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# Structure of deep-sea pelagic fish assemblages in relation to the Mid-Atlantic Ridge (45°–50°N)

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## Abstract

Pelagic fishes from depths of 250 to 3200 m from 45°N to 50°N were sampled during a mid-Atlantic cruise in 1982. These clustered into 6 assemblages, which were related to the Mid-Atlantic Ridge, the continental shelf edge and oceanic habitats. Spatial distribution of clusters coincided with SST and surface chlorophyll patterns. Cluster distribution further coincided with published mid-depth hydrography indicating that hydrographic recirculation features were an important determinant of community structure. Over the ridge, Melamphaidae, Serrivomeridae, Stomiidae and Centrolophidae increased in abundance. Horizontally, the myctophid *Benthosema glaciale* indicated the transition from temperate-subtropical to temperate-subarctic waters. The gadid *Micromesistius poutassou* and the alepocephalid *Xenodermichthys copei* were characteristic species for the shallow shelf edge assemblage. Vertically, extended depth ranges were stated for assemblages above MAR and the southern leg, as indicated for the species *Gonostoma bathyphilum*, and *Schedophilus medusophagus*. This was further tested for the saccopharyngid *Saccopharynx ampullaceus*. The increase of gelatinous plankton feeders over the ridge, in particular for *S. medusophagus*, is discussed with respect to a probable increase of gelatinous plankton abundance in the area considered. An error model was developed to address the contamination problem with respect to non-closing devices.

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**Keywords:** North Atlantic; Mesopelagic zone; Bathypelagic zone; Abyssopelagic zone; Recirculation

## 1. Introduction

As part of the ‘western transition zones’ (Olson, 2001), the Mid-Atlantic Ridge (MAR) at 45–50°N is located at the latitudinal boundary between

temperate and subarctic waters. Notwithstanding investigations on bottom fishes at MAR (Vinnichenko et al., 1994; Vinnichenko, 1998; Hareide and Garnes, 2001), hitherto no quantitative investigations have been carried out for pelagic fishes (albeit qualitatively: Kukuev et al., 2000).

For pelagic fish communities off MAR, pioneering investigations have focussed either on local

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process studies (Badcock and Merrett, 1976; Roe et al., 1984; Roe and Badcock, 1984) or on species distributions (e.g. Krefft, 1974; 1976; Hulley, 1981). In the western North Atlantic, Gulf Stream and Sargasso Sea environments have been investigated (Backus et al., 1970; Jahn and Backus, 1976; Backus and Craddock, 1982; Boyd et al., 1986; Conte et al., 1986). East of MAR at 20°W, oceanographic investigations have been carried out within the Atlantic Meridional Transect program (Badcock and Merrett, 1977; Aiken and Bale, 2000). Shelf edge fish assemblages have been studied at Rockall Trough and Porcupine Bank with regard to pelagic and benthopelagic fishes (Gordon and Duncan, 1985; Merrett et al., 1986; 1991; Gordon and Bergstad, 1992; Hulley, 1992; Hillgruber and Kloppmann, 2000) and interactions between them (Mauchline and Gordon, 1983; 1984; 1991).

Distribution boundaries for pelagic animals usually coincide with zones of marked change in the physical and chemical properties of the water (Jahn and Backus, 1976). The basic zoogeographical methodology is to define categories linked to water masses and coastal affiliation (Backus et al., 1970; Backus et al., 1977; Figueroa et al., 1998). Amongst others, oxygen concentration, water density and timing and quality of production were considered essential determinants for fish distribution (Badcock and Merrett, 1976; Krefft, 1976). In the eastern North Atlantic, fish populations from subtropical and temperate waters are generally transported northwards, where boundaries are set up by secondary subpolar fronts at > 50°N (Krefft, 1976). Oxygen-depleted Mediterranean water is encountered in the northeastern Atlantic. John and co-workers (John and Zelck, 1998b; John et al., 2001) suggested that distributions of fish larvae were affected by oxygen-depleted waters. However, for the Arabian Sea ambiguous effects were shown (Craddock and Haedrich, 1973; Kinzer et al., 1993; Butler et al., 2001). Over MAR, hotspots of increased primary production (Behrenfeld and Falkowski, 1997; Falkowski et al., 1998) and of unutilized, exported production (Eppley and Peterson, 1979) appear, which fuel deep-water trophic processes (see Merrett, 1987). After the grazing-down of the

surface spring bloom, subsurface chlorophyll maxima may develop, consisting of picophytoplankton (Longhurst, 1995; Falkowski et al., 1998). Longhurst (1995) gives a regional estimate of 13% of total primary production attributed to subsurface chlorophyll production in the North Atlantic Current province during summer (NADR province in Longhurst's terminology). A generally positive production-fish abundance link has been suggested (Falkowski et al., 1998).

Recognizing that MAR in the South Atlantic constitutes an ecosystem boundary for meso- and epipelagic assemblages (John and Zelck, 1998a), 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. Data diaries are accessible in the archives of the Federal Research Centre for Fisheries, Hamburg.

## 2. Materials and methods

### 2.1. Regional hydrography

MAR constitutes a significant longitudinal hydrographical boundary (e.g. Sy, 1988). Correspondingly, differences appear in the circulation patterns at either side of MAR (Bower et al., 2002). These are reflected by different kinetic energy spectra of the current systems, indicating a rapidly evolving system west of MAR and a slow system east of MAR (Losee et al., 1989; LeTraon, 1991).

West of MAR, due to interactions with near surface subpolar waters off Newfoundland (Labrador Current with Labrador Sea Water, LSW), the warmer North Atlantic Current (NAC) branches up into several eastward arms, which together determine a recirculation pattern west of MAR, i.e. the Newfoundland Basin Gyre, and the northern mid-latitude frontal systems, i.e. Mid-Atlantic Front (MAF) and the Southern Sub-Polar Front (SSAF, see Fig. 1, Schmitz and McCartney, 1993; Kearns and Rossby, 1998; Caniaux et al., 2001).

The eastern basins are fed by NAC-derived weaker currents bearing water from the lower

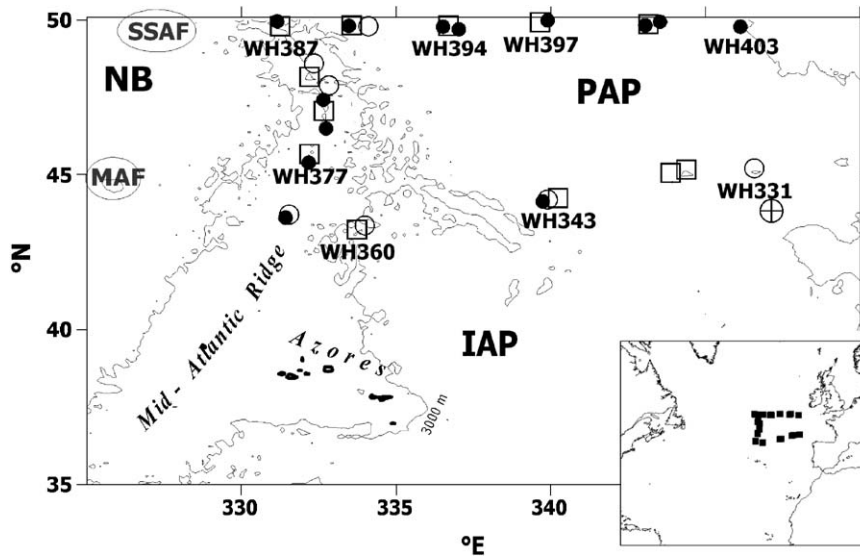


Fig. 1. Trawling stations, topography and location of fronts. Frontal systems as indicated by the literature: Position of Mid-Atlantic Front (MAF) and Southern Sub-Polar Front (SSAF) after Caniaux et al. (2001). Black dots indicate hauls < 1000 m depth, circles hauls from 1000 to 2000 m depth, and squares hauls > 2000 m. Station names at intervals, full account in Table 1. The encircled cross indicates a reference station from Roe et al. (1984). Insert picture shows position in North Atlantic. Topography and longitudinal scale obtained from [http://topex.ucsd.edu/marine\\_topo/mar\\_topo.html](http://topex.ucsd.edu/marine_topo/mar_topo.html). PAP—Porcupine Abyssal Plain, IAP—Ibero-Abyssal Plain, NB—Newfoundland Basin. Depth contour at 3000 m.

thermocline across MAR at a rate of app. < 5% of the total NAC flux (Schmitz and McCartney, 1993). In the intermediate layers (> 1000 m depth), Antarctic Intermediate Water (AIW) together with Mediterranean Outflow Water (MOW) entrain the area from the south (van Aken, 2000a). The influence of AIW south of Rockall Trough is evidenced by the proliferation of high silicate concentrations in northward deep and intermediate currents which upwell at the shelf edges of the Porcupine Bank and the Rockall Trough and thus supply the euphotic zone with silicate rich water (Schmitz and McCartney, 1993; Holliday et al., 2000). The deep water in the Porcupine Abyssal Plain eastward of MAR (PAP, see Fig. 1) is partly replenished from Labrador Deep Water flowing across the Gibbs–Fracture zone (52°N) and from the Iceland–Scotland Overflow Water (van Aken, 2000b). Over PAP, a counter-clockwise deep current mixes waters of southern and northern sources (Schmitz and McCartney, 1993).

## 2.2. Environmental data

As climatological reference data set on a  $1^\circ \times 1^\circ$  grid, four stratified parameters from the World Ocean Atlas 1998 at <http://www.ferret.noaa.gov/nopp/> (Conkright et al., 1998, hereafter WOA98) were analyzed by means of principal components analysis to define habitat types: temperature, chlorophyll, oxygen saturation and silicate, the last as proxy to indicate possible modifications in the composition of the phytoplankton, i.e. the diatom/flagellate ratio (Falkowski et al., 1998). Since primary production in the ocean is nutrient limited, chlorophyll is likely to represent the respective patterns for N,P-nutrients (Campbell and Aarup, 1992).

For the year 1982, together with shipborne surface salinity and temperature data (Table 1), Reynolds and COADS sea surface temperature (SST) time-series data were deployed (NOAA-CIRES 2000, <http://ferret.pmel.noaa.gov/NVODS>). Satellite images were digitized as retrospective

Table 1

Station data for the RV *Walther Herwig* cruise 52, June 5–20, 1982, shipborne oceanographical measurements and cluster affiliation

Station	Bottom depth (m)	Catching depth (m)	Position North (°)	Position East (°)	Start of haul (Winch arrested)	End of haul (Start of heaving)	Daytime classification <sup>b</sup>	Surface temperature <sup>a</sup> (°C)	Surface salinity <sup>a</sup> (ppt)	Affiliation to clusters			Raw S# <sup>c</sup>	Raw n# <sup>e</sup>
										original <sup>c</sup>	2%cont <sup>d</sup>	4%cont <sup>d</sup>		
WH331	4100	1800	45.21	346.58	15:45	16:45	D	14.82	35.6	A	A	A	53	295
WH335	3600	2250	45.17	344.375	7:20	8:20	D	14.31	35.62	A	A	A	39	315
WH336	4700	3200	45.06	343.87	13:30	14:30	D			A	A	A	51	274
WH343	4500	3200	44.25	340.24	7:00	8:00	D	14.38	35.71	B	B	-	64	592
WH344	4000	1100	44.20	339.91	13:07	13:37	D			B	B	B	50	324
WH345	4100	800	44.14	339.74	15:15	15:45	D			B	-	-	44	379
WH359	3100	1230	43.36	333.99	8:40	9:10	D	14.69	35.79	B	B	B	78	739
WH360	3000	2600	43.23	333.74	13:25	13:55	D	14.7	35.79	B	B	-	60	405
WH369	2400	700	43.62	331.43	14:45	15:15	D	14.9	35.87	B	-	-	46	578
WH370	2200	1550	43.71	331.55	16:45	17:25	D			B	B	B	75	694
WH375	2500	900	45.39	332.175	8:50	9:20	D	13.45	35.67	F	-	-	72	1425
WH377	3400	3200	45.67	332.20	11:50	12:21	D			F	F	F	65	1322
WH378	2550	250	46.49	332.74	5:25	5:55	M	13.16	35.61	C	C	C	26	951
WH380	3200	2800	47.06	332.67	15:40	16:10	D			F	F	F	72	959
WH381	3500	250	47.42	332.65	5:15	5:50	M	14.56	35.65	C	C	C	20	347
WH383	1875	1370	47.89	332.83	15:40	16:20	D	14.56	35.65	F	F	-	72	828
WH384	3350	3200	48.16	332.20	7:15	7:45	D	13.36	35.59	F	F	F	68	1179
WH385	2000	1000	48.595	332.35	15:10	15:40	D			F	-	-	69	1203
WH387	4300	3200	49.80	331.26	7:25	7:55	D	12.4	35.33	F	F	F	54	1254
WH388	3100	900	49.955	331.16	15:10	15:40	D			D	D	D	56	1436
WH390	3800	500	49.81	333.48	5:20	5:50	M	13.2	35.4	D	D	D	52	2648
WH391	4200	3200	49.83	333.57	8:30	9:00	D	13.2	35.46	F	F	F	63	2203
WH392	4200	1000	49.80	334.11	14:10	14:40	D			D	D	D	61	2641
WH393	4050	460	49.78	336.52	4:30	4:45	M	13.2	35.35	D	D	D	48	918
WH394	4125	3200	49.81	336.70	7:25	7:55	D			F	F	F	48	636
WH396	4100	870	49.70	337.03	13:10	13:25	D			D	D	D	46	399
WH397	3500	3200	49.93	339.655	7:20	7:40	D	13.3	35.48	F	F	F	58	666
WH399	4400	800	49.99	339.90	13:10	13:25	D			D	D	D	51	439
WH400	4800	480	49.83	343.055	4:30	4:45	M	13.9	35.45	E	-	-	45	457
WH401	4800	3200	49.87	343.16	7:20	7:50	D			F	F	F	67	1023
WH402	4750	950	49.94	343.53	13:10	13:25	D			D	D	D	46	496
WH403	3850	500	49.78	346.13	3:30	3:45	M	14.5	35.36	E	-	-	37	335

<sup>a</sup>Shipborne measurements not recorded at all stations.<sup>b</sup>Dawn (M) from beginning of nautical twilight to sunrise +1 h, D—day, meteorological data from the US Naval Observatory Astronomical Applications Department ([http://aa.usno.navy.mil/data/docs/RS\\_OneYear.html](http://aa.usno.navy.mil/data/docs/RS_OneYear.html)).<sup>c</sup>ref. to Fig. 6A.<sup>d</sup>2%cont and 4%cont refer to assumed levels of contamination of 2% and 4 %, respectively, for treatment of assumed contamination see text.<sup>e</sup>Raw S (species numbers) and raw n (individuals caught) obtained in haul prior to rarefaction and scaling. n excluding *Cyclothone* spp.

estimates of surface chlorophyll distributions. According to Longhurst (1998, p. 19), surface images can be taken as sound descriptors of regional biological oceanography. Images were obtained from <http://seawifs.gsfc.nasa.gov/SEA-WIFS.html> from the Nimbus 7—Coastal Zone Colour Scanner archives (CZCS). For 1982, a composite April through June was analyzed, since the image for June contained a large number of blank spots.

### 2.3. Biological sampling

The aim of the FRV *Walther Herwig* cruise 52 in June 1982 (see Table 1, and Post, 1987, pp. 57–61) was the study of the bathy- and benthopelagic fishes of the Mid-Atlantic-Ridge north of the Azores. The course comprised a southern and a northern leg on parallels of latitude, and a transverse along the Mid-Atlantic Ridge (Fig. 1). Deep stations were trawled during daytime, while shallow stations were trawled at dawn (Table 1).

A 1600 meshes pelagic trawl (MT 1600) was deployed, spanning 20 m vertically and 30 m horizontally, equipped with two 8 m<sup>2</sup> Süberkrüb doors. Except for one station (St. 331), an inlet was fixed to the codend with 10 mm stretched mesh size (Post, 1987, p.6). This configuration is likely to underestimate the abundance of specimens < 30 mm SL (Gartner et al., 1989). The application of large commercial nets in connection with the FRV *Walther Herwig* cruises has been widely discussed (Krefft, 1974; 1976; Merrett et al., 1986). During retrieval, the net was hauled speedily in order to avoid contamination of deep hauls with specimens from shallower depths (Krefft, 1976). For a nominal trawling speed of 3.5 kn, ship speed was usually reduced to 2.5 kn during lowering, and to 1.5 kn during retrieval of the net (Krefft, 1967). WH52 fishing protocols indicate beginning, time at depth and end of a station. For a mesopelagic haul (St. 390, 500 m catching depth), pre- and post-fishing station time added up to 20 and 40 min, to 50 and 40 min for a bathypelagic haul (St. 383, 1370 m catching depth) and to 60 min and 3 h 45 min for an abyssopelagic haul (St. 391, 3200 m), respectively. After retrieval, the forenet area was carefully sampled by hand before winding it to the

drum (Post, 1987, p. 8). Codend content was flushed into containers. Samples were pre-preserved in 2% formalin for 12 h prior to further processing.

### 2.4. Community analysis

Following Jahn and Backus (1976), analysis was carried out excluding *Cyclothone* spp. (Gonostomatidae), for which methodology was insufficient. Further, singletons with respect to the whole data set were excluded.

Diversity measures were calculated from untransformed data. We employed Hill's diversity indices  $N_0$  and  $N_2$  (Hill, 1973; Magurran, 1988), which gradually differ in their indicative value for rare and common species. The general form is

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

with  $a=0,1,2,\dots$ , and  $p_i$  denoting the proportion of abundance for each species  $i$ .

For  $a=0$ ,  $N_0$  is the number of species.  $N_0$  was estimated as the rarefied number of species in a sample of 250 specimens (ES250), which was the smallest overall sample size, avoiding sample size bias in the assessment of species numbers (e.g. Gordon, 1986; Fock, 2000; Gotelli and Colwell, 2001). For  $a=1$ ,  $N_1$  is the exponential Shannon–Wiener index  $H'$ , which was employed in its more familiar form  $H'_{10} = -\sum p_i \log_{10} p_i$  to facilitate comparisons with other studies where  $H'$  was used instead of  $N_1$ . 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).

For multivariate analysis, samples were scaled to a trawling time of 1 h. The PRIMER software package was employed (Clarke and Gorley, 2001). Group average cluster analysis was conducted on Bray–Curtis similarities. Clusters were obtained by cutting certain joints at levels of 50–60% similarity (Digby and Kempton, 1987, p. 138). Ordination by non-metrical multidimensional scaling (NMDS) was used to substantiate cluster analysis. NMDS is appropriate for scaling heterogeneous communities (Merrett, 1987). SIMPER was applied to identify characteristic species, non-parametric

ANOSIM to evaluate the significance of the chosen level of partitioning. SIMPER firstly analyses contributions to within-cluster similarity. The six top ranking species were tabulated and referred to as consolidating species. Secondly, species are considered which perform stable differences between two clusters. These were referred to as discriminating species, and tabulated until 25% cumulative dissimilarity was reached. For the ANOSIM of all clusters (i.e. general  $R$ ), a Bonferroni-corrected significance level  $\alpha''$  for multiple comparisons was applied (Sokal and Rohlf, 1995):

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

where  $k$  is the number of cluster–cluster comparisons.

### 2.5. Contamination effects

In non-closing devices, deep samples are likely contaminated with specimens from shallower depths. In this study, the probable effect of contamination was analyzed qualitatively and quantitatively. Qualitatively, systematic discrepancies in vertical species distributions were investigated. Quantitatively, a linear error model was developed after Watanabe et al. (1999), who showed that retrieval contamination in non-closing devices can be reduced to <2% of total catch for samples from 700 m. For the model, we assumed for each 500 m depth difference between samples either 2% or 4% contamination in terms of abundance. This changes Bray–Curtis similarity by ca 1% and 2%, respectively. To analyze stability of the original clusters, entries in the Bray–Curtis similarity matrix were modified according to the depth difference and the cluster output was regenerated. Consistent cluster configurations were indicated. Deviating partitions were not affiliated with new clusters, since after modification relationships are merely virtual (Table 1, ‘2%cont’ and ‘4%cont’).

### 2.6. Validation of community analysis

Complementary hypothesis testing was conducted with an additional data set (see Heyen

et al., 1998; i.e. ‘testing another population in similar manner’-method in Myers, 1998). Congruence of results is likely to increase the robustness of interpretation. For complementary hypothesis testing, the depth distribution of *Saccopharynx ampullaceus* in the North Atlantic was analyzed to indicate whether a consistent vertical pattern in accordance with given cluster distribution patterns emerged. Data obtained with comparable methodology from the FRV *Anton Dohrn* Sargasso Sea-expedition in 1979, the FRV *Walther Herwig* Overflow-expedition in 1973 transecting the northern MAR from 64°N to the PAP, and respective data from the 1982 cruise were merged. In the North Atlantic, *S. ampullaceus* is abundant at depths of 1000–3000 m (Bertelsen and Nielsen, 1986). Known southern distribution limits are about 10°N 20°W and 36°N 63°W (data references in Froese and Pauly, 2001). Only the significance of locations <2000 m being clustered above MAR was tested with the  $r^2$ -statistic after Solow (1989) with a randomization procedure ( $n=101$ ), since the coverage for abyssopelagic stations was not sufficient.

## 3. Results

### 3.1. Hydrographical conditions with respect to the 1982 survey

PCA reveals that four main gradients determine different habitat types. The first type (Fig. 2A) is assigned to the western section of the southern leg (ref. to St. 359–370): temperature (i.e. 50 and 200 m) and oxygen saturation (i.e. 50 m) in the upper water layer are relatively high, surface chlorophyll is relatively low. The second type, i.e. the northern leg and the northernmost part of the transverse (ref. to St. 387–403, Fig. 2B), are characterized by increasing values for surface chlorophyll and silicate (i.e. 50 and 200 m). The central part of the transverse (ref. to St. 375–385) as third type of habitat (Fig. 2C) is characterized by a subsurface chlorophyll maximum (i.e. 50 and 75 m). The fourth type (Fig. 2D) covers the easternmost section of the southern leg (referring to stations 331–345), characterized by higher water

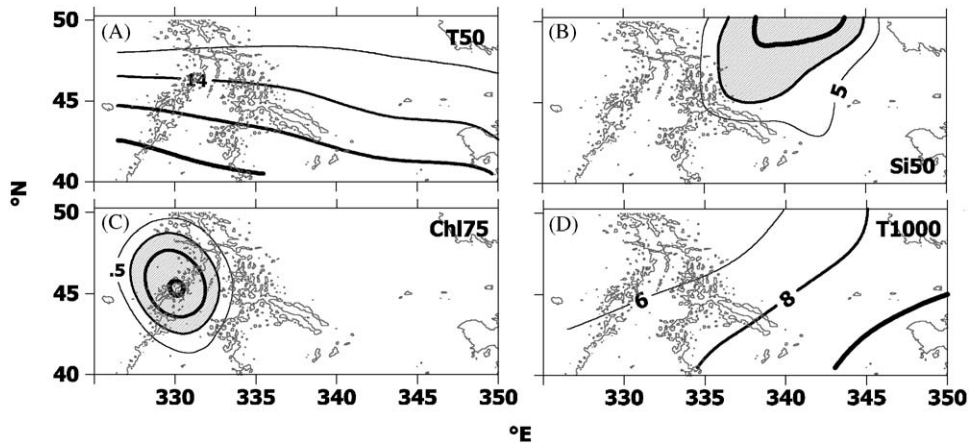


Fig. 2. WOA98—characteristics of habitat types. A—southern leg with positive relationship to surface layer temperature, e.g. T50 (contour lines 13–16); B—northern leg with positive relationship to silicate, e.g. Si50 (contour lines 5–6); C—central part of transverse with subsurface chlorophyll maximum, e.g. Chl75 (contour lines 0.5–0.8); D—southern leg influenced by Mediterranean Outflow Water, e.g. T1000 (contour lines 6–10). Concentrations in  $\mu\text{M}$ , temperature in  $^{\circ}\text{C}$ , parameter digits indicate depth.

temperatures in the meso- and bathypelagic layers (i.e. 500 and 1000 m, 1500 m) and oxygen saturation in shallower layers. In turn, this habitat is negatively related to deep-water oxygen saturation owing to MOW influence.

Shipborne measurements during the cruise (Table 1), however with unknown accuracy, COADS SST data and the inspection of CZCS satellite images supplement the climatology with respect to specific conditions in 1982. The coldest and most fresh surface water masses were met at the western and northwestern stations of the cruise, stations 375–377 and 387–393 (Table 1). In turn, the warmest and most saline waters were found at the southeastern stations. COADS SST data resemble this pattern (Fig. 3A), indicating that surface isotherms in June 1982 followed a SW–NE direction. This contrasts the normal NW–SE orientation of surface isotherms (e.g. Fig. 2A) in the WOA98 climatology. Evidence for an anomaly is further provided from the distribution of SST anomalies in 1982 ( $\delta$  SST, Fig. 3B). Positive anomalies were encountered in the eastern section of the investigation area. Negative SST anomalies extended from northwest to southeast. The track of the negative anomalies is congruent with the main path of LSW as it enters the eastern basin (Paillet et al., 1998). COADS SST data

represented only 60% of variability of shipborne SST data (in terms of linear regression), and thus are rather likely to depict only a general figure. COADS SST time series for a box  $45^{\circ}\text{N}/330.5^{\circ}\text{E}$  ulc– $40^{\circ}\text{N}/334.5^{\circ}\text{E}$  lrc reveal that the cruise was preceded by a relatively warm period which followed a cold period from 1968 to 1979 (Fig. 3C).

Combining stations by means of geographic and abiotic proximity, five groups of stations can be discerned from standardized shipborne data (Fig. 4). In accordance with the distribution of habitat types from Fig. 2, two groups are outlined each for the southern (f1, f2) and the northern leg (f4, f5) and one for the central part of the transverse (f3). Four stations (381, 383, 387, and to some extent 397) cannot be unambiguously affiliated with either one group. The spring surface chlorophyll distribution for 1982 (Fig. 5A) substantiates the interpretation that station 387 is a likely outlier to f4, and that station 397 rather belongs to f5 than to f4. Apparently, groups f1 to f5 coincide with salient differences in chlorophyll concentrations and steep separating gradients. f3 was characterized by low chlorophyll concentrations, f1 by low concentrations combined with a high-concentration center. Peak concentrations were reached in f4 and even more in f5. MAF

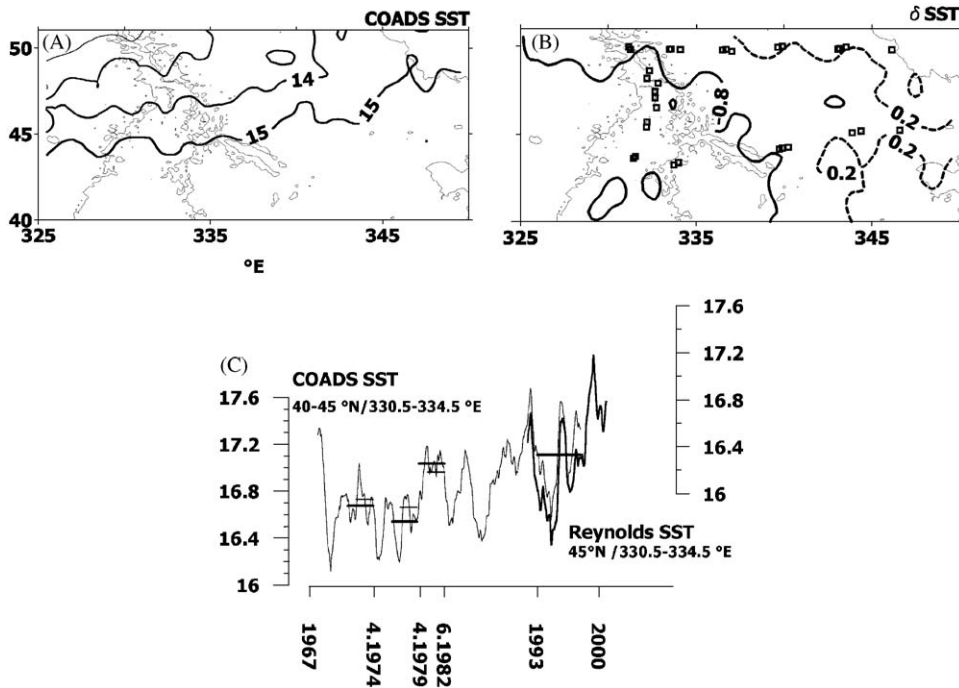


Fig. 3. Trend and distribution of COADS SST and anomalies in June 1982. A—isotherms 12–15°C, B—anomaly isotherms ( $\delta$  SST) for  $-0.8$  and  $+0.2^\circ\text{C}$  calculated as  $\text{COADS}_{\text{June82}} - \text{WOA98}_{\text{June}}$ , C—COADS SST time series from  $40^\circ$  to  $45^\circ\text{N}$  above MAR as 12 month-moving average. Horizontal lines in C indicate 2-(short) and 3-(long)-year SST averages prior to the sampling dates of the 1974 cruise of Roe and Badcock (1984), the 1979-Sargasso Sea expedition (Hulley and Krefft, 1985) and the 1982 WH52 cruise, referring to the southern leg of the WH52 cruise. Further indicated is a mean value for 1993–97 likely to be representative of the conditions during the circulation experiment of Bower et al. (2002). COADS time series end in 1997, Reynolds SST deployed for further extrapolation (ends in 2000).

and SSAF determined chlorophyll patterns at the western flank of MAR. Chlorophyll concentrations in f1, f3, MAF, and f5 were higher in 1982 as compared to the 9-years spring average 1978–86 (Fig. 5B). Further chlorophyll spots in 1981 not developed in 1982 (s1,s2, Fig. 5C) indicate considerable spatial inter-annual variability.

### 3.2. Structure of the fish assemblages

The analysis of community structure with 6 clusters (Table 1, Fig. 6A) can be justified by NMDS (Fig. 6C). Specific assemblages were associated with the southern leg approaching MAR (cluster B) and the northern leg abutting on the continental shelf (cluster E). The shallowest hauls were joined (cluster C). Further, assemblages were related to the central part of the transverse,

i.e. the Mid-Atlantic Ridge proper (most of cluster F). Matching hydrographic structure (Fig. 4) and cluster distributions indicate, that the distribution of clusters fairly resembles hydrographic structure (Fig. 7). Transitions f1/f2, f2/f3, f3/f4 are resolved. The analysis of cluster structure (Tables 2 and 3) by means of ANOSIM 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, accordingly in Table 3.

*Cluster A:* This cluster was confined to the easternmost section of the southern leg likely under influence by MOW (Fig. 2D) and water mass f1. The gonostomatid *Gonostoma bathyphilum* was the prominent consolidating species. In relation to cluster F with a similar average



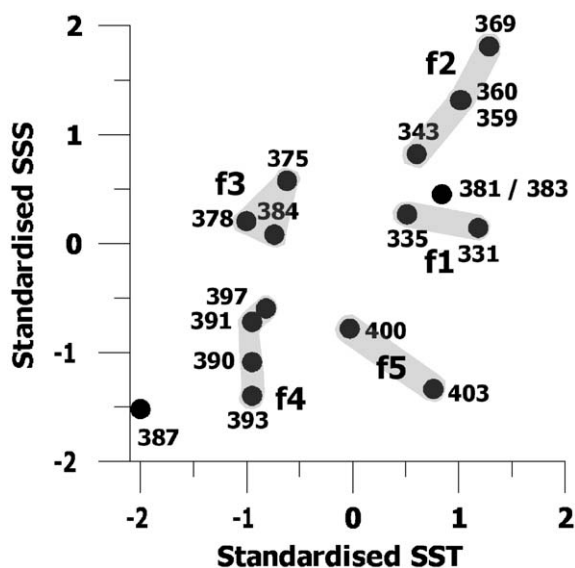


Fig. 4. Property–property plot for standardized SSS and standardized SST (zero mean and unit variance). Group classification f1 to f5 according to geographical and environmental proximity. Stations 381, 383 not assigned to either group. Stations 387 and 397 discussed in text.

sampling depth, comparably lower abundances for the consolidating species *G. bathyphilum* ( $140.33 \text{ n h}^{-1}$  trawling) as well as for *Lampanyctus crocodilus* ( $7.33 \text{ n h}^{-1}$  trawling) were found. The average standardized number of species was high ( $\text{ES250} = 44.3$ ), but due to dominance of *G. bathyphilum* diversity measures  $H'_{10}$  and  $N_2$  were relatively low.

Cluster B occupied the western section of the southern leg and was affiliated with habitat type depicted in Fig. 2A and water mass f2. The northern boundary for this assemblage was set by the transition f2/f3. It was dominated by myctophids (e.g. *Electrona risso*, *Diaphus rafinesquii*) and sternoptychids (*Argyrolepecus olfersi*) as consolidating species (Table 2). Main discriminating species were *Benthoosema glaciale* with respect to northern clusters and *Gonostoma bathyphilum* with respect to deep 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.  $\text{ES250} = 46.4$ ) with a comparably low score in abundance ( $926 \text{ n h}^{-1}$  trawling).

Cluster C joined the shallowest stations affiliated with the deep-chlorophyll maximum habitat above MAR (Fig. 2C) and water mass f3. With  $505.71 \text{ n h}^{-1}$  trawling, *Diaphus rafinesquii* contributed 43.42% of total abundance. Myctophids contributed 61.05% of total abundance. Compared to the neighboring cluster F (Tables 2 and 3), *Benthoosema glaciale* was less abundant in cluster C ( $71.29\text{--}195.68 \text{ n h}^{-1}$  trawling), whereas *D. rafinesquii* was more abundant ( $505.71\text{--}52.89 \text{ n h}^{-1}$  trawling). Discrimination was achieved mainly through species absent from this species-poor shallow assemblage. Correspondingly, diversity measures were low (e.g.  $\text{ES250} = 19$ ).

Cluster D assembled hauls from different times of day. Mean sampling depth at dawn was 480 m (shallow assemblage) and 904 m (deep assemblage) during daytime. Cluster D was confined to the northern leg and affiliated with the habitat type rich in surface chlorophyll and silicate (Fig. 2B) and water masses f4 and f5. It represented stations of highest abundance during dawn and daytime with relatively low values for the diversity measures  $\text{ES250}$ ,  $H'_{10}$  and  $N_2$ . *B. glaciale* dominated with  $631.14 \text{ n h}^{-1}$  trawling, followed by *M. muelleri* with  $389.43 \text{ n h}^{-1}$  trawling. Stomiids were characterized by high abundance (*C. sloani* 248.29, *S. boa ferox* 309.43  $\text{ n h}^{-1}$  trawling). Its southern boundary coincides with f3.

*Cluster E*: This mesopelagic assemblage was strictly associated with shallow hauls at the easternmost end of the northern leg and f5 approaching the continental shelf edge. The consolidating sternoptychids and myctophids accounted for 55.7% of total abundance (Table 2). With respect to the neighboring clusters D and F, blue whiting *M. potassou* was an important discriminating species (Table 3). The centrolophid *Schedophilus medusophagus*, present in D and F, was missing in cluster E (Table 3).

Cluster F covered wide parts of the transverse and deep hauls of the northern leg, representing 11 from 32 stations. Above MAR, it was affiliated with the deep-chlorophyll maximum habitat (Fig. 2C) and water mass f3. It combined features from mesopelagic as well as from abyssopelagic hauls. Next to stomiids, *Benthoosema glaciale* as a subpolar-temperate and *Gonostoma bathyphilum*

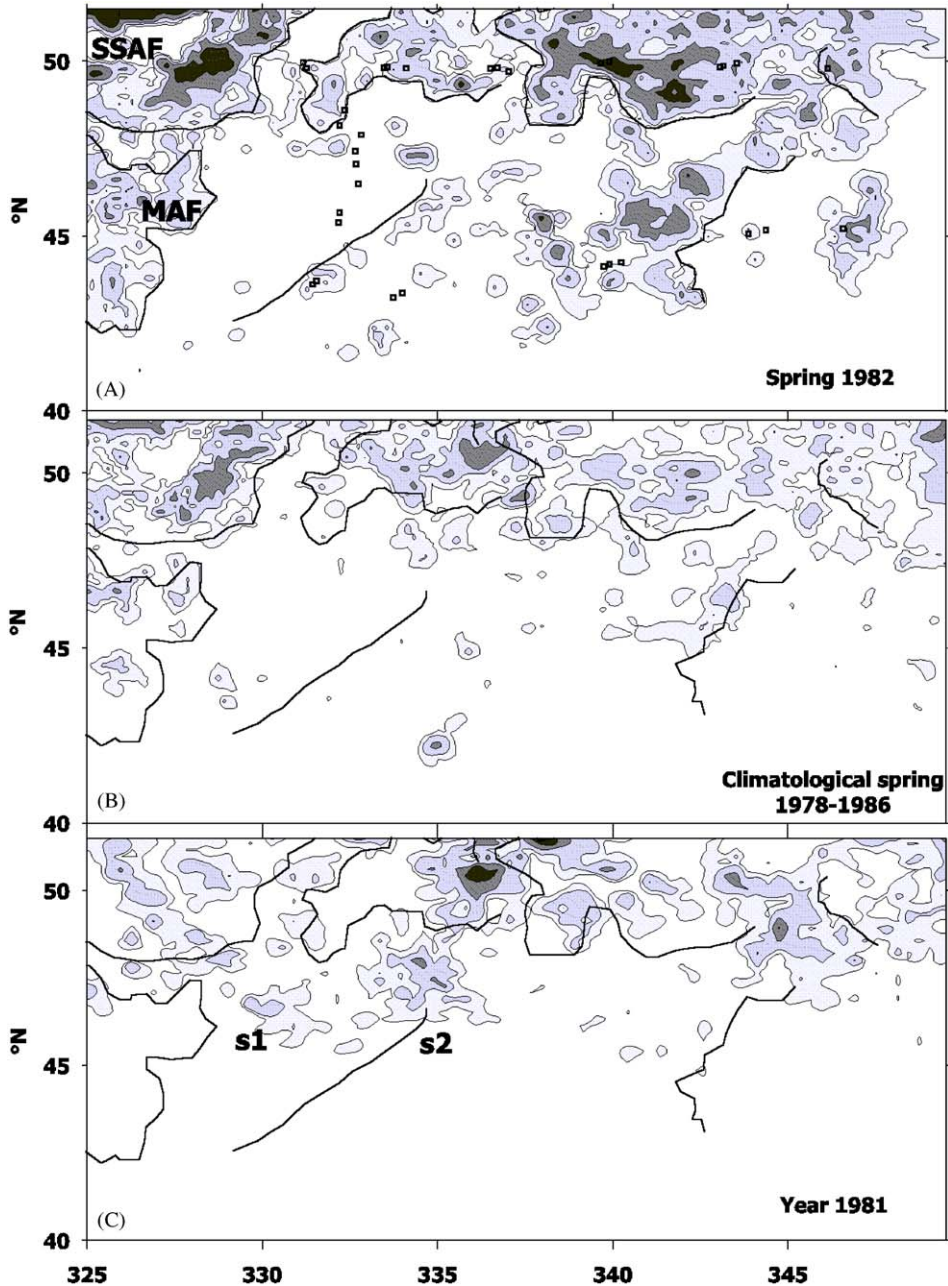


Fig. 5. Surface chlorophyll distributions derived from CZCS images. A—spring 1982 (April–May–June), B—climatological spring 1978–1986, C—whole year composite for 1981. In A, assumed frontal positions and water mass boundaries indicated by bold lines and superimposed in B and C for convenience. SSAF and MAF identified according to Fig. 1. Stations indicated by squares. Chlorophyll contours start with ‘high’ level according to Longhurst(1998), i.e.  $0.8 \text{ mg Chl m}^{-3}$ , then increase two-fold (1.6), five-fold (4.0) and ten-fold (8.0).

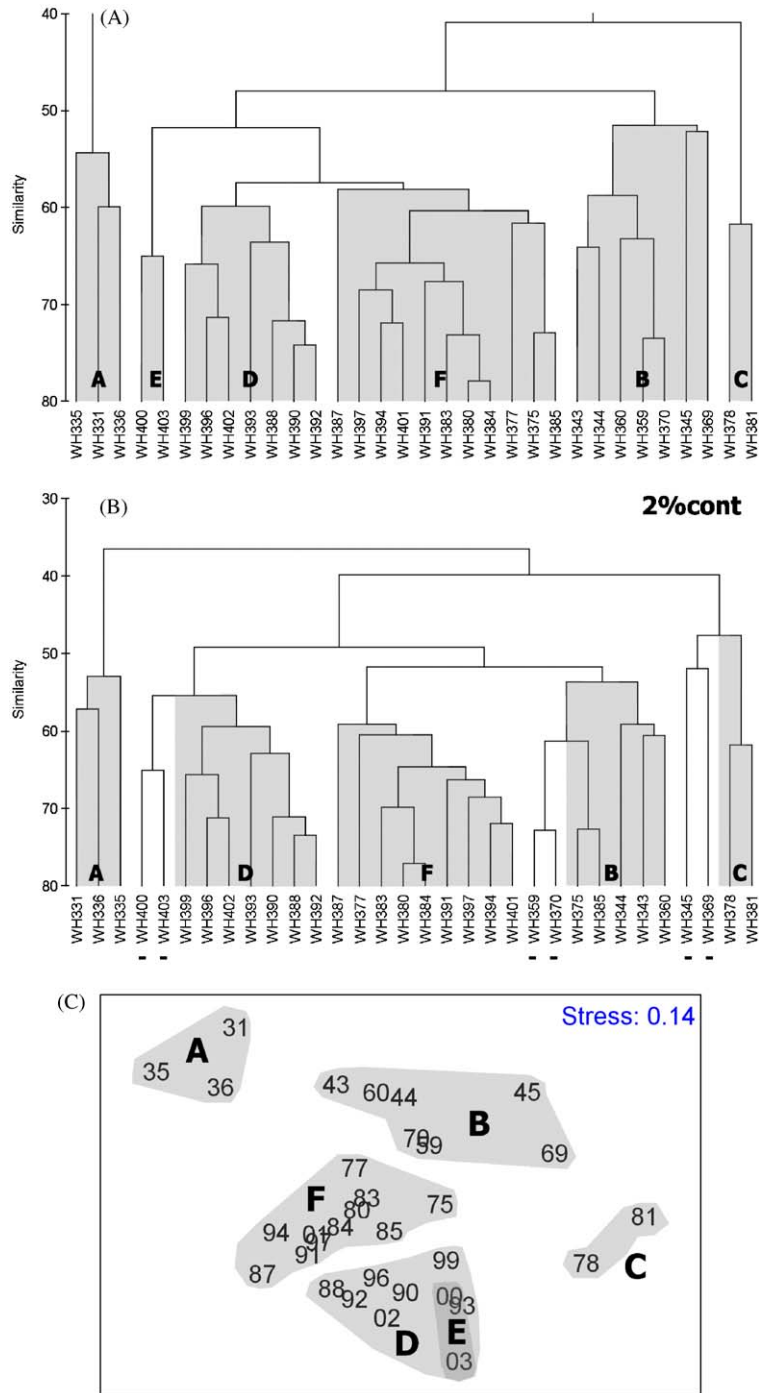


Fig. 6. Classification results. (A) Cluster ordination of original  $\sqrt{\sqrt{-}}$ -data—cluster denotation at x-axis according to Table 1. (B) Cluster ordination under the 2% contamination error model—deviating partitions indicated by '-'. (C) NMDS ordination of original  $\sqrt{\sqrt{-}}$ -data—first digit in stations names removed to improve readability. Grouping according to Fig. 6 A. Stress (0.14) is reduced in a three-dimensional analysis (0.10), separating cluster E from D by means of the third axis.

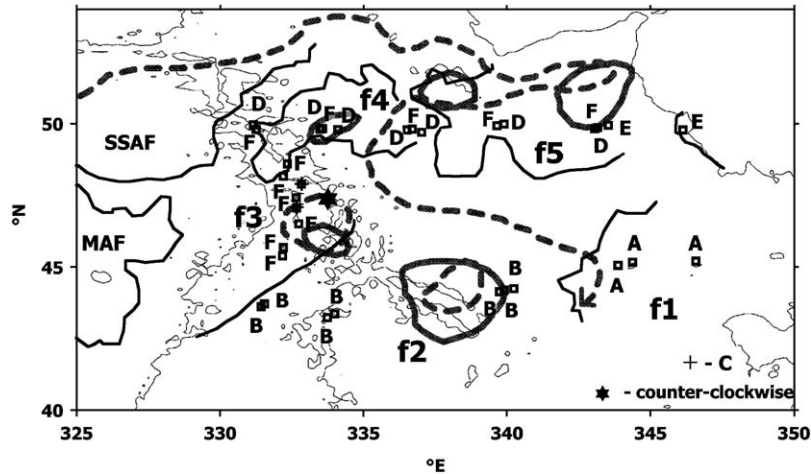


Fig. 7. Synthesis of hydrography and cluster distribution in 1982, compared to recent current investigations from 1993–2001. Cluster denotation after Table 1, water mass denotation according to Fig. 4 and water mass delimitation (bold black lines) after Fig. 5 A. Bold grey streamlines indicate clockwise recirculation cells at thermocline depth (600 m), broken thin grey streamlines indicate flow patterns at about 1750 m, either as recirculation cells or non-recirculating southward flow (arrow tip). East of the non-recirculating flow counter-clockwise streamlines appear. Streamlines partially redrawn from Bower et al. (2002). Asterisk indicates counter-clockwise deep recirculation for f3. The 600-m-recirculation for f3 re-appears in an analysis of Lavender et al. (2000, Fig. 2).

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 abundance of  $143.38 \text{ n h}^{-1}$  trawling compared to cluster A with a similar average depth and an abundance of  $0.67 \text{ n h}^{-1}$  trawling. Further species important in terms of consolidation and discrimination were *Scopelogadus beanii* and *Serrivomer beanii* with an average abundance of 102.15 and  $63.48 \text{ n h}^{-1}$  trawling, respectively.

### 3.3. Assessment of contamination effects

From a qualitative perspective, sampling results of four abundant species differentiated by depth and area are considered with respect to zero catches, extreme values and effects on SIMPER (see Fig. 8). Except for *Gonostoma bathyphilum*, several deeper hauls with zero abundance were recorded though the respective species were present at shallower depths. This would not have been expected if samples were severely contaminated.

For *G. bathyphilum*, sampling results were reproducible for the transverse and the northern leg.

Secondly, most extreme abyssopelagic values were singled out and considered for their possible effect in biasing the remaining data. Coincidences of extreme values between species were further considered. For *Benthoosema glaciale* in each of the three sub-areas, the most extreme abyssopelagic value was low compared to the other mesopelagic and bathypelagic records and always accompanied by several zero or minute abyssopelagic counts. This also holds for *Maurolicus muelleri* on the northern leg. For the transverse, the most extreme abyssopelagic value for *M. muelleri* was higher than any other value. But in absolute terms the whole ensemble comprised only low values and thus its low discriminating abundance above MAR is not contentious. For *Chauliodus sloani*, the most extreme abyssopelagic values for the southern leg and the transverse conformed to trends as indicated in the respective panels of Fig. 8. Trends were consistent though opposite and would not have been affected from singling out the most extreme abyssopelagic values in

Table 2

Cluster statistics and top 6 ranking consolidating species for each cluster.

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 <sup>-1</sup> )	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 <sup>-1</sup> )	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 <sup>-1</sup> 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' <sub>10</sub>	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
N <sub>2</sub>	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 pelecanoioides</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>Bentosema glaciale</i> 71.29 (7.93 %) <i>Symbolophorus veranyi</i> 67.29 (7.93 %) <i>Diaphus holti</i> 96.86 (7.48 %)	<i>Bentosema glaciale</i> 631.1 (6.05 %) <i>Stomias boa 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>Maurolicus muelleri</i> 385.43 (4.06 %)	<i>Lampanyctus crocodilus</i> 314.0 (7.34 %) <i>Lobianchia gemellarii</i> 222.0 (6.70 %) <i>Argyropelecus hemigymmus</i> 92.0 (5.45 %) <i>Argyropelecus olfersi</i> 84.0 (5.38 %) <i>Nansenia</i> sp. 96.0 (5.17 %)	<i>Stomias boa ferox</i> 165.43 (4.21 %) <i>Gonostoma bathyphilum</i> 390.63 (3.92 %) <i>Scopelogadus beanii</i> 102.15 (3.71 %) <i>Bentosema 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 %)	

Ordered measures for clusters indicate average / minimum / maximum value, respectively. Ordered measures for consolidating species indicate average abundance per 1 h trawling and percentage by similarity contributed by the species (in brackets).

Table 3  
Discriminating species for the cluster analysis of root-root transformed data.

Species	1st abun	2nd abun	%dissim
First cluster A–second cluster B			
<i>Diaphus rafinesquii</i>	0.33	59.93	2.48
<i>Sternoptyx diaphana</i>	0	20.43	2.16
<i>Symbolophorus veranyi</i>	0	29.29	2.13
<i>Gonostoma denudatum</i>	0	10.64	1.91
<i>Diaphus metapoclampus</i>	0	12.71	1.88
<i>Gonostoma bathyphilum</i>	140.33	88.36	1.67
<i>Hygophum benoiti</i>	0	12.00	1.63
<i>Electrona risso</i>	6.00	85.43	1.57
<i>Ceratoscopelus maderensis</i>	1.33	54.57	1.56
<i>Diaphus holti</i>	3.33	39.64	1.50
<i>Poromitra crassiceps</i>	12.33	5.57	1.49
<i>Chauliodus sloani</i>	7.33	42.50	1.43
<i>Bolinichthys supralateralis</i>	0.33	5.79	1.28
<i>Poromitra capito</i>	3.33	21.50	1.24
<i>Scopelogadus beanii</i>	1.00	19.50	1.14
First cluster A–second cluster D			
<i>Benthoosema glaciale</i>	1.00	631.14	3.97
<i>Maurollicus muelleri</i>	0	385.43	3.43
<i>Gonostoma bathyphilum</i>	140.33	2.29	2.92
<i>Stomias boaferox</i>	5.33	309.43	2.81
<i>Notoscopelus kroeyeri</i>	0	117.71	2.67
<i>Chauliodus sloani</i>	7.33	248.29	2.37
<i>Symbolophorus veranyi</i>	0	99.43	2.31
<i>Nansenia</i> sp.	2.67	277.71	2.02
<i>Diaphus rafinesquii</i>	0.33	68.57	1.96
<i>Sagamichthys schnakenbecki</i>	0	19.14	1.85
First cluster A–second cluster F			
<i>Benthoosema glaciale</i>	1.00	195.68	2.72
<i>Scopelogadus beanii</i>	1.00	102.15	2.28
<i>Stomias boaferox</i>	5.33	165.43	2.25
<i>Chauliodus sloani</i>	7.33	170.05	2.07
<i>Diaphus rafinesquii</i>	0.33	52.89	2.03
<i>Schedophilus medusophagus</i>	0.67	143.38	1.89
<i>Lampanyctus macdonaldi</i>	0.67	52.09	1.86
<i>Symbolophorus veranyi</i>	0	15.12	1.73
<i>Nansenia</i> sp.	2.67	218.41	1.69
<i>Bathylagus</i> sp1	0.67	25.84	1.60
<i>Gonostoma bathyphilum</i>	140.3	390.63	1.47
<i>Lampadena speculigera</i>	0	6.26	1.39
<i>Sagamichthys schnakenbecki</i>	0	9.50	1.38
<i>Serrivomer beanii</i>	5.0	63.48	1.25
First cluster B–second cluster C			
<i>Lampanyctus crocodilus</i>	23.86	0	2.57
<i>Gonostoma bathyphilum</i>	88.36	0	2.52
<i>Diaphus rafinesquii</i>	59.93	505.71	2.34
<i>Diaphus metapoclampus</i>	12.71	0	2.06
<i>Schedophilus medusophagus</i>	11.43	104.86	2.05
<i>Benthoosema glaciale</i>	5.50	71.29	1.94
<i>Serrivomer beanii</i>	29.36	0.86	1.82

Table 3 (continued)

Species	1st abun	2nd abun	%dissim
<i>Bolinichthys supralateralis</i>	5.79	0	1.78
<i>Eurypharynx pelecanooides</i>	16.07	0	1.72
<i>Lestidiops similis</i>	0	43.00	1.65
<i>Sternoptyx diaphana</i>	20.43	0.86	1.64
<i>Poromitra capito</i>	21.50	1.0	1.62
<i>Opisthoproctus soleatus</i>	6.07	0	1.56
First cluster B–second cluster D			
<i>Maurolicus muelleri</i>	0	385.43	3.32
<i>Benthoosema glaciale</i>	5.50	631.14	3.20
<i>Stomias boaferox</i>	7.36	309.43	2.47
<i>Notoscopelus kroeyeri</i>	2.57	117.71	2.07
<i>Nansenia</i> sp.	2.71	277.71	2.06
<i>Myctophum punctatum</i>	1.43	49.14	2.04
<i>Lampanyctus macdonaldi</i>	0	47.71	1.85
<i>Gonostoma bathyphilum</i>	88.4	2.29	1.84
<i>Gonostoma denudatum</i>	10.6	0	1.60
<i>Sternoptyx diaphana</i>	20.4	0.86	1.50
<i>Chauliodus sloani</i>	42.5	248.29	1.44
<i>Bolinichthys supralateralis</i>	5.79	0	1.35
<i>Poromitra capito</i>	21.5	9.71	1.32
<i>Sagamichthys schnakenbecki</i>	1.86	19.14	1.28
First cluster B–second cluster E			
<i>Nansenia</i> sp.	2.71	96	2.64
<i>Benthoosema glaciale</i>	5.50	168	2.26
<i>Gonostoma bathyphilum</i>	88.36	0	2.11
<i>Lampanyctus crocodilus</i>	23.86	314	1.98
<i>Myctophum punctatum</i>	1.43	36	1.94
<i>Serrivomer beanii</i>	29.36	0	1.94
<i>Micromesistius poutassou</i>	0	14	1.87
<i>Diaphus metapoclampus</i>	12.71	0	1.72
<i>Sagamichthys schnakenbecki</i>	1.86	30	1.67
<i>Protomyctophum arcticum</i>	0.00	6	1.51
<i>Hygophum benoiti</i>	12.00	0	1.49
<i>Bolinichthys supralateralis</i>	5.79	0	1.48
<i>Ceratospinelus maderensis</i>	54.57	8	1.46
<i>Eurypharynx pelecanooides</i>	16.07	0	1.45
First cluster B–second cluster F			
<i>Gonostoma bathyphilum</i>	88.36	390.63	2.17
<i>Benthoosema glaciale</i>	5.50	195.68	2.0
<i>Lampanyctus macdonaldi</i>	0	52.09	2.00
<i>Stomias boaferox</i>	7.36	165.43	1.91
<i>Poromitra crassiceps</i>	5.57	51.68	1.68
<i>Nansenia</i> sp.	2.71	218.41	1.67
<i>Scopelogadus beanii</i>	19.50	102.15	1.65
<i>Borostomias antarcticus</i>	0.14	17.86	1.60
<i>Schedophilus medusophagus</i>	11.43	143.38	1.53
<i>Bathylagus</i> sp1	1.50	25.84	1.45
<i>Chauliodus sloani</i>	42.50	170.05	1.38
<i>Hygophum benoiti</i>	12.00	0.18	1.34
<i>Maulisia microlepis</i>	1.29	22.41	1.33
<i>Myctophum punctatum</i>	1.43	8.94	1.21

Table 3 (continued)

Species	1st abun	2nd abun	%dissim
<i>Bolinichthys supralateralis</i>	5.79	0.90	1.20
<i>Eurypharynx pelecanaoides</i>	16.07	42.95	1.10
First cluster C–second cluster D			
<i>Maurolicus muelleri</i>	1	385.43	3.55
<i>Lampanyctus crocodilus</i>	0	104.29	3.53
<i>Notoscopelus kroeyeri</i>	0	117.71	3.25
<i>Stomias boaferox</i>	25.86	309.43	2.62
<i>Diaphus rafinesquii</i>	505.71	68.57	2.50
<i>Lampanyctus macdonaldi</i>	0	47.71	2.33
<i>Nansenia</i> sp.	22.0	277.71	2.31
<i>Sagamichthys schnakenbecki</i>	0	19.14	2.25
<i>Benthoosema glaciale</i>	71.29	631.14	2.16
<i>Normichthys operosus</i>	1	53.71	2.04
First cluster C–second cluster F			
<i>Gonostoma bathyphilum</i>	0	390.63	3.82
<i>Scopelogadus beanii</i>	0	102.15	3.01
<i>Lampanyctus crocodilus</i>	0	68.44	2.74
<i>Eurypharynx pelecanaoides</i>	0	42.95	2.25
<i>Diaphus rafinesquii</i>	505.71	52.89	2.23
<i>Lampanyctus macdonaldi</i>	0	52.09	2.14
<i>Malacosteus niger</i>	0	22.62	2.08
<i>Poromitra crassiceps</i>	0	51.68	2.08
<i>Serrivomer beanii</i>	0.86	63.48	2.07
<i>Bathylagus</i> sp1	0	25.84	1.96
<i>Borostomias antarcticus</i>	0	17.86	1.83
First cluster D–second cluster E			
<i>Maurolicus muelleri</i>	385.43	20	3.09
<i>Chauliodus sloani</i>	248.29	26	2.96
<i>Serrivomer beanii</i>	41.43	0	2.51
<i>Lampanyctus macdonaldi</i>	47.71	0	2.44
<i>Xenodermichthys copei</i>	1.71	30	2.22
<i>Arctozenus risso</i>	20.57	0	2.16
<i>Symbolophorus veranyi</i>	99.43	2	2.14
<i>Micromesistius poutassou</i>	1.14	14	1.96
<i>Schedophilus medusophagus</i>	21.71	0	1.93
<i>Nansenia</i> sp.	277.71	96	1.91
<i>Nannobranchium atrum</i>	9.71	0	1.82
<i>Notoscopelus kroeyeri</i>	117.71	6	1.62
First cluster D–second cluster F			
<i>Gonostoma bathyphilum</i>	2.29	390.63	3.77
<i>Maurolicus muelleri</i>	385.43	32.0	2.93
<i>Eurypharynx pelecanaoides</i>	0.57	42.95	2.21
<i>Nansenia</i> sp.	277.71	218.41	2.04
<i>Notoscopelus kroeyeri</i>	117.71	10.41	1.82
<i>Benthoosema glaciale</i>	631.14	195.68	1.74
<i>Poromitra crassiceps</i>	2.0	51.68	1.70
<i>Bathylagus</i> sp1	1.43	25.84	1.62
<i>Scopelogadus beanii</i>	36.0	102.15	1.51
<i>Melanostomias bartonbeani</i>	3.43	11.91	1.32
<i>Lampanyctus macdonaldi</i>	47.71	52.09	1.30



Table 3 (continued)

Species	1st abun	2nd abun	%dissim
<i>Schedophilus medusophagus</i>	21.71	143.38	1.30
<i>Maulisia microlepis</i>	6.29	22.41	1.27
<i>Electrona risso</i>	214.57	74.83	1.22
First cluster E–second cluster F			
<i>Gonostoma bathyphilum</i>	0	390.63	3.73
<i>Serrivomer beanii</i>	0	63.48	2.62
<i>Schedophilus medusophagus</i>	0	143.38	2.26
<i>Eurypharynx pelecanoides</i>	0	42.95	2.19
<i>Scopelogadus beanii</i>	4.0	102.15	2.18
<i>Chauliodus sloani</i>	26.0	170.05	2.09
<i>Lampanyctus macdonaldi</i>	0	52.09	2.09
<i>Poromitra crassiceps</i>	0	51.68	2.03
<i>Bathylagus</i> sp1	0	25.84	1.92
<i>Nansenia</i> sp.	96.0	218.41	1.88
<i>Maulisia microlepis</i>	0	22.41	1.71
<i>Micromesistius poutassou</i>	14.0	0.45	1.61

Only cluster pairs with significant differences according to ANOSIM considered. For each species average abundance in first cluster (1st abun) and second cluster (2nd abun) and contribution to overall dissimilarity (%dissim) listed. Abundances in  $\text{n h}^{-1}$  trawling. Cluster combinations A–C, A–E and C–E not tabulated due to insignificant results.

either case. But, the most extreme samples coincided for *M. muelleri*, *C. sloani* and *B. glaciale* in one case (St. 384), so this station is probably subject to noticeable contamination. Since St. 384 is not marginal with respect to cluster F, spatial relationships remain unaffected. Note that St. 384 was special according to its minute nominal sampling distance to the bottom, i.e. 150 m (Table 1). For the northern leg, one extreme abyssopelagic value appeared for *C. sloani*. This value coincided with the extreme value for *M. muelleri*, but the degree of probable contamination for *M. muelleri* differed by an order of magnitude. Since a clear vertical separation in terms of dominance groups was found over the northern leg (f4, f5), a general biasing effect owing to contamination is not expected with respect to f1–f3.

Thirdly, with respect to SIMPER, contamination is likely to be of minor importance for consolidating species, since these deliver stable contributions to cluster characteristics. Contamination is more likely among the discriminating species. Especially species with minute abundances like *Diaphus rafinesquii* and *Bolinichthys supralateralis* in cluster A with  $0.33 \text{ n h}^{-1}$  trawling are probable candidates for indicating contamination.

In turn, species with zero abundances and abundant species are reasonable candidates for non-biased discrimination, especially if gradients are considered. This can be exemplified for *Benthoosema glaciale*, a good discriminator between clusters A and F. Its abundance is minute in cluster A ( $1.00 \text{ n h}^{-1}$  trawling, likewise  $5.5 \text{ n h}^{-1}$  trawling in cluster B) compared to F ( $195.68 \text{ n h}^{-1}$  trawling), and thus probably subjected to contamination in A. But the conclusion in terms of a significant difference between A and F is not questionable.

Quantitatively, the outcome of the error model shows that under the 2% contamination regime delimitations for clusters A–D persist (Fig. 6B). Cluster E becomes closely related to D, and cluster F sheds its southernmost station. A crossing-over appears between f2 and f3, with stations 345 and 369 aligning themselves to cluster C, and vice versa, stations 375 and 385 aligning themselves to cluster B. Still, stations of very different catching depth combine into clusters. The remaining cluster F becomes more compact. Due to the depth-dependent algorithm, the severe 4% contamination regime further disintegrates clusters with respect to depth strata. The remaining B-cluster

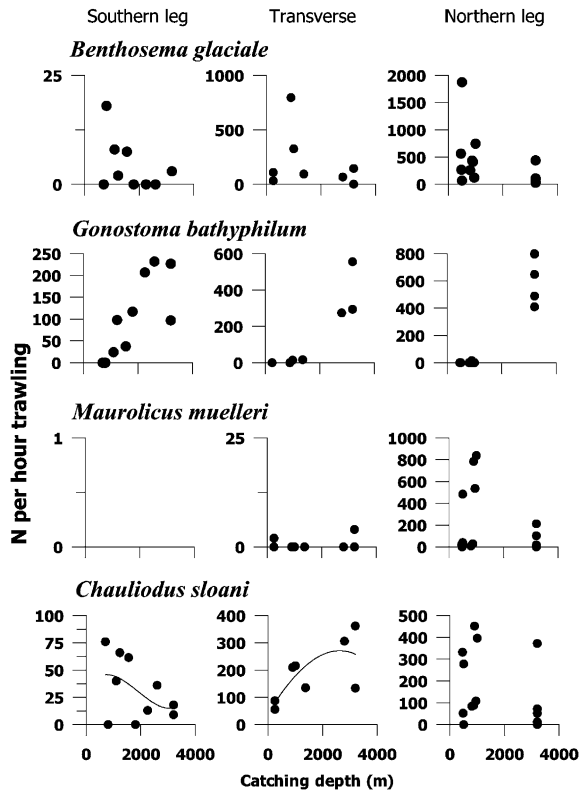


Fig. 8. Sampling results by depth and by area for abundant species. Assignment to areas not congruent with clusters: southern leg stations 331–370, transverse stations 375–385, northern leg stations 387–403. No bathypelagic hauls were carried out in the northern leg. Polynomial regression to provide tentative depth dependent trends for *C. sloani*.

comprises bathypelagic stations, and the remaining F-cluster abyssopelagic stations. Still, A, C, and D are stable, as is the separation between F and D (Table 1).

### 3.4. Dominance patterns and vertical structure

Percentage by abundance on family level (Table 4) 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 five types of dominance patterns can be discerned. The first type considers

deep-water taxa (Table 4, pattern 1). Gonostomatids excluding *Cyclothone* spp. were leading in cluster A which consisted of bathy- and abyssopelagic stations and further contributed to clusters B and F. The second type (Table 4, pattern 2) comprises myctophids and sternoptychids predominating in meso- and bathypelagic clusters B–E. Whereas predominance for myctophids was strongest in the assemblages C and E sternoptychids had their highest share in the northern assemblages D and E. The third type of dominance (Table 4, pattern 3) indicates a northern and ridge component. Microstomatids and stomiids are concerned, abundantly present in clusters D and F over the ridge and the northern leg. However, the abundance for the microstomatid *Nansenia* sp. was highly variable in these assemblages so that it did not achieve a consolidating status (see Table 2). The fourth type (Table 4, pattern 4) considers taxa related to assemblages of the ridge. This concerns in the first line centrolophids. The centrolophid *Schedophilus medusophagus* was an important discriminating species for cluster F. The fifth dominance pattern (Table 4A, pattern 5) considers a ridge and southern component, i.e. taxa abundant in B. Taxa with this dominance scheme were melamphids, serrivomerids, and eurypharyngids. These taxa were nearly absent in the upper mesopelagic zone represented by cluster C. In particular, *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 and fifth type over MAR with regard to the increased abundance data given in Table 2 is likely to indicate that the ecological function of this assemblage has changed with respect to specific features of the MAR environment (e.g. subsurface chlorophyll maximum, Fig. 2C).

Further considering a depth stratified distribution of dominance patterns with respect to water masses corroborates the statement of a specific ridge assemblage in f3. Four strata are illustrated: upper (250 m) and lower mesopelagic zone, bathypelagic and abyssopelagic zone (zones are separated by a slash, missing entries are represented by an asterisk, and dominance patterns are from

Table 4

Percentage by abundance on family level for clusters from analysis of root–root transformed data.

Cluster	A	B	C	D	E	F
<i>Relative abundances excluding Cyclothone spp.</i>						
Group 1						
Gonostomatidae	47.81	11.27	0.32	0.18	0.38	17.77
Group 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
Group 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
Group 4						
Centrolophidae	0.22	1.54	8.40	0.68	0.00	6.15
Group 5						
Melamphidae	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
Group 6						
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

Dominance patterns 1 to 5 described in text. Group 6 consists of families without specific affiliation. Major affiliation indicated by boxes.

Table 4). For f1 no mesopelagic hauls were made, resulting in a \*/\*/1,5/1,5 vertical pattern. For f2 a \*/2,5/2,5/2,5 pattern is obtained. F3 is characterized by 4,2/4,3,5/4,3,5/4,3,5, the only water mass with upper mesopelagic hauls. F4 is characterized by \*/3,2\*/4,3,5 and f5 at its eastern end by \*/2\*/4,3,5. This shows, that in f4 and f5 the hauls represented by cluster F are overlaid by shallower and different clusters D and E, whereas in f1, f2, and f3 the vertical structure was rather homogeneous in terms of statistics, in f3 especially with respect to dominance pattern 4.

The complementary analysis of the distribution of *Saccopharynx ampullaceus* in the North Atlantic reinforces the statement of elevated and vertically mixed faunas above MAR (Fig. 9). Above MAR, minimum catching depth rises to 1000 m, whereas off-MAR minimum catching depth above PAP is 2550 m. Analysis for the bathypelagic stations reveals ( $r^2$ -statistic is two-dimensional) significant

clustering of elevated sampling locations of *S. ampullaceus* above MAR ( $p < 0.01$ ).

## 4. Discussion

### 4.1. Methodology

Deep hauls with non-closing devices suffer from contamination with shallower living specimens. Three approaches to search for systematic indications of contamination, to justify the SIMPER analysis and to assess the value of the data base were conducted. For the cluster analysis, results under the 2%-contamination regime model confirm the present analysis. The 4%-contamination regime is unreasonably rigid, implying that for a 3200 m-haul about 25% of total abundance are subject to contamination. Though contamination

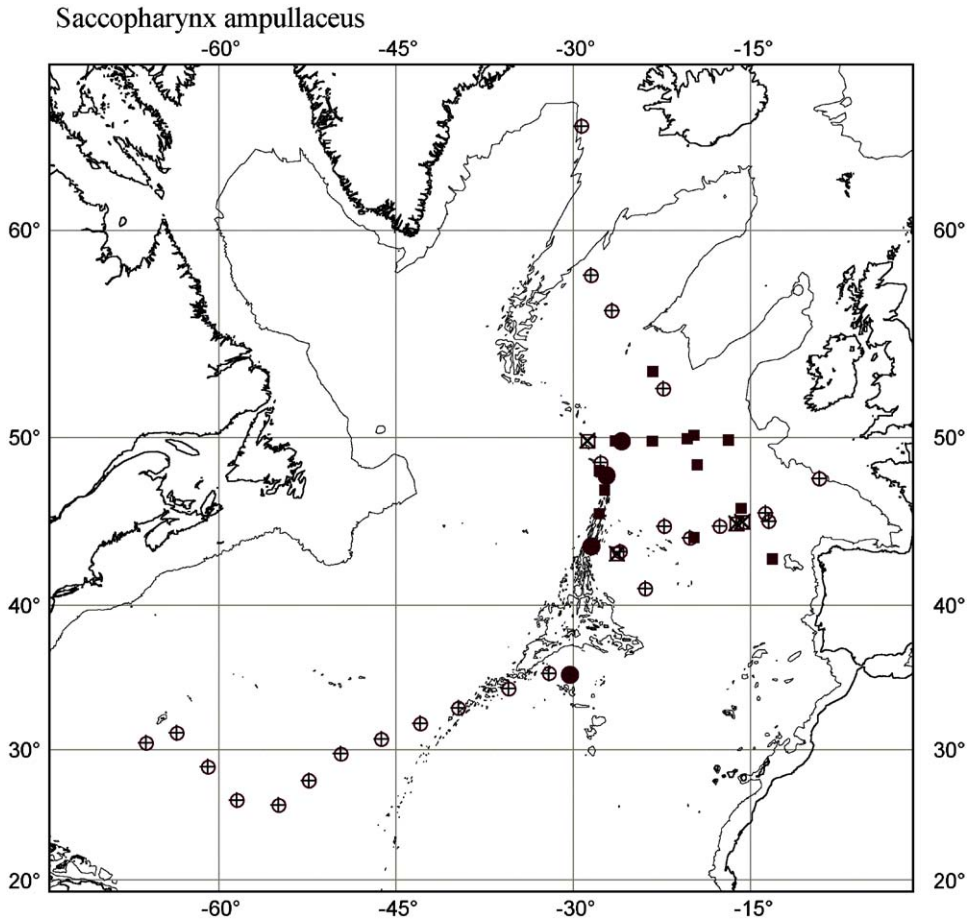


Fig. 9. PANMAP projection of the distribution of *Saccopharynx ampullaceus* in the North Atlantic applied for complementary hypothesis testing. Records deeper than 2000m indicated by squares, bathypelagic records by dots. Crossed symbols indicate zero records, filled symbols indicate positive records. Depth contour at 2000 m.

cannot be precluded, we conclude that the data base renders reasonable analysis.

#### 4.2. Relationships between the pelagic environment and MAR

The distribution of deep-sea fish assemblages fairly followed the distribution of characteristics of the oceanic surface layer as indicated by salinity–temperature relationships and surface chlorophyll (Fig. 7). The faunistic analysis was capable of resolving water masses f1, f2, f3, and f4 plus f5 as a whole, since cluster E was only present in the

easternmost section of f5. As WOA98 data elucidated, these water masses represented different habitat types.

The congruence between deep-sea fish assemblages and surface water mass characteristics especially along the transverse and the southern leg requires anticipation that surface structures are linked to deep-water processes and that these processes were persistent enough to establish vertical alignment. A surface-deep water link was shown by means of changes in potential vorticity along a meridional section at 30°W attributed to NAC and Azores Current coinciding with

corresponding SST changes (Longhurst, 1998, p. 121). Kinetic energy spectra of the eastern North Atlantic indicate dominating periods > 100 days and length-scales of 80–160 km (Losee, et al. 1989; LeTraon, 1991), i.e. the range of mesoscale eddies (Colling, 2001, p. 73), which in turn determine surface chlorophyll distribution during vernal stratification (Longhurst, 1998, p. 121). These dimensions would be sufficient for fish assemblages of all bathymetric zones to align themselves to surface features, since particle flux from the surface down to 3200 m takes about 30 days (from Sargasso Sea, Deuser, 1986).

What causes eddy formation over MAR? Anomalous topography may 'precondition' up- and downwelling (DiBatista et al., 2002), thus break up flows and establish vertical transport. Anomalously high kinetic eddy energy was found above MAR at 44–50°N (Sy et al., 1992) and recent mid-depth current measurements (Lavender et al., 2000; Bower et al., 2002) revealed a set of hitherto unexpected embedded recirculations at the thermocline (600 m) and at 1750 m depth above and east of MAR (indicated in Fig. 7). It was suggested that MAR determined their position. Circulation patterns are subject to climate variability, e.g. spreading of LSW into the mid-latitude North Atlantic (Reid et al., 1998) and contraction of the subpolar gyre (Bower et al., 2002), both in relation to the North Atlantic Oscillation. Taking into account climate variability, there is an astounding congruence between the 1993 and 2001 recirculations (after Bower et al., 2002) and the 1982-distribution of water masses, both measured during periods of high regional SST and thus comparable in terms of climatology (Fig. 3C). Another congruence appears between the deep non-recirculating pattern and the distribution of cluster F along the northern leg of the cruise (Fig. 7). We assume that this pattern also represents deeper-water circulations, since the interplay between inflow through the Gibbs Fracture Zone and the counter-clockwise basin circulation is likely to be limited by the depth of the ridge crest (about 3500 m). This indicates that fish assemblage structure depends on hydrographic structure in relation to MAR. Further, topographically fixed eddies in relation to f3 and f4

with associated up- and downwelling features may provide nutrients to the surface layer for enhanced surface and subsurface production above MAR (s1 and s2, Fig. 5).

#### 4.3. Environmental relationships for fish assemblages

Three assemblages are influenced by MAR topography, i.e. clusters B, D, and F (incl. C), and further E by the shelf edge. Cluster A at the border between Porcupine Abyssal Plain and Ibero Abyssal Plain is likely to be influenced from Mediterranean Outflow Water. The lowered oxygen contents of MOW at 500–1500 m probably has an influence on fish abundance, especially for St. 331 with a catching depth of 1800 m. For *Gonostoma bathyphilum*, the decrease in abundance for cluster A compared to cluster F is presumably linked to the reduced oxygen contents of the Mediterranean outflow water there, since *G. bathyphilum* is known not to enter deep waters devoid of oxygen in the Arabian Sea (Craddock and Haedrich, 1973). Compared to the Arabian Sea (<0.2 ml/l), the WOA98 oxygen concentration at 1000 m in the deep NE Atlantic (>4 ml/l) still is moderate, so that we suggest that the general increase of abundance over the ridge associated with cluster F at comparable mean catching depth rather reflects ridge specific processes and a gradient of production there.

Assemblage B is located at a likely deep recirculating water column, indicated by two clockwise recirculations in f2 (Fig. 7). Vertical transport due to centered downwelling and marginal upwelling would explain the relative vertical homogeneity of the faunal assemblages and the marginal bands of increased surface chlorophyll.

Assemblage D found its southwestern limit in f3 and was mainly associated with f4 and f5, a homogeneous water body probably rich in AIW derived silicate. As for Rockall Trough (Hulley, 1992), *Notoscopeus kroeyeri* was the dominant species there, more abundant in cluster D than in cluster E (Table 3). A link between cluster D and the Rockall Bank area was probably established. A southward current is indicated at Rockall Bank

at the western trough side (Fig. 8 in Mauchline, 1986). Thermocline recirculations (Fig. 7) do not reach the bathypelagic zone, paralleling the separation of cluster D from cluster F along the northern leg.

Assemblage E was located near the shelf edge and probably influenced by the shelf-edge current. This hypothesis is supported by the presence of the gadid *Micromesistius poutassou* (Table 3), a mesopelagic dweller over depths of 400–3000 m and benthopelagic at depths <400 m (after Gordon, 1986; Svetovidov, 1986; Merrett et al., 1991). According to Gerber (1993), the area along the continental shelf from 45°N to 55°N is the characteristic distribution area for juvenile blue whittings. Fish lengths of 68–138 mm indicate juvenile specimens during the present cruise. 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 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. stations in conjunction with the continental slope comparable to Sts. 400 and 403. Species composition for myctophids and sternoptychids partly resembled the species of cluster E. Another feature in common with Roe and Badcock (1984) was the relatively high abundance of the alepocephalid *Xenodermichthys copei*. Because of its reproduction biology with the positioning of benthopelagic eggs, *X. copei* is associated with continental slopes (Markle and Quero, 1986).

The analysis revealed a certain assemblage above MAR in f3, i.e. cluster F. As in f2, two eddies are present indicating a deep recirculating water column; however, the turning directions for the two eddies are opposite (Fig. 7). Assuming vertical exchange, fish assemblages were rather homogenous throughout the sampled water column. The significantly extended depth range of *Saccopharynx ampullaceus* above MAR (Fig. 9) supported this. A further eastward extension of F along the northern leg coincides with a northern

deep circulation pattern, separating it from clusters D and E. Cluster F was characterized by an increase of abundance for Melamphaidae, Serrivomeridae, Eurypharyngidae and Stomiidae. In particular, Centrolophidae increased over MAR (clusters C and F, Table 4). Melamphaidae (Gartner and Musick, 1989) and Centrolophidae (e.g. Macpherson and Roel, 1987) are to some degree feeding on gelatinous plankton. In turn, Serrivomeridae are facultatively and Stomiidae obligatorily piscivorous. This indicates a considerable shift in prey utilization 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. 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, because of upwelling of deep-water populations in the two-eddy system or as a response to increased subsurface production (Fig. 2 C), gelatinous plankton abundance may increase. Our own unpublished data 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 0.02–79) than for oceanic habitats (on average <1 with a range of 0.12–1.0). Correspondingly, Biggs et al. (1981) found an increase of gelatinous plankton in the NE Atlantic from 18°W to 36°W associated with MAR.

A further modification of food web structure appears with respect to the presence of benthopelagic predators in cluster F. *Serrivomer beanii* (Serrivomeridae) and *Scopelogadus beanii* (Melamphaidae) are subjected to predation by roundfish (grenadiers: Haedrich and Henderson, 1974; cod: Casas and Paz, 1996). The former suggested that larger grenadiers leave the bottom habitats and advance their prey in the water column. During the cruise, the only four specimens of *Coryphaenoides rupestris* caught were sampled on stations 381–388 over the ridge, supporting the view that over MAR their presence was correlated with their prey.

#### 4.4. Zoogeographical affiliation

In this study, the border between clusters B and F marked a considerable change in terms of zoogeographical composition.

With respect to stomiids, abundance was considerably low for *Stomias boa ferox* in clusters A and B, contrasting the distribution of *Chauliodus sloani*. This refers to Kreffft's (1976) classification assigning *S. boa ferox* to a North-temperate-subtropical pattern and *C. sloani* to a broader biantitropical pattern. *C. sloani* is a widespread species also present in the Indian and Pacific Ocean, whereas *S. boa ferox* is restricted to the North Atlantic (Gibbs, 1986; Butler et al., 2001).

*Lampanyctus crocodilus*, present only in the North Atlantic, finds its northern limit in temperate waters off Iceland (Nafpaktitis et al., 1977; Hulley, 1981) and can be characterized as a temperate species. Abundances per  $\text{h}^{-1}$  trawling increased steadily from the southern leg (cluster A—7.33, cluster B—23.86) over the transverse (cluster F—68.44) to the northern leg (cluster D—104.29, cluster E—314). Our data suggest a considerable increase of abundance towards the shelf slope along the northern leg. The temperate-subtropical congener *L. pusillus* (Hulley, 1981) was markedly present only in cluster B ( $4.3 \text{ n h}^{-1}$  trawling). Off Fuerteventura, the latter was dominating over *L. crocodilus* (Badcock, 1970). A further consolidating species for cluster B was *Lobianchia gemellarii* (Table 2), a tropical-subtropical species (Nafpaktitis et al., 1977). Comparably, *Ceratoscopelus maderensis* was a consolidating and discriminating species only for cluster B. *C. maderensis* is a temperate-subtropical species, and its discriminating function with respect to cluster B proves, that cluster B comprised a temperate-subtropical species composition, which is substantiated by water mass classification (Fig. 4).

*Benthoosema glaciale* contributed notably to the northern clusters, but not to clusters A and B. It was a powerful discriminating species for cluster F towards cluster B (Table 3). Likewise, *B. glaciale* was the most abundant species in slope waters at the northern flank of the NAC in the western North Atlantic (Backus and Craddock, 1982), but

of negligible abundance in Gulf Stream and northern Sargasso Sea waters (Jahn and Backus, 1976). It is a subpolar-temperate species (Nafpaktitis et al., 1977; Hulley, 1981) and thus likely to indicate the extension of temperate-subarctic waters in the area of investigation. Contrasting the present study, *Benthoosema glaciale* was the predominant myctophid in the 1974 cruise of Roe and Badcock (1984) and the 1979 study of Hulley and Kreffft (1985), both at latitudes comparable to the southern leg (see crossed circle in Fig. 1). Albeit the former linked the southward shift for this species to a springtime southward shift of the thermohaline front associated with the North Atlantic Current and the eastern subtropical gyre (Roe et al., 1984), Fig. 3C shows that both deviating studies were carried out during periods of low regional SST, probably establishing a general southward shift for subarctic-temperate species. Further south, *B. glaciale* was found only in the Mauretanian upwelling area (Badcock, 1981).

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