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Deep-sea pelagic ichthyonekton diversity in the Atlantic Ocean and the adjacent sector of the Southern Ocean

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Abstract

Species richness of pelagic deep-sea fishes was analysed for 66 stations. For local and regional richness latitudinal gradients were present, asymmetric between North and South Atlantic. Lowest values were indicated for the Antarctic stations. The analysis of local-regional richness relationships indicated that assemblages were saturated. In support of the productivity-diversity hypothesis, a strong hump-shaped relationship to primary production was indicated. Regional effects on local richness were indicated in that a regionalisation in accordance to Merrett's (1987) hypothesis on the effect of seasonal productivity improved the model significantly. For regional richness, historical influences by means of the overlap between tropical and boreal faunas could not be precluded.

## Introduction

According to the Convention on Biological Diversity (CBD) enacted during the 1992 Rio Earth Summit, biodiversity is "the variability among living species from all sources ... and the ecological complexes of which they are part; this includes diversity within species, between species and ecosystems". This means all variability in the natural world (Angel 1993). Currently, changes and trends of biodiversity have become central interest of research also including overfishing of marine resources and its subsequent effect on associated ecosystem services (Price 2001, Hutchings & Baum 2005, Worm et al. 2006). In this study, biodiversity is analysed in terms of numbers of species in a sample, its large-scale patterns and underlying causative factors.

Large-scale patterns of biodiversity and community diversity patterns are complementary "as each one loses much of its meaning that both have when taken together" (Margalef 1997, p. 115). Accordingly, an explicit link between local determinism, regional and historical processes for generating diversity has been postulated, embedded within a multi-scale framework (Gage 2004, Ricklefs 2004).

Local determinism predicts that (1) diversity is strongly correlated to environmental aspects, (2) local diversity in similar habitats is similar irrespective of regional affiliation, (3) local diversity at some level is irrespective of the regional species pool, i.e. saturated (Angel 1997, Ricklefs 2004).

For the Atlantic, regional processes affecting faunal diversity by means of species composition and by changes of life history traits were first introduced to deep-sea ecology by Merrett (1987), revealing an abrupt change for deep-sea demersal fish assemblages located at 34-41°N. Northern species were characterized by relatively large bodysize, high fecundity, and negative buoyancy and vice versa. He hypothesized that these differences were attributed to an increased seasonality in primary production in the North with intensive vernal pulses of organic matter to the deep-sea. Angel (1991, 1993, 1997) reinforced this argument with

respect to similar changes in the plankton at ca 40°N and emphasized the general importance of this feature for ocean diversity.

The global pattern of biodiversity is that latitudinal species diversity gradients (LSDGs) decline towards the poles (Hillebrand 2004). In the oceanic realm, biodiversity gradients have been described with respect to latitude and vertically with respect to depth (Angel 1997, Levin et al. 2001, Macpherson 2002). Specific analyses for selected ecological groups of fishes yielded more complex figures (Worm et al. 2005). Compared to terrestrial habitats, the number of species in the oceanic pelagic environment is low, since extensive mixing through the major oceanic current systems provides sufficient gene-flow to hinder speciation (Angel 1997).

Among the more than 30 hypotheses to explain LSDGs (Willig et al. 2003), in the marine world the species richness-energy hypothesis has prevailed over mechanistic (Smith & Gaines 2003, Kendall & Haedrich 2006) or purely evolutionary concepts (Roy et al. 1998). On the one hand, the species richness-energy hypothesis proposes a link to diversity in terms of a productivity-diversity relationship with temperature as a proxy for productivity (e.g. Fraser & Currie 1996, Roy et al. 1998). Productivity-diversity relationships for fishes appear to be hump-shaped (Mittelbach et al. 2001) or negative (Macpherson 2002). Alternatively, local richness-temperature relationships have been attributed to features such as epipelagic water column structure (Rutherford et al. 1999), thermal fronts (Worm et al. 2005), developmental modes (Roy et al. 2000, Astorga et al. 2003), or to faster metabolic and evolutionary rates (Allen et al. 2002). Still, the complexity of the matter leaves broad room for controversy (metabolic rate: Huston 2003, Storch 2003, evolutionary time : Briggs 2006).

From published data, regional diversity for Atlantic pelagic fishes reaches a maximum from ca 40 °N to 15 °S with 400 pelagic species per 5°-band (Macpherson 2002). A corresponding local diversity maximum of ca 150 species for the upper 2000 m occurs at 18 °N 25 °W (Angel 1993).

This study comprises hitherto unrecognized data for bathypelagic fishes spanning from the Southern Ocean to the Arctic sector of the North Atlantic. Community structure has been analysed to some extent (Krefft 1974, 1976, Hulley & Krefft 1985, Fock et al. 2004).

The extreme habitat is considered almost pristine at the time of sampling and offers unique opportunities to the study. First, due to sampling depth this study overcomes sources of error encountered for investigations of shallow pelagic fauna, i.e. seasonal incompleteness of species inventories especially at high latitudes and mixing of local communities with expatriates due to eddy advection (Angel 1997). Bathy- and abyssopelagic fauna has non-seasonal modes of development (Mauchline 1991) and eddies at depth are likely bound by bottom topography (Bower et al. 2002). Second, many surface bound factors so far employed to explain diversity patterns do not apply at bathypelagic depths, providing validation opportunities of the different aspects of the species richness-energy hypothesis (Rex et al. 2001).

## Material and methods

Climatological reference data at 1°-resolution from the World Ocean Atlas 2001 were interpolated to station coordinates (WOA, <http://ferret.pmel.noaa.gov/NVODS/servlets/dataset> (Conkright et al. 2002)). Sea temperature at 1750 m and the sea temperature difference between 500 m and 1750 m were considered to indicate local environmental conditions and water column stability. Surface chlorophyll was taken as one proxy for productivity. At higher spatial resolution compared to WOA measurements, VGPM cloudiness-corrected primary production estimates (see Behrenfeld & Falkowski 1997) based on SEAWIFS remote sensing were applied as a further productivity measure (at [http://marine.rutgers.edu/opp/production/html\\_files/annu\\_glb\\_T\\_cld\\_inh1.html](http://marine.rutgers.edu/opp/production/html_files/annu_glb_T_cld_inh1.html)). Satellite derived measures are reliable proxies for productivity and regional biological oceanography (Longhurst 1998, Marañón et al. 2000), and indicative of decadal variability in ocean primary production (Gregg et al. 2003). Longhurst's biogeographical scheme (Longhurst 1998) was further applied to characterize regional oceanography.

66 bathypelagic stations with a nominal catching depth of 1200 to 2400 m were selected (Fig. 1, Table 1) representing the same type of habitat (Srivastava 1999, her method 3, Willig et al. 2003). Data were retrieved from hand-written cruise diaries archived at the Federal Research Center for Fisheries (BfaFi), Germany. Sampling was carried out between 1968 and 1986. Sampling and taxonomic analysis followed a standard protocol with great continuity also in the personnel involved (Post 1987). Except for three hauls in 1976, when a non-closing 23 m x 25 m MT1000 was deployed, a non-closing 20 m x 30 m MT1600 was used. Time-at-depth varied between 15 minutes and 2 hours.

Sampling from the same depth stratum presumably leads to the same degree of background contamination from shallower depths for all samples and thus omits confounding contamination effects. Diel vertical migration was not considered (Mauchline 1991, but see Angel 1997). The fauna comprised micronektonic as well as larger fishes. Taxonomic

resolution was harmonized between cruises, i.e. epipelagic taxa were omitted (e.g. Lampridae, Exocetidae, Pomacanthidae, genera *Macroramphosus*, *Antigonia*, *Capros*, *Zenopsis*). Genera *Cubiceps* and *Cyclothone* were not resolved to species level. Two extraordinary catch numbers were considered background contamination and omitted, i.e. 10000 *Maurolicus muelleri* from station 463\_86 and 3500 *Electrona carlsbergi* from station 21\_II\_76.

To account for potential mid-domain effects (MDEs), a presence/absence (p/a)-MDS ordination was carried out. Prior to analysis, single- and doubletons were omitted from the data set (McKelvie 1985), amounting to 435 taxonomic units. The mid-domain effect predicts that in bounded environments random mixing of species distribution ranges generates diversity peaks near or in the center of the gradient (Colwell et al. 2004). Homogeneous ordinations reflecting a gradient ('horseshoe-effect', Digby & Kempton 1987) would indicate the possibility of MDEs. Ordinations were carried out with the PRIMER software package (Clarke & Gorley 2001).

For diversity analysis, 685 taxonomic units were analyzed, including single- and doubletons. Local species richness (SL) was determined as individual-based rarefaction species numbers to overcome sample size bias (Gotelli & Colwell 2001), normalized to 100 specimens (ES100). Rarefaction sample size range for deep-sea fauna has been between 50 and 200 (Rex et al. 1997, Wilson 1998). Rarefaction overestimates richness if species are not distributed randomly (e.g. benthos, Gray 2002). This is not assumed in this study considering the large nets deployed. Total number of species per sample (S), specimens caught (N), Shannon-Wiener diversity ( $H'$ , base e) and evenness for  $H'$  ( $J'$ ) were tabulated for each station.

Regional species richness (SR) was calculated for 5° to 10°-latitudinal bands (Macpherson 2002), depending on station coverage. Regional species richness was calculated stepwise for 2 to 5 ('5p') samples pooled per latitudinal band. These were analysed by means of  $\log(\text{samples})-\log(\text{SR})$  accumulation curves by region for scale effects (Srivastava 1999,

Willig et al. 2003). In log-log plots, parallel slopes indicate scale invariance of local-regional relationships and non-saturation of local communities.

SL-SR plots for all regions combined corrected for spatial pseudoreplication were analyzed for SL saturation effects, i.e. non-linearity (Srivastava 1999). The fit ( $r^2$ ) of a linear and a non-linear (power) model with the same number of parameters were compared (Cresswell & Vidal-Martinez 1995). To account for artificial saturation effects due to an area effect for SR (Caley & Schluter 1997), the SR-area correlation was calculated excluding the Antarctic for which the size of the province relevant to the fauna analyzed could not be determined (Clarke & Johnston 2003).

SR estimates were calculated as sample-based jackknife2-estimates with EstimateS<sup>1</sup> also estimating 'unseen' species. To account for sample-size bias, i.e. the range of mean time-at-depth, SR estimates for the South Atlantic zone '45-55S' with an average of 0.5 hours time-at-depth were rescaled to 0.8 hours in order to compare with the other SR-values (see Table 2).

Sample size as scaled time-at-depth  $t^b$  was rescaled after

$$\log (SL/SR) = \log a + b \cdot \log (t) + c \cdot |lat|,$$

adopted from He et al. (2005, eq. 3). For simplicity, the parameter  $a$  representing initial immigration and extinction rates in relation to  $t^b$  and SR was assumed constant. Further variability was treated as function of absolute latitude ( $lat$ ).

Local determinism, regional processes, and historical events are the three main driving forces for diversity to be considered and tested in this study. With expected decadal variability in pelagic assemblages (Watanabe & Kawaguchi 2003), diversity relationships were graphically analyzed with a LOESS smoother without prejudging the shape and monotonicity of the relationships. For local-regional relationships, the hypothesis tested was whether a model of locally determined diversity performed better than a regionally partitioned model of local

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<sup>1</sup> R. K. Colwell (2001) EstimateS: statistical estimation of species richness and species from samples. Version 6. <http://viceroy.eeb.uconn.edu/estimates>

diversity according to Merrett's (1987) hypothesis. Partitioning of local assemblages was tested with a randomization test based on the sum of squared errors. Inference of historical influences was based on comparisons of tabulated palaeo-oceanographic events in particular for high latitudes with SL- and SR-distribution patterns. For historical influences, the stability-time hypothesis predicts that stable conditions enhance diversity (Willig et al. 2003). Further, historical faunal expansions should generate zones of overlap in accordance with recent oceanography.

## Results

MDS revealed distinct aggregation of stations indicating a discontinuous and non-random community structure (Fig. 2). A compact northern group north off 40°N was evident ('N' in Fig. 2), separated from a northern subtropical group and a tropical assemblage. The southernmost group ('S', latitudes 51-57) was neighbored by an assemblage at 35-45 °S. The distinct geographical pattern proves that diversity gradients are not likely subject to random mixtures of species and thus of distribution ranges, which would be expected under the mid-domain effect.

Local species richness SL(ES100) was significantly correlated with evenness J' ( $r = 0.76$ ) and Shannon-Wiener diversity H' ( $r = 0.93$ ) (Table 1 for data). This indicates a relationship between local species richness and assemblage structure. Hereafter, only SL and its relationship to SR are further considered. Lowest SL values were encountered at the northern- and southernmost stations (Fig. 1). The latitudinal SL gradient was asymmetric with a break at 35°N and a broad shoulder at mid-latitudes in the South (Fig. 3). At high latitudes, SL was comparably higher in the North than in the South. At the equator, data structure is not clear. Whereas the smoothed curve slightly declined across the equator, the original SL values indicated a V-like depression partly reflecting differences in regional currents (Fig. 3).

The transition from local (SL) to regional richness (SR) was scale-dependent and not confounded by area size (SR-area correlation  $r^2 = 0.02$ , calculation not shown). The log-log slope coefficients from the species accumulation curves were low at high latitudes and had an indifferent trend towards low latitudes (Table 2). High-latitude SR increased less with the number of samples than SR at other latitudes. As a consequence, latitudinal SR-gradients were steeper than SL-gradients. The resulting SR-pattern was more asymmetric than for SL. Highest SR was observed at the southern Subtropical Gyre and the northern Equatorial region (Fig. 3). Patterns were fairly similar when 3 (3p) and 5 (5p) samples were pooled, so that extrapolation had no confounding effect. Even with rescaled values, high latitude SR at 45-55° was lower in the South (SR(p5) = 166) than in the North (SR(5p) = 190, Table 2). Scale dependence for the log-log accumulation curves indicated saturation for local communities. Saturation for SL, i.e. non-linearity was also evident in the SL-SR plot for all regions combined. The fit for the power function was better ( $r^2 = 0.9$ ) as compared to the linear function ( $r^2 = 0.81$ ). A quadratic function yielded the best fit ( $r^2 = 0.92$ , Fig. 4). Both terms of the quadratic function were significant (first order term  $p = 0.0016$ , quadratic term  $p = 0.014$ ).

From the environmental conditions potentially causative for local determinism, only productivity showed a robust relationship to SL both for WOA chlorophyll and VGPM primary production (Fig's 5 b, c). Due to outliers, the hump-shaped pattern was less pronounced for primary production (Fig 5 c) than for chlorophyll (Fig 5 b). Outliers were the stations of the Southern Ocean either as single (Fig. 5 b : St 21\_II\_76) or as a group (Fig 5 c shaded area). The coherence between the southernmost stations was also evident with respect to environmental temperature (Fig. 5 d) and water column stability (Fig. 5 e). However, for the latter two factors no general relationship to SL was evident.

To analyse regional effects, stations were regrouped according to Merrett's hypothesis with a sharp 40° latitude border corresponding to high and low seasonal increases of primary

production (Table 2). For the North Atlantic, regrouping was justified by the MDS community analysis. In the South Atlantic, regrouping splitted up the stations from the southern Sub-Tropical Convergence. As a first result, regrouping removed the outlying position of the southernmost group of stations in the SL-primary production plot (Fig. 5 c) and constitutes similar hump-shaped figures for both groups (Fig. 6 a). The chosen regrouping was significant in that SSE was at minimum at 40° in stepwise partitioning (Fig. 7). The randomization test for 40° latitude was significant ( $p < 0.01$ ,  $n = 101$  trials). This indicates that at low latitudes  $< 40^\circ$  maximum SL was reached at lower productivity, that at high latitudes  $> 40^\circ$  maximum SL was reached at higher productivity and that maximum SL at high latitudes was smaller than maximum SL at low latitudes. As for SL, regrouping SR values into the same scheme resulted in 2 hump-shaped curves (Fig. 6 b).

Geological history of the Atlantic Ocean is unlikely to explain observed patterns for SL (Table 3). The Southern Ocean and the South Atlantic have been relatively more connected to adjacent oceans than the North Atlantic. During the most recent 4 My, conditions have been more stable in the Southern Ocean than in the Arctic North Atlantic. Despite the very different histories, the poleward decline of SL is qualitatively similar in the North and the South Atlantic. Moreover, opposite to the pattern expected from the stability-time hypothesis, relatively stable long-term conditions in the Antarctic did not increase the number of pelagic fish species as compared to the North Atlantic with higher SL numbers by latitude.

However, for SR the expansion of boreal faunas towards low latitudes during the last 60 My BP (Table 3) presumably created an overlap between tropical and boreal faunas with higher diversity in the zone of overlap. The three latitudinal peaks of SR with maximum values at 30°S, 10°N in the eastern central Atlantic and 35 °N in the Mid-Atlantic (Fig. 3) coincided with the modern tropical-boreal border, which is asymmetric across the North Atlantic, and the borders of subtropical provinces (Fig.1).

## Discussion

The analysis revealed a clear LSDG for local (SL) and regional (SR) species richness of deep-sea Atlantic pelagic fishes, related to productivity in support of the productivity-diversity hypothesis. The productivity-diversity relationship was significantly improved when nested within a regional framework with regard to seasonality of production (see Merrett 1987, Angel 1997). The productivity-SL relationship was robust despite expected decadal variability. For SR, further historical effects, i.e. overlap between boreal and tropical faunas could not be precluded. No evidence for the stability-time hypothesis was inferred. As for MDE, the mechanistic explanation of the LSDG was rejected. MDEs failed to explain ocean diversity gradients (Smith & Brown 2002, Kendall & Haedrich 2006), albeit supporting evidence in other habitats (Colwell et al. 2004). Rapoport's rule linking diversity reciprocally to distributional range size, was ineffective to explain marine LSDGs (Rohde et al. 1993, Smith & Gaines 2003, Kendall & Haedrich 2006) and was not investigated in this study. The resulting SL- and SR-patterns are congruent with other LSDGs in that there is a depression of SL at the equator (foraminiferans, Rutherford et al. 1999, tintinnids, Dolan et al. 2006), in that there is a North-South asymmetry in species richness (Chown et al. 2004), with greater diversity in the subtropical South Atlantic than in the corresponding part of the North Atlantic (deep-sea gastropods and isopods, Rex et al. 1997, foraminiferans, Culver & Buzas 2000, tintinnids, Dolan et al. 2006), and in that species richness by latitude is lower in the Antarctic than in the North Atlantic (fishes, Macpherson 2002). Generally, the Antarctic fish fauna is low in diversity (Clarke & Johnston 2003).

The asymmetry in species richness between the North and South Atlantic could not be explained. However, palaeo-ecological redistribution pathways during the last 50 My give a possible cue to the understanding of this phenomenon in that the major deep-water pathways

originated in the West Pacific and led into the South Atlantic before entering the North Atlantic (Miranov 2006).

From the causative factors, no effect of geological history on the SL-gradient was inferred, contrary to the stability-time hypothesis. For Pacific and Atlantic gastropods respective results were obtained (Roy et al. 1998).

In turn, for the SR-gradient the Eocene expansion of boreal faunas would lead to overlap patterns likely to resemble the SR-gradient for the South and the North Atlantic presented here. Three findings augment this interpretation.

First, peaks appeared for both hemispheres corresponding to the boreal expansions from both poles, but not for other zones.

Second, due to the strong asymmetry of the northern tropical-boreal boundary, i.e. reaching about 10°N in the eastern central Atlantic and 30°N in the Mid-Atlantic (Briggs 1970), both peaks or breaks in the North Atlantic SR-gradient can be explained by the same underlying process. The proposed overlap of faunas along the asymmetric tropical-boreal boundary implies a longitudinal gradient for SR, which was shown for Atlantic foraminiferans (Rutherford et al. 1999) and in a meta-analysis (Hillebrand 2004). The asymmetry is evidenced e.g. through the occurrence of the subpolar-temperate myctophid *Benthosema glaciale* off Africa (Badcock 1981). The SR peak in the eastern central Atlantic coincided with the peak found by Angel (1993) at 18°N 25°W. Corresponding to the break at 32.5°N for SR and at 35°N for SL for the Mid-Atlantic, a broad zone of overlap of distribution ranges for West Atlantic gastropods was indicated from 25°N to 42°N with a peak at 35°N (Roy et al. 1998). In the West Atlantic, species richness of flabelliferan isopods, an evolutionary new deep-sea group mostly confined to the mid-latitude South Atlantic, collapses at about 35°N (in Wilson 1998). The SL break at 35 °N coincided with the frontal system of the Subtropical Convergence (Longhurst 1998). Convergence zones are important for the generation of local species maxima at the surface (Angel 1993, McClatchie et al. 1997). The associated

Subtropical Gyre extends from the surface into the intermediate layer (ca. 1800 m, Schmitz & McCartney 1993) likely also to delimit bathypelagic fauna. In the South Atlantic, the SR-maximum at 30°S coincided at depth with the zone of interleaving for North Atlantic Deep water and Antarctic Intermediate water (Colling 2001). As for SR-maxima, species richness maxima for euphausiids in the South Atlantic occurred at 30°-35°S (Gibbons 1997). The underlying process of boreal expansion is further reflected in that tropical teleost fishes have greater latitudinal ranges than high-latitude species, a likely reminiscence of ancient high-latitude water temperature conditions (Rohde et al. 1993).

Third, the overlap for deep-sea fishes in this study is not observed in species collations of fish fauna from shallower depths (e.g. Macpherson & Duarte 1994, Macpherson 2002). This is presumably related to the increased rate of speciation in shallow tropical habitats during the last 7 My due to habitat development of the neritic zone, i.e. uplift of the Central American isthmus (Crame 2001, Buzas et al. 2002, Briggs 2006). This should not apply to deep-sea habitats. Increased tropical speciation rates were not observed in this study, since the increased steepness of LSDGs for SR as compared to SL (Hillebrand 2004) was attributed to lower log-log slope values at high latitudes, but not to consistently high log-log slopes at lower latitudes. Storch et al. (2005) found a negative relationship between productivity and log-log slopes for avifauna, i.e. decreasing steepness with increasing productivity.

From the environmental factors analysed, only productivity was consistently linked to the SL-gradient both in the over-all (Fig. 5 b, c) and the regionalised analysis (Fig. 6 a). Consistent productivity-diversity explanations for LSDGs have been provided for deep-sea foraminiferans (Thomas & Gooday 1996, but differently in Rutherford et al. 1999) and planktonic tintinnids (Dolan et al. 2006). Local deep-sea diversity changes in time series were significantly linked to changes in productivity (Cronin & Raymo 1997, Ruhl & Smith 2004). In turn, Danovaro et al. (2004) failed to prove the productivity-diversity relationship, however based on indirect

data for surface productivity. Sedimentation processes take about 1 month to transport organic matter from the surface to the abyssal bottom (Deuser 1986), linking the one surface process to the deep-sea environment within a reasonable time frame.

Margalef (1997, p. 113) and Levin et al. (2001, p. 79) have provided complementary successional-functional hypotheses for the hump-shaped productivity-diversity relationship. At low resource levels, food supply limits the number of populations in a community. As resources increase until optimum supply level, more populations can be maintained. Excess and often pulsed supply allows only few opportunistic species to further increase, so that competitive exclusion depresses diversity. The increase of diversity has implications for the distribution of interaction strengths in communities, leading to an increase of weak interaction strengths (McCann 2000). Weak interactions serve to limit energy flow in a potentially strong resource-consumer relationship and thus inhibit runaway consumption. Thus, strong seasonal pulses of resource input hinder the constitution of weak interactions and thus depress the number of species. The community concept emphasizes that patterns of biodiversity emerge from how organisms utilize resources (scaling laws, Ritchie & Olf 1999).

A strong environmental SL-correlate was an indicator for local determinism (Ricklefs 2004). Local determinism was also indicated by non-linearity in SL-SR plots (see Fig. 4) and non-parallel log-log slopes (Table 2). Here, the degree of local determinism is relatively high and accounts for 19 % in the SL-SR plot (linear  $r^2 = 0.81$ ), since the maximum share for local determinism was 30 % in linear SL-SR plots under the constraint of fully competitive organization for model communities (linear  $r^2 = 0.7$ ) (Hillebrand 2005). Significant quadratic terms in SL-SR regressions only appeared when > 60 % of the communities were competitively controlled (Hillebrand 2005). For coral reefs, and sampling SR in a similar way from own local data instead of applying published collations, a low degree of local determinism was indicated (i.e. high linear  $r^2 = 0.94-0.99$ , Karlson et al. 2004). This probably points at the importance of different types of communities (sessile vs. mobile) and the effect

of vicinity to speciation hotspots as was the case for the coral reef study. The present study gives no indication how community type is linked to the diversity gradient. The regionalization of SL according to Merret's hypothesis (1987) into two different regimes partially reflected changes in community composition as indicated in the MDS-plot, where five groups were discerned (Fig. 2). This points at different processes for community composition and for community diversity. Species composition of oceanic assemblages is related to water mass structure (Jahn & Backus 1976, Fock et al. 2004) and thus biogeochemical partitioning of the ocean (see Table 2, after Longhurst 1998).

At the SL-SR interface, observations (Chase & Leibold 2002) and modeling results (Steiner & Leibold 2004) indicate that a hump-shaped productivity-diversity relationship for SL turns into a positive linear relationship for SR. This was due to high species turnover or  $\beta$ -diversity at high productivity (Chase & Leibold 2002). In this study, the SR-productivity curve was curvilinear, and turnover by means of the log-log slope coefficient was not positively related to productivity, e.g. the zone SATL with a high value for productivity had a comparably small slope coefficient (Table 2). The linear SR-productivity relationships published for Atlantic fishes so far are likely subject to incompletely covered gradients (Fock 2003) or to analysis constraints (Macpherson 2002).

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## Figures

Fig. 1 Station locations.

Station bubbles indicate local species richness SL. Bold full line: Recent border between tropical and boreal faunas (Briggs 1970), bold broken lines: border of mesopelagic subtropical seas (North: southern Sargasso Sea and southern African Sea, South: South Atlantic Subtropical Sea/Transitional zone) (Backus et al. 1977, Herman 1979). Scale bar indicates annual primary production ( $\text{g C m}^{-2} \text{yr}^{-1}$ ).

Fig. 2 MDS community ordination

Ordination for presence/absence data (stress 0.13). Numbers indicate station latitudes. 'N' and 'S' indicate meridional orientation.

Fig. 3 Latitudinal gradients in local and regional species richness and location of oceanographic features.

Lower panel : SL, upper panel : SR values at different accumulation levels, thin line = 3 samples pooled (3p), bold line = 5 samples pooled (5p). Squares indicate extrapolated values, arrow indicates values rescaled to larger sample size for the southernmost zone. ACC - Antarctic Circumpolar Current, EC - Equatorial Counter Current, NEC - North Equatorial Current, SEC - South Equatorial Current, SF - Subpolar Front, STC - Subtropical Convergence.

Fig. 4 Analysis of local-regional species richness relationship

SR as 5-sample aggregates for regional richness. Line indicates regression with quadratic fit and 95%-CI. For SR, zonal affiliation indicated according to Table 1 and Table 2.

Fig. 5 Local species richness relationships

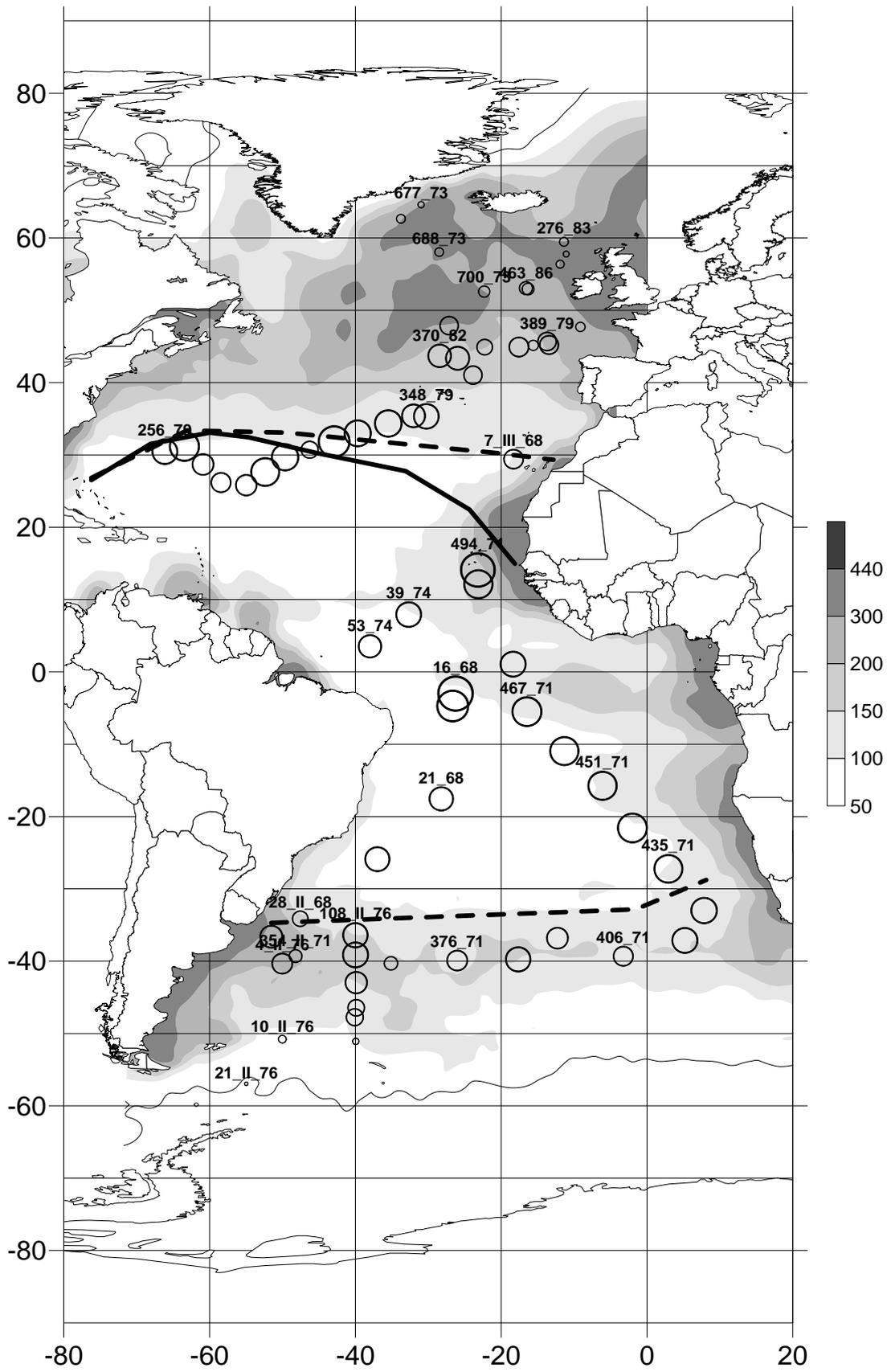
Species richness SL(ES100) in relation to (a) latitude, (b) surface chlorophyll, (c) primary production, (d) sea temperature at 1750 m, (e) temperature difference between 500 and 1750 m. Non-parametric LOESS smoother fitted. Shaded area indicates southernmost stations.

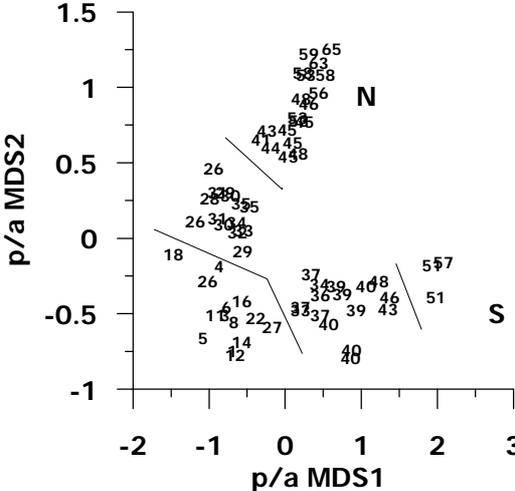
Fig. 6 Regionalisation of local (SL) and regional richness (SR)

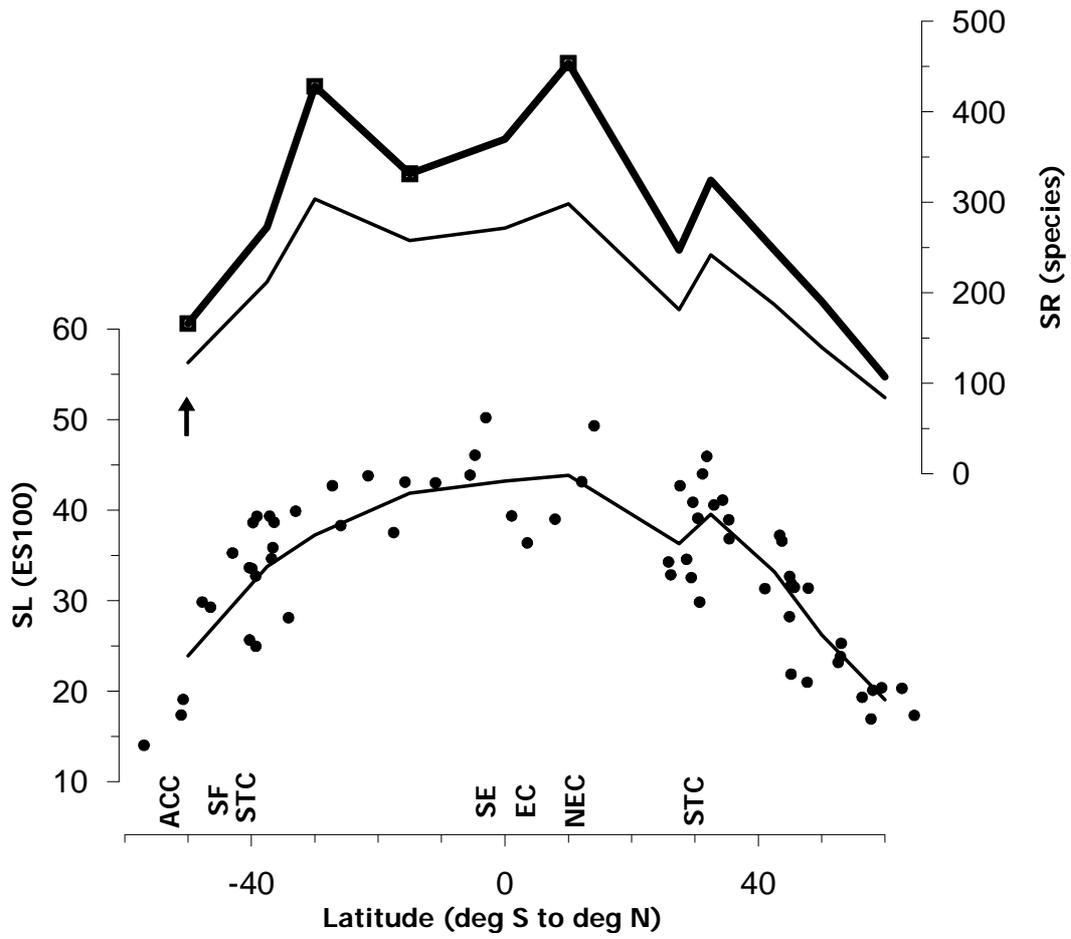
Open circles – stations  $> 40^\circ$  latitude, dots – stations  $< 40^\circ$  latitude. Non-parametric LOESS smoother fitted.

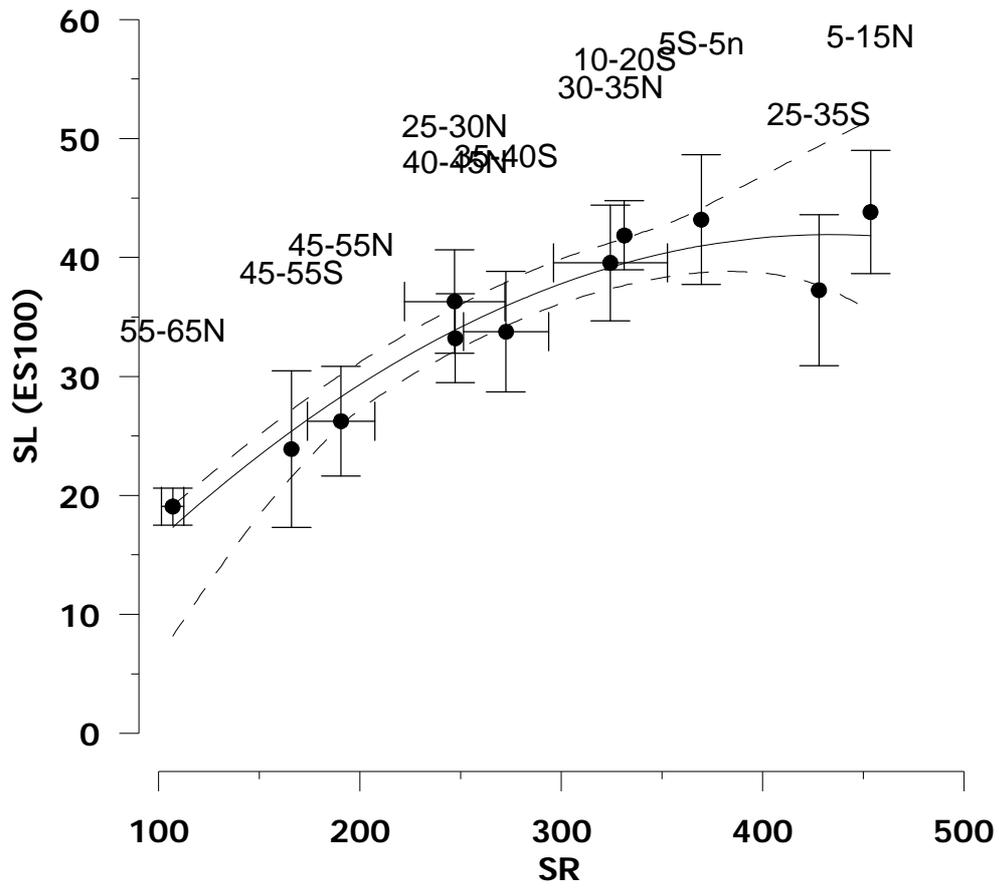
Fig. 7 Sum of squared errors for LOESS fits for different regionalisations

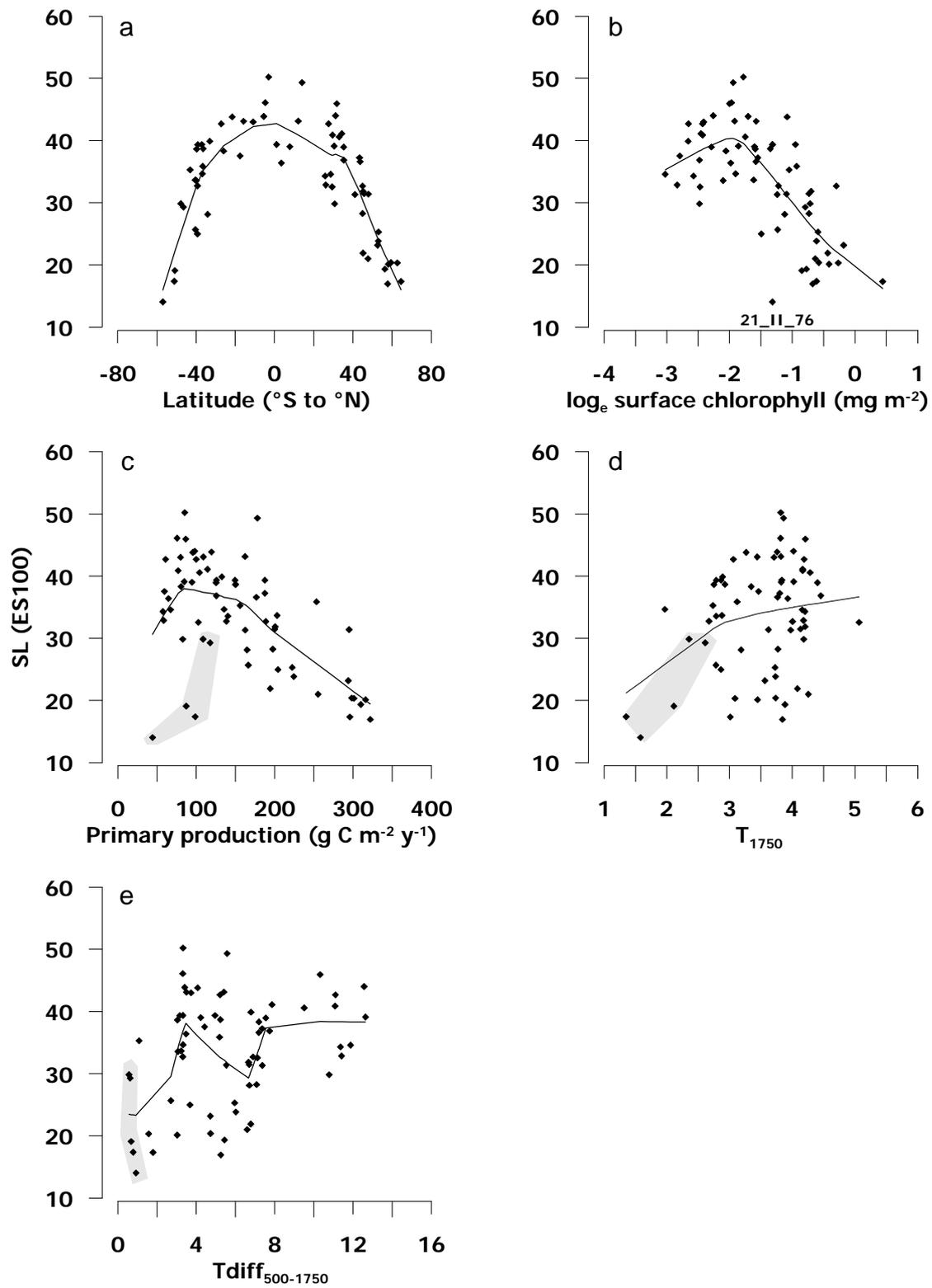
x-axis indicates latitudinal partitioning. 'No'-partitioning refers to Fig. 5a, partitioning at '40'-degrees latitude refers to Fig 6.

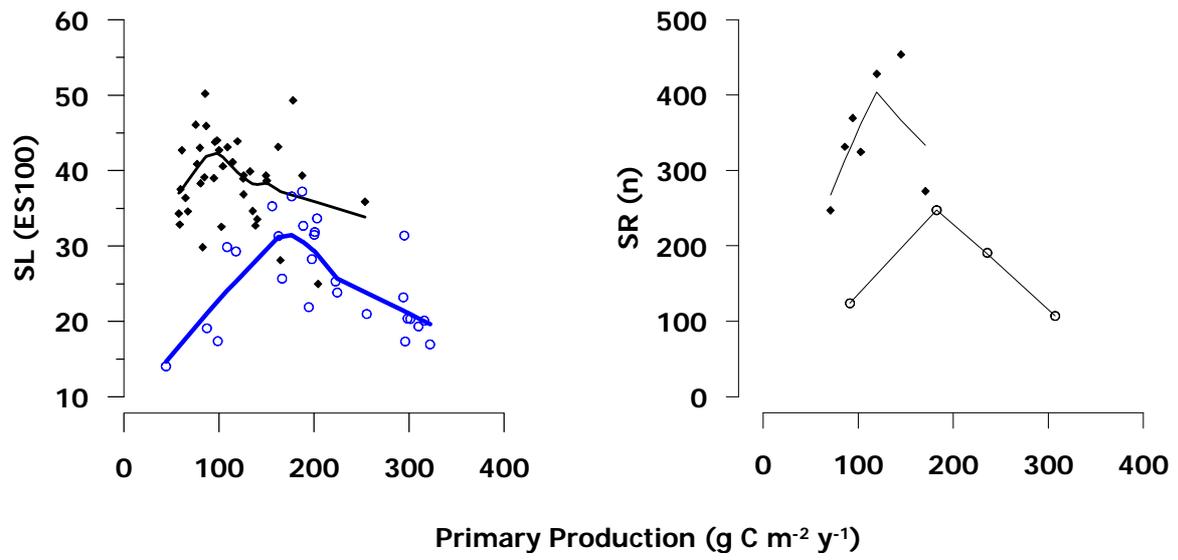












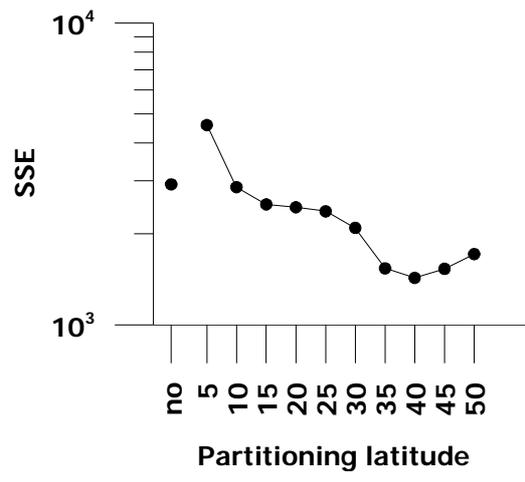


Table 1 : Station data, zonal affiliation, total number of species per sample (S), total number of specimens (N), local species richness SL (ES100), evenness (J') and Shannon Wiener diversity (H').

STATION_ID	Zonal affiliation	Year	MONTH	DAY	lat	lon	FISHING DEPTH	BOTTOM Depth	SPEED (0.1 kn)	START_TIME (local time)	STOP_TIME (local time)	Remarks	S (n)	N (n)	SL (ES100)	H'	J'
21_II_76	45-55S	75	11	28	-56.95	54.97	2200	4200	37	17:10	17:40	MT1000	23	627	14.04	1.54	49
99_II_76	45-55S	76	1	4	-51.08	39.95	2300	3500	35	16:00	16:30		28	808	17.37	2.5	0.75
10_II_76	45-55S	75	11	22	-50.78	50.02	2050		35	17:45	18:15	MT1000	34	975	19.09	2.46	0.7
101_II_76	45-55S	76	1	5	-47.75	40.08	2000	5550	30	15:50	16:20		60	749	29.85	3.15	0.77
102_II_76	45-55S	76	1	6	-46.45	39.88	2000		35	16:25	16:55		62	789	29.28	3.1	0.75
104_II_76	-	76	1	7	-42.97	39.88	2350			15:50	16:20		63	453	35.28	3.44	0.83
4_II_76	35-40S	75	11	19	-40.33	50.03	2350	5000	25	17:50	18:20	MT1000	77	946	33.66	3.16	0.73
367_71	35-40S	71	3	9	-40.3	35.12	1850	4800	40	21:00	22:00		71	1408	25.67	2.84	0.67
376_71	35-40S	71	3	11	-39.92	26.03	2000		25	20:15	21:45		95	965	33.56	3.36	0.74
384_71	35-40S	71	3	13	-39.75	17.67	2000		25	20:45	21:15		47	142	38.63	3.25	0.84
406_71	35-40S	71	3	19	-39.32	3.25	2000		25	20:00	21:00		69	715	32.72	3.31	0.78
354_II_71	35-40S	71	3	6	-39.3	48.2	2000	5300	40	22:00	22:30		72	1225	24.97	2.84	0.66
106_II_76	35-40S	76	1	8	-39.13	39.98	1850			18:10	18:40		82	548	39.32	3.53	0.8
412_II_71	35-40S	71	3	21	-37.13	-5.2	2200		40	20:00	21:30		77	450	39.34	3.66	0.84
395_71	35-40S	71	3	17	-36.82	12.28	2000		40	01:45	03:45		69	464	34.65	3.42	0.81
30_68	35-40S	68	2	16	-36.62	51.53	2000	3000	35	23:40	00:40		69	497	35.87	3.49	0.82
108_II_76	35-40S	76	1	9	-36.42	40	2400			15:40	16:10		72	414	38.66	3.58	0.84
28_II_68	25-35S	68	2	14	-34.13	47.57	2000	4000	37.5	00:45	01:15		82	978	28.12	2.87	0.65
427_71	25-35S	71	3	30	-33	-7.83	2000		33	21:00	22:00		92	572	39.89	3.56	0.79
435_71	25-35S	71	4	1	-27.23	-2.93	2000		35	21:00	22:00		101	528	42.7	3.75	0.81
24_II_68	25-35S	68	2	10	-25.9	36.98	2000		35	23:45	00:15		60	233	38.31	3.47	0.85
443_71	10-20S	71	4	3	-21.58	2	2100	4500	30	20:25	21:25		106	590	43.8	3.88	0.83
21_68	10-20S	68	2	7	-17.55	28.22	2000	5000		23:05	23:35		39	107	37.53	3.23	0.88
451_71	10-20S	71	4	5	-15.75	6.1	1900		30	20:50	21:50		111	868	43.1	3.87	0.82
459_71	10-20S	71	4	7	-10.95	11.33	1900		30	19:52	20:52		86	400	43.01	3.8	0.85
467_71	5S-5n	71	4	9	-5.5	16.47	1900		25	20:00	21:00		112	912	43.88	3.91	0.83
17_68	5S-5n	68	2	4	-4.72	26.65	2000			11:55	12:55		81	374	46.08	3.87	0.88
16_68	5S-5n	68	2	3	-3	26.27	2000			19:15	19:45		96	420	50.22	4.05	0.89
478_71	5S-5n	71	4	12	1.07	18.37	2100		20	20:20	21:20		128	1264	39.37	3.5	0.72
53_74	5S-5n	74	7	23	3.53	38	2000	4140	22	21:00	21:15	step-haul	57	226	36.39	3.28	0.81
39_74	5-15N	74	7	21	7.92	32.68	2000	4840	16	19:40	20:25	step-haul	61	190	39.01	3.22	0.78
12_II_68	5-15N	68	1	30	12.12	23.13	2000	5000		22:35	23:05		113	890	43.14	3.91	0.83
494_71	5-15N	71	4	16	14.08	23.2	1900		25	20:30	21:30		127	859	49.32	4.12	0.85
293_79	25-30N	79	4	22	25.82	54.97	2000	5600	40	15:05:00	16:00:00		55	244	34.29	2.93	0.73
284_79	25-30N	79	4	21	26.18	58.43	2000	5600	25	15:00:00	16:00:00		41	177	32.86	3	0.81
301_79	25-30N	79	4	23	27.63	52.37	2000	5400	40	14:55:00	15:45:00		61	199	42.69	3.41	0.83
276_79	25-30N	79	4	20	28.68	60.9	1800		25	15:10:00	16:00:00		66	385	34.58	3.32	0.79
7_III_68	25-30N	68	1	22	29.42	18.3	2000		35	00:42	01:12		86	752	32.55	3.31	0.74

308_79	25-30N	79	4	24	29.67	49.64	2000	5200		15:35:00	16:30:00	72	304	40.87	3.59	0.84
256_79	30-35N	79	4	15	30.45	66.13	1800	4800	30	04:45:00	05:45:00	131	1297	39.11	3.65	0.75
314_I_79	30-35N	79	4	25	30.72	46.27	2000	4270	20	16:37:00	17:35:00	51	270	29.84	2.69	0.69
268_79	30-35N	79	4	19	31.18	63.45	1650	4760	25	15:10:00	15:55:00	88	435	44.01	3.82	0.85
321_79	30-35N	79	4	26	31.85	42.92	1950	3450	20	16:30:00	17:25:00	100	463	45.95	3.89	0.84
329_79	30-35N	79	4	27	32.98	39.68	1950	3900		15:35:00	16:30:00	86	485	40.57	3.63	0.82
338_79	30-35N	79	4	28	34.35	35.48	1300	2220	13	17:00:00	18:00:00	102	614	41.11	3.73	0.81
348_79	30-35N	79	4	30	35.33	30.27	1900	2760	20	06:40:00	07:10:00	84	602	38.94	3.62	0.82
345_79	30-35N	79	4	29	35.4	32.02	1800	2530	20	17:00:00	17:50:00	77	459	36.85	3.41	0.78
361_79	40-45N	79	5	2	41.03	23.87	2000	3580	15	11:35:00	12:30:00	70	640	31.33	3.15	0.74
359_82	40-45N	82	6	9	43.36	25.98	1230	3100	30	08:40:00	09:10:00	84	747	37.23	3.58	0.81
370_82	40-45N	82	6	10	43.7	28.44	1550	2200	40	16:45:00	17:25:00	84	705	36.59	3.56	0.8
371_79	40-45N	79	5	3	44.9	22.27	2000	3975	20	16:38:00	17:30:00	62	497	28.24	2.91	0.7
380_79	40-45N	79	5	4	44.92	17.57	1900	4400	20	17:20:00	18:20:00	61	436	32.69	3.16	0.77
335_82	45-55N	82	6	6	45.15	15.6	2250	3600	30	07:20:00	08:20:00	41	318	21.89	1.8	0.48
331_82	45-55N	82	6	5	45.21	13.43	1800	4100	30	15:45:00	16:45:00	56	297	31.85	2.81	0.7
389_79	45-55N	79	5	5	45.68	13.7	2000	4760	20	17:13:00	18:10:00	51	406	31.48	3.17	0.81
398_79	45-55N	79	5	6	47.7	9.13	2000	3970	20	18:37:00	20:00:00	42	629	20.99	2.66	0.71
383_82	45-55N	82	6	13	47.87	27.14	1370	2100	30	15:40:00	16:20:00	79	833	31.38	3.21	0.74
700_73	45-55N	73	9	24	52.58	22.33	1250	3940	30	18:40:00	19:10:00	36	472	23.19	2.55	0.71
464_86	45-55N	86	7	9	52.94	16.31	2300	3430	30	12:30:00	13:30:00	60	1142	23.84	2.74	0.67
463_86	45-55N	86	7	9	53.06	16.61	1800	3450	30	08:45:00	09:45:00	52	771	25.3	3	0.76
321_83	55-65N	83	5	18	56.37	11.91	1500	2600	40	06:45:00	08:00:00	39	772	19.33	2.49	0.68
291_83	55-65N	83	5	13	57.77	11.09	1500	2100	40	07:00:00	08:00:00	44	1795	16.94	1.91	0.5
688_73	55-65N	73	9	21	58.05	28.5	2100	2300	30	20:15:00	20:45:00	30	387	20.11	2.6	0.77
276_83	55-65N	83	5	9	59.46	11.39	1300	1650	40	18:02:00	19:02:00	37	436	20.38	2.71	0.75
681_73	55-65N	73	9	20	62.65	33.75	2100	2810	30	10:45:00	11:45:00	33	506	20.32	2.51	0.72
677_73	55-65N	73	9	19	64.6	30.98	2000	2440	25	10:42:00	11:12:00	22	320	17.33	2.38	0.77

Table 2 : Zonal environmental statistics and regional diversity and seasonal changes in primary production.

Zonal statistics calculated as means over all stations in the respective zone except for SR(5p). Seasonal changes indicate the min –max difference according to descriptions given by Longhurst (1998). ( ) indicate re-scaled values for 0.8 h sample size. \* extrapolated

Zone	Lat. midpoint (S-N)	Average annual primary production (g C m <sup>-2</sup> y <sup>-1</sup> )	Av. Temperature difference 500-1750 m	Average Temperature at 1750 m	Species accumulation curves: Log-log slope	Average time-at-depth (h)	Average local richness (SL)	Regional richness SR(5p)	Seasonal change in primary production
45-55S	-50	91.36	0.72	3.84	0.365	0.5	23.9	123.8* (166)	5x (SANT)
40-45S									4x (SSTC)
35-40S	-37.5	170.80	3.72	3.86	0.494	0.95	33.8	272.6	1.5 x (SATL)
25-35S	-30	119.54	6.48	4.22	0.6744	0.75	37.3	428.0*	
10-20S	-15	86.06	3.93	4.32	0.4931	0.88	41.9	331.3*	
5S-5N	0	94.24	3.37	2.73	0.6075	0.75	43.2	369.5	1.2 x (WTRA)
5-15N	10	144.92	5.07	3.50	0.8203	0.75	43.8	453.6*	1.2 x (NATR)
25-30N	27.5	70.68	10.66	3.12	0.6026	0.82	36.3	247.0	
30-35N	32.5	102.74	9.87	2.76	0.5774	0.86	39.5	324.4	2.5 x (NAST)
40-45N	42.5	182.54	7.18	3.91	0.5495	0.76	33.2	247.4	5.5 x (NADR)
45-55N	50	235.84	6.12	2.00	0.6066	0.95	26.2	190.6	8 x ( ARCT)
55-65N	60	307.28	3.64	3.83	0.477	0.88	19.1	107.0	

Biogeographical provinces: SANT - Subantarctic Water Ring, SSTC - Southern Subtropical Convergence, SATL - South Atlantic, WTRA - Western tropical Atlantic, NATR - North Atlantic Trade Winds, NAST - North Atlantic Subtropical Gyre, NADR - North Atlantic Drift, ARCT - Atlantic Arctic. Coastal provinces not considered for primary production calculations.

Table 3 : Evolutionary effective changes in the Atlantic Ocean and adjacent polar seas (after Briggs 1970, Wilson 1998, Clarke 2003, Clarke *et al.* 2004, Gage 2004, Haug *et al.* 2005)

My BP – million years before present, ACC – Antarctic Circumpolar Current

Time period	Antarctica	Arctica
60 My BP	Climatic deterioration : start of cooling period for entire Atlantic Ocean, mid-latitudinal expansion of boreal faunas towards equator	
40-50 My BP		Formation of Bering land-bridge impedes exchange with Pacific fauna and leads to species impoverishment of Atlantic boreal fauna
33-34 My BP	Formation of ice-sheets	
25-30 My BP	Opening of Drake passage establishes ACC and starts Antarctic isolation; before this, Antarctic confluence with Indian, Pacific and Atlantic Ocean should have increased 'effective area' for speciation and exchange and thus lead to enhanced diversity.	
14-16 My BP	Evolution of anti-freeze capacities, radiation of the teleost family Notothenoidea	
3-4 My BP	Relatively stable glaciation, Milankovitch variability of environmental conditions (period length 19000 – 400000 y)	Breakdown of land-bridge, immigration of northern Pacific species; rapid shifts in oceanic conditions due to warm-cold oscillations. Fluctuations of iceberg production (Heinrich-events, period length 10000 y)
2-3 My BP to present		Formation of ice-sheets