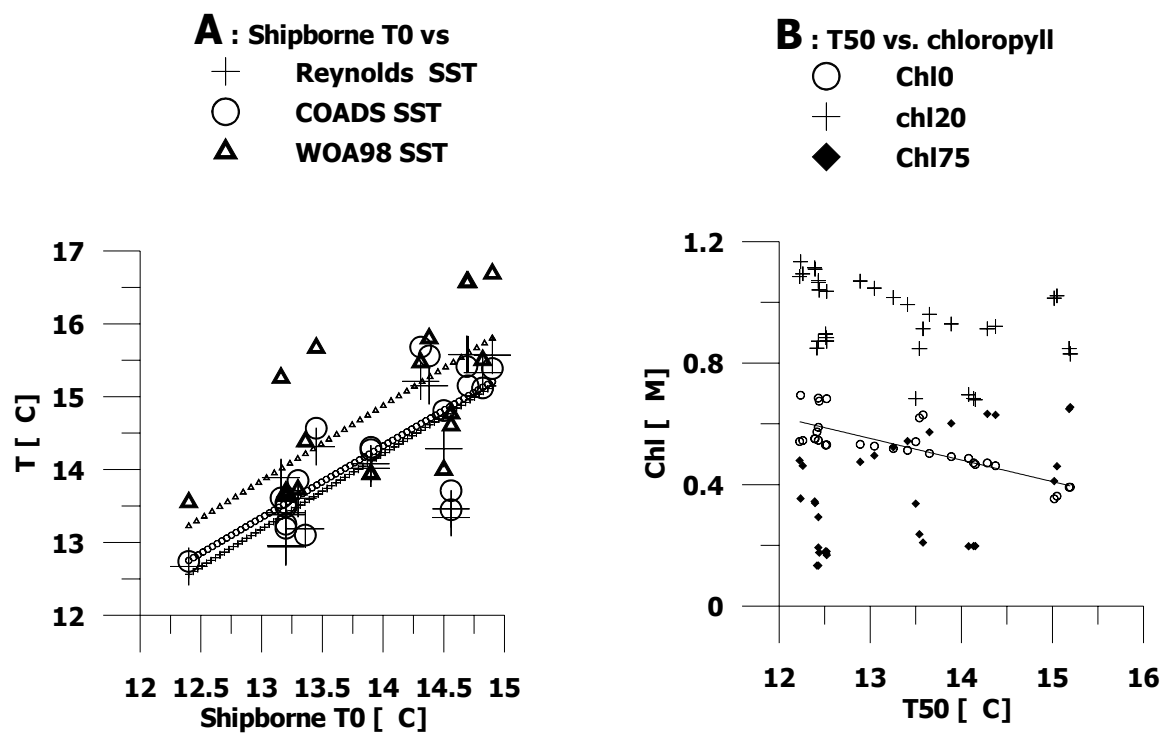


FIGURE 3

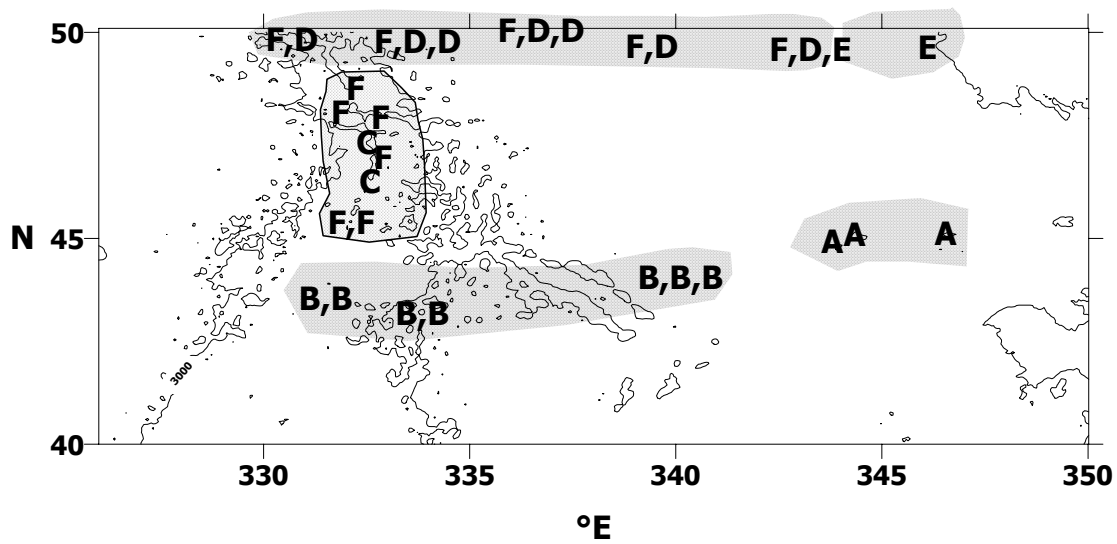


FIGURE 4

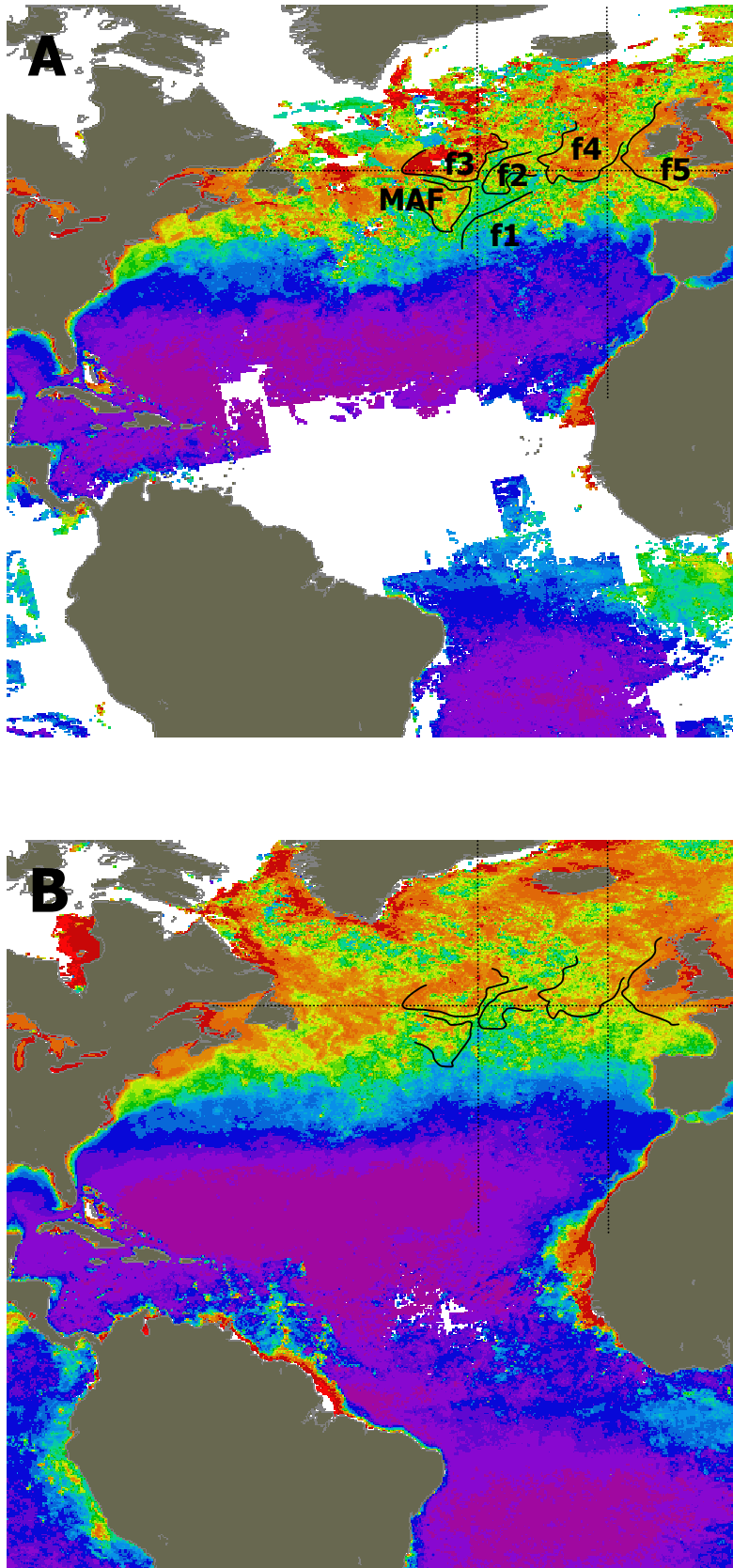


FIGURE 5