

Structural and functional aspects of the benthic communities in the deep Angola Basin

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ABSTRACT: During the RV 'Meteor' expedition 'DIVA I' the macro- and megafaunal communities were studied in 6 areas of the deep Angola Basin in July 2000. Water depths varied between 5162 and 5497 m. The macrofauna was dominated by polychaetes, peracarids and bivalves; the megafauna by ophiurids, bivalves and actinurians. Abundance and biomass of macro- and megafauna were similar to other non-oligotrophic deep sea areas >4000 m. Predatory polychaetes, peracarids and facultative surface deposit feeders or predatory sipunculids occurred in similar ratios in all areas. Facultative subsurface deposit-feeding or predatory nematodes and oligochaetes increased towards the northern Areas 4 to 6. The percentage of surface-deposit and interface-feeding organisms such as polychaetes and ophiurids, which dominated in Areas 2 and 3, decreased towards the north. For megafauna, the ratio of organisms feeding as suspension feeder or predator as well as surface-deposit feeder increased from south to north. In the northern Areas 4 to 6, high numbers of bivalves occurred, which feed as surface or subsurface deposit feeders. TOC and chlorophyll *a* contents in sediment, as well as macro- and megafaunal abundance and biomass, were lower in the southern Areas 1 to 3 than in the northern Areas 4 to 6. These differences seem to be connected to the different water masses north and south of the Angola–Benguela Front, which cross the transect of our 6 study sites. In the north, the Angola Basin is a highly productive region fed by the South Equatorial Counter Current and water masses from the Zaire (Congo) River, whereas in the south, the cold Benguela Oceanic Current is less productive. The structure and function of the benthic fauna in connection with sediment data give evidence for differences in food supply north and south of the front.

KEY WORDS: Angola Basin · Deep sea · Macrofauna · Megafauna · TOC · Chlorophyll *a* · Food availability · Benguela Oceanic Current

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INTRODUCTION

The circulation in the eastern South Atlantic Ocean is dominated by the Benguela Current system, which is part of the anticyclonic Subtropical Gyre. At about 30°S the Benguela Current separates into the Benguela Oceanic Current and the Benguela Coastal Current, which is influenced by the coastal upwelling regime. With flow velocities of 10 to 20 cm s⁻¹, the cold Benguela Oceanic Current crosses the Walvis Ridge and feeds the South Equatorial Current, whereas the Benguela Coastal Current meets the warm Angola Current at about 16°S, forming the Angola–Benguela Front in coastal regions. The South Equatorial Counter

Current results in a cyclonic gyre in the surface waters of the Angola Basin, which meets the cold Benguela Oceanic Current and extends the Angola–Benguela Front towards the open Angola Basin (Reid 1989, Petersen & Stramma 1991, Speer et al. 1995, Jansen et al. 1996, Wefer et al. 1996, Larqué et al. 1997).

The Angola Basin is situated off the Namibian and Angolan coast north of the Walvis Ridge. Water depths reach almost 5500 m. The water column in the basin is strongly stratified due to different water masses entering the area. The surface waters down to 200 m depth are characterised as the South Atlantic Subtropical Surface Water. Between 200 and 1400 m water depth the South Atlantic Central Water, the Antarctic Inter-

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mediate Water and the Upper Circumpolar Deep Water occur. Below 1400 m the Angola Basin is filled with North Atlantic Deep Water, which is modified by injections of Antarctic Bottom Water through deep gaps in the mid-Atlantic ridge system (Reid 1989, Shannon & Chapman 1991, Larqué et al. 1997) as well as by the Namib Col Current (Speer et al. 1995). In the north of the basin the influence of the Zaire (Congo) River plume can be detected in the water column up to 800 km from the coast (van Bennekom & Berger 1984, Larqué et al. 1997).

Intensive research in oceanography, geochemistry, microbiology, benthology and fisheries biology has been carried out in the Benguela upwelling system in coastal Namibian waters (Alva & Vadon 1989, Macpherson 1991, Holmes et al. 1996, Bernard et al. 1999, Schmidt et al. 2000). But there is only little information available for the deep Angola Basin. Foraminifera and meiofauna have been investigated only in coastal regions (Mackensen et al. 1995, Soltwedel & Thiel 1995, Schmiedl & Mackensen 1997, Schmiedl et al. 1997, Soltwedel 1997); macro- and megafauna only at 3 stations in the offshore SW Angola Basin by Vinogradova et al. (1990). Studies on meiofauna and megafauna at the Walvis Ridge, the southern border of the Angola Basin, have been carried out by Dinert (1973), Monniot & Monniot (1976) and Fedorov & Karamyshev (1991).

To fill the gap, the 'Meteor' Expedition Me 48/1—'DIVA I' (July 6 to August 2, 2000) took place in the Angola Basin to study the biodiversity and ecology of the benthic communities in extreme water depths of about 5500 m.

MATERIALS AND METHODS

Sampling and sample treatment. Megafauna: The megafauna was collected in 6 areas with a modified Agassiz-trawl of 3.5 m width (Fig. 1, Table 1). Depths varied between 5162 and 5497 m. The trawl was run twice in each area. The mesh size in the cod end measured 1 cm between stretched meshes. A fore-rope was let out 200 m, at which point a 500 kg weight was attached before the rope was lowered further. Based on our earlier experience, we paid out a rope length of 1.8 times the water depth to reach the sea floor. The sea bed was trawled for 2 to 3.5 h at 2 knots, which equals a trawled area of at least 26 300 to 45 500 m². Taxa number (on class level) is given as mean per haul, and abundance and biomass (g wet weight) are standardised per towed area of 10 000 m².

Macrofauna: Macrofauna samples were taken in 5 areas with a 0.25 m² USNEL box corer (Fig. 1, Table 2). Depths varied between 5433 and 5494 m. It being winter in the southern hemisphere, very stormy

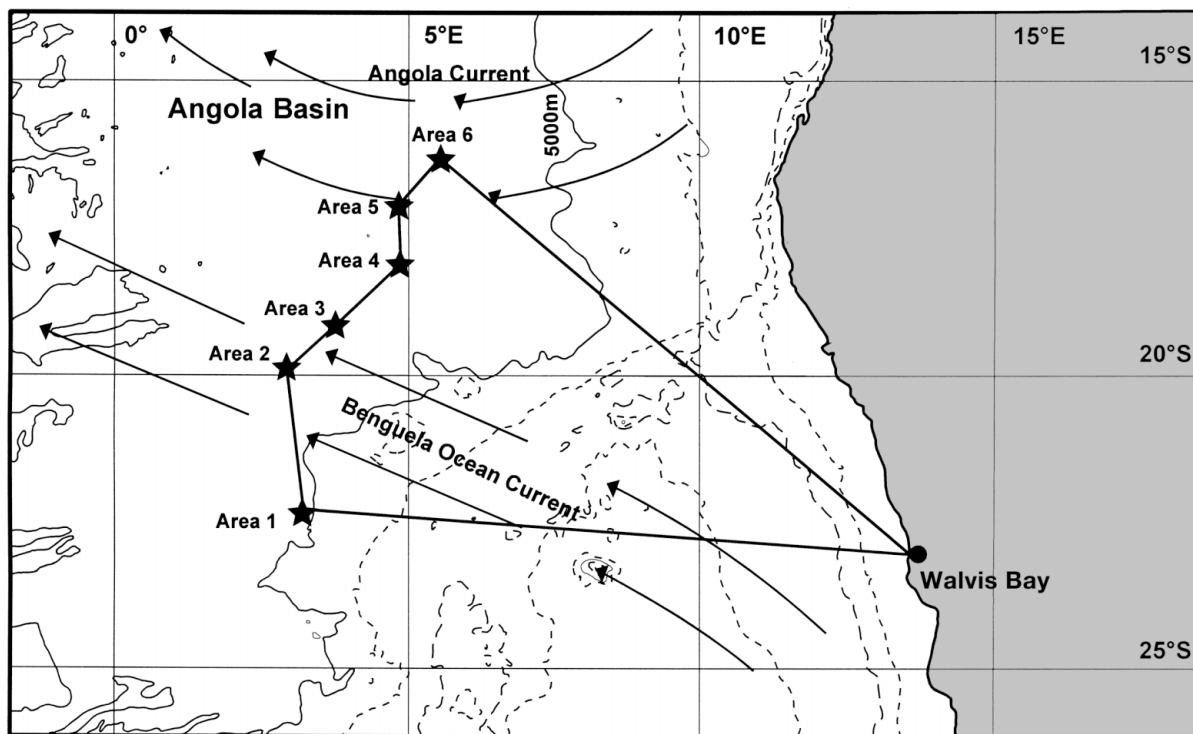


Fig. 1. Map of areas for 'Meteor' Expedition Me 48/1—'DIVA I'

Table 1. Station coordinates for sampling of megafauna (start positions)

Area	No. of trawls	Latitude (S)	Longitude (E)	Depth (m)
1	2	22° 22.644'	003° 20.156'	5162
		22° 20.640'	003° 23.567'	5162
2	1	20° 00.733'	003° 02.230'	5497
3	2	19° 12.897'	003° 48.569'	5469
		19° 13.484'	003° 50.063'	5468
4	2	18° 18.979'	004° 42.728'	5439
		18° 19.430'	004° 42.059'	5443
5	1	17° 07.514'	004° 42.882'	5460
6	3	16° 14.991'	005° 27.000'	5430
		16° 15.771'	005° 27.170'	5432
		16° 25.238'	005° 27.170'	5430

weather and a strong swell made sampling in Areas 1 and 4 extremely difficult. Unfortunately, we could obtain no box core sample in Area 1 and only 1 box core in Area 4. In the other areas, 4 to 5 box cores were taken for quantitative analysis.

The uppermost 20 cm of all samples were washed over a 0.5 mm mesh and fixed in 4 % formaldehyde sea water solution.

Biomass and taxonomy. Biomass is given as wet weight in order to save the unique organisms for taxonomy.

The organisms collected were identified to family or genus level, and, where possible, preliminarily to species level. Identification and description of species is still in progress.

Feeding modes. The feeding modes of taxa were determined according to information in the literature for families or genera (e.g. Fauchald & Jumars 1979, Lincoln 1979, Gage & Tyler 1991, Hartmann-Schröder 1996).

Oceanography. Water temperature and salinity were obtained by using a self-registrating CTD probe (Falmouth Instruments), which was fixed at the USNEL box corer while sampling.

Sediments. Sediment data are available for Areas 2, 3, 5 and 6 only. Samples were taken from the box core using plastic tubes. Out of 1 box core, 2 Plexiglas tubes (5 cm diameter) were taken for sediment analyses

(% <63 µm fraction) and for analyses of the contents of total carbon (TC), total organic carbon (TOC) and pigments.

The core was sliced into different layers. For the present study, only data for the surface sediment (5 mm) were used. The samples for mud, sand and TOC contents were dried on board at 50°C and the samples for analysis of pigments were frozen at -20°C.

Sediment fractions. In the lab the mud fraction was separated by wet sieving over a 63 µm mesh.

TOC and TC contents. The dried samples were homogenised. An aliquot of 10 mg of the sediment was combusted at 1010°C in a C/N analyser (Heraeus vario EL). For TC content, total sediment was analysed. Prior to TOC analysis, the samples were kept for 24 h in a desiccator with concentrated HCl to eliminate carbonate (Hedges & Stern 1984).

Eh profiles. A second tube taken from the same box core was used to measure the Eh profiles in the different sediment depths (2 cm steps) using a Portamess 651-2 Microprocessor (Knick).

Phytopigments. In addition to the box core samples, samples for the analysis of phytopigments were taken from parallel-run multicorers. If available, 1 tube each from 2 multicorers (10 cm diameter) was used for analysis of phytopigment as well as TOC content, the latter for comparison with box core data.

Surface sediments (upper 5 mm) for pigment analysis were kept at -20°C, those designated for TOC analysis were dried on board at 50°C.

Phytopigments (e.g. chlorophyll *a* and derivatives) were extracted from 5 g sediment with 5 ml 90 % acetone. After incubation of the suspension for 1 h at 4°C in darkness, it was mixed for 1 min, followed by ultrasonication in a water bath for 3 min at medium power. To remove particles the suspension was centrifuged for 25 min at 1745 × *g* at 0°C. Pigments were analysed in the supernatant by high performance liquid chromatography (HPLC) as described by Wallerstein & Liebezeit (1999). Standards (Sigma) were used for the quantification of chlorophyll *a* and pheophorbides.

Statistics. For correlations between faunal and environmental parameters the Pearson Product Moment correlation was used.

Table 2. Station coordinates for sampling of macrofauna, and sediment data (–: no sediment samples available)

Area	No. of box cores taken	Latitude (S)	Longitude (E)	Depth (m)	Temp. (°C)	TOC (%)	TC (%)	Chl <i>a</i> (µg g ⁻¹)	<63 µm (%)	>63 µm (%)	Eh (mV)
2	4	19° 58.291'	002° 59.682'	5494	2.50	0.41	8.7	1.72	98.94	1.06	111
3	5	19° 07.123'	003° 51.885'	5468	2.49	0.41	8.86	1.77	98.2	1.8	117
4	1	18° 16.677'	004° 44.361'	5437	–	–	–	–	–	–	–
5	4	17° 07.969'	004° 41.997'	5465	2.48	0.51	8.6	1.91	95.45	4.55	94
6	5	16° 17.024'	005° 27.021'	5433	2.48	0.62	8.01	1.67	95.23	4.77	171

For multidimensional scaling (MDS) the PRIMER v5 package was used (Clarke & Warwick 1994). The abundance data similarities between stations were calculated using the Bray-Curtis coefficient. No transformation was used.

Canonical correspondence analysis (CCA) was performed with CANOCO 4 software (Microcomputer Power). CCA was applied to evaluate correlation between environmental variables, species and variance in site pattern. The Monte Carlo permutation test was used to check the statistical validity of these associations.

RESULTS

Oceanography. The water temperature in the upper 100 m water column at all stations varied between 19 and 20°C and dropped continuously down to 4°C at 900 m and 2.5°C at 3000 m depth. A constant temperature of 2.48°C was measured between 3000 m water depth and the sea floor (Fig. 2).

The salinity in the upper 100 m water column was around 35.8 and dropped constantly down to 34.4 at about 780 m depth. Then it increased again up to 34.8 at about 1700 m depth and remained constant towards the sea floor.

Sediments. The sediment of all stations was white to light beige. In Areas 2 and 3 mud contents in the surface layer reached almost 99%, in deeper layers up to 99.95%. At Areas 5 and 6 about 95% mud was found; contents decreased towards 12 cm sediment depth down to about 90%, and increased again towards deeper layers up to 98 or 99% (Table 2). The sediment, especially in Areas 2 and 3, contained high amounts of globularian foraminiferans. Therefore, the TC contents of sediment were higher (8.7 and 8.86%) in the southern than in the northern areas (8.6 and 8.01%) (Table 2).

Eh profiles. All sediment layers were well oxygenated down to the studied sediment depth of 20 cm.

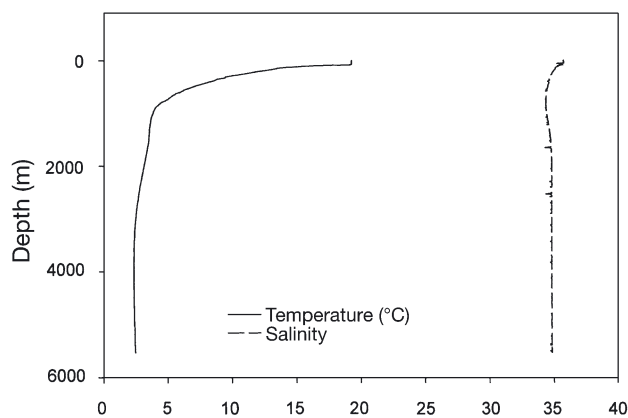


Fig. 2. Temperature and salinity gradients

The values were lowest at the sediment surface and increased towards deeper sediment layers. In Areas 2 and 3, 111 to 117 mV were measured in surface sediment, in Areas 5 and 6, 94 and 171 mV, respectively (Table 2).

TOC and TC content. The TOC content in Areas 2 and 3 was lowest, at 0.41%, and increased towards Areas 5 and 6 up to 0.51 and 0.62%, respectively (Table 2). TOC contents were used for box core samples, as values for sediments taken from box cores and multicorers were identical.

The TC content was higher in Areas 2 and 3 (8.7 and 8.86%) than in Areas 5 and 6 (8.6 and 8.01%) (Table 2).

Chlorophyll a and derivatives. 1.72 and 1.77 µg chlorophyll a per g sediment were measured in surface sediment in Areas 2 and 3 (Table 2), 1.91 µg chlorophyll a per g sediment at Area 5 and 1.67 µg chlorophyll a per g sediment in Area 6. Chlorophyll a contents were used for box core samples because values for sediment taken from box cores and multicorers were almost identical.

Megafauna. Taxa and abundance: A total of 25 taxa on class level were found in the 6 areas. The mean taxa number per haul varied between 9 and 11 in Areas 1 to 3, and increased up to 13 or 14 in Areas 4 to 6 (Fig. 3).

The mean abundance was lower in Areas 1 to 3, with 14 to 46 ind. 10 000 m⁻² than in Areas 4 and 5 with 72 to 96 ind. 10 000 m⁻², respectively. In Area 6 abundance decreased again down to 36 ind. 10 000 m⁻² (Fig. 3).

Ophiurids dominated the megafaunal community only in Area 1 (Table 3). In Area 2 decapods and actinarians were the most abundant groups. In Areas 3 to 6 bivalves and actinarians dominated.

Biomass: The lowest mean biomass was found in Areas 1 and 2 with 111 and 33 g wet weight 10 000 m⁻² (Table 3). In Areas 3 and 6 biomass was rather similar, with 176 and 179 g wet weight 10 000 m⁻². Highest biomass was found in Areas 4 and 5 with 259 and 246 g wet weight 10 000 m⁻², respectively.

In Areas 1 and 2 actinarians, decapods, ophiurids, fish and 'others' made the largest contributions to biomass. In Area 3 biomass was dominated by actinarians, asteroids and fish. In Areas 4 to 6 biomass of bivalves, asteroids and holothurians increased, while values for actinarians and fish remained high.

Macrofauna. Taxa and abundance: A total of 58 taxa on class and family level was found in the 5 areas. The mean taxa number per 0.25 m² varied between 25 in Area 4 (1 box only) and 36 to 42 in Areas 2 and 6 (Fig. 4).

The mean abundance was low in Area 2 with 32 ind. 0.25 m⁻² and increased towards Areas 4 to 6 up to 88 and 94 ind. 0.25 m⁻² respectively (Fig. 4).

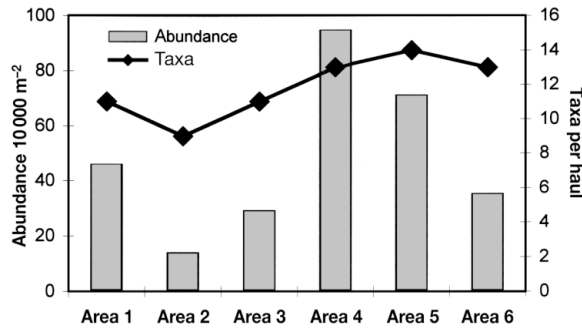


Fig. 3. Megafaunal mean number of taxa per haul and abundance per 10 000 m²

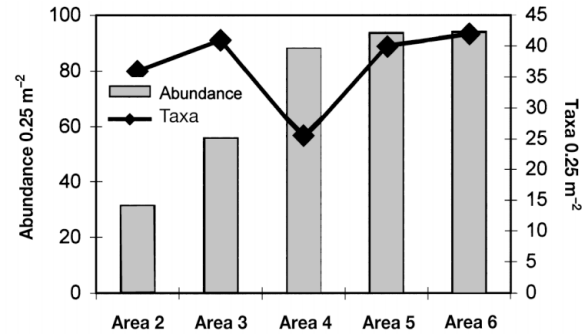


Fig. 4. Macrofaunal mean number of taxa and abundance per 0.25 m²

Polychaetes dominated the communities in all areas (Table 4). Nematoda and Peracarida were more abundant in Areas 4 to 6. Porifera, Mollusca and Sipunculida were less but homogeneously abundant at all sites.

Biomass: The mean biomass was also lowest in Areas 2 and 3 with 65.4 and 165 mg wet weight 0.25 m⁻² and highest at Area 4 with 654.5 mg wet weight 0.25 m⁻² (Table 4). In Areas 5 and 6 biomass decreased again down to 496 and 324.6 mg wet weight 0.25 m⁻².

Bivalves dominated the biomass (Table 4), and specimens of the families Arcidae and Glycymeridae caused the increase in biomass in Areas 4 to 6.

Multivariate analyses. The MDS shows that the macrofaunal communities of Areas 2 to 4 are dissimilar, but Areas 5 and 6 are almost identical (Fig. 5A). The pattern for the megafauna reflects that Areas 1 and 2 are dissimilar to each other as well as to the other areas, which are rather similar (Fig. 5B).

Since environmental data are only available for Areas 2, 3, 5 and 6, the CCA can only provide a restricted picture. However, the plots for macro- and megafauna reveal a similar picture and are therefore

combined in Fig. 6. The gradients are slight and thus of minor importance. Nonetheless, the analysis reveals that the arrows for environmental variables account, in conjunction with the sites, for 76.2 % (macrofauna) and 83 % (megafauna) of the variance of the weighted averages of the 4 areas with respect to the 7 environmental variables. The first axis reveals gradients for macro- and megafaunal community structure influenced by mud content ($r = 0.99$), depth ($r = 0.59$), TOC ($r = -0.76$), and TC ($r = 0.56$). The second axis reflects a gradient influenced by Eh ($r = 0.97$) and chlorophyll *a* ($r = -0.85$) for megafauna only. All these gradients follow the latitudinal gradient of the 6 sample sites.

Fauna and environmental parameters. The correlations between faunal and environmental parameters are weak because of the low numbers of parameters. Nevertheless, they confirm the results obtained with CCA. Significant correlations (5 or 1 % level) were found between depth and macrofaunal abundance and taxa number ($r = -0.9$), TOC ($r = -0.92$), TC ($r = 0.8$), mud content ($r = 0.83$) as well as between macrofaunal abundance and TOC ($r = 0.88$) or mud content ($r = -0.98$). Chlorophyll *a* contents did not correlate with any macrofaunal or sediment parameter, but did with

Table 3. Mean megafaunal abundance (ind. 10 000 m⁻²) and biomass (g wet weight 10 000 m⁻²) in Areas 1 to 6

	Area 1		Area 2		Area 3		Area 4		Area 5		Area 6	
	Abund.	Biomass	Abund.	Biomass	Abund.	Biomass	Abund.	Biomass	Abund.	Biomass	Abund.	Biomass
Actinaria	1.01	19.75	5.86	7.86	6.57	22.09	11.06	46.46	8.09	38.83	2.15	9.35
Bivalvia	0.5	0.65	0.23	0.07	7.54	6.02	59.34	47.4	31.18	26.02	8.83	6.66
Decapoda	1.68	14.18	2.93	10.73	0.97	0.61	1.81	19.3	3.85	19.2	2.98	3.14
Ophiuroida	36.67	31.38	1.13	1.16	5.99	5.94	5.23	7.94	3.08	11.94	2.77	2.96
Asteroida	1.18	2.6	0.68	2.95	1.74	17.74	2.42	40.77	1.92	36.18	1.84	28.94
Holothuroida	1.01	10.21	0	0	1.94	37	0.4	12.84	3.08	48.85	5.01	20.61
Fish	1.85	12.42	1.8	6.5	1.55	82.42	3.42	24.72	2.31	15.99	4.09	9.17
Others	2.53	19.5	1.35	3.32	3.09	4.28	12.27	59.12	18.48	48.59	7.9	97.72
Sum	46.43	110.69	13.98	32.59	29.39	176.1	95.95	258.55	71.99	245.6	35.57	178.55

Table 4. Mean macrofaunal abundance (ind. 0.25 m⁻²) and biomass (mg wet weight 0.25 m⁻²) in Areas 2 to 6

	Area 2		Area 3		Area 4		Area 5		Area 6	
	Abund.	Biomass	Abund.	Biomass	Abund.	Biomass	Abund.	Biomass	Abund.	Biomass
Porifera	–	–	2.2	6.94	5	29.13	6.75	19.15	3	100.94
Hydrozoa	–	–	–	–	–	–	0.25	0.51	–	–
Anthozoa	0.25	43.40	0.4	35.81	–	–	1	123.75	–	–
Nemertini	0.25	0.01	–	–	–	–	–	–	–	–
Nematoda	2.75	0.10	3.2	0.11	12	0.40	18	0.60	15.8	0.51
Oligochaeta	0.25	0.01	–	–	2	18.92	–	–	0.4	0.16
Polychaeta	20.5	3.17	37.6	5.70	36	8.66	43.5	7.62	50.6	23.45
Sipunculida	0.5	0.46	1.6	1.23	3	8.06	2.75	5.27	1	4.38
Harpacticoida	0.75	0.05	1.2	0.17	2	0.07	3.5	0.55	1.8	0.47
Peracarida	2	0.29	3	0.83	20	4.10	10.5	2.15	9	1.99
Crustacea	0.25	0.06	0.2	0.01	–	–	–	–	–	–
Caudofoveata	0.25	0.16	0.8	0.34	–	–	0.75	0.43	–	–
Scaphopoda	0.75	0.74	1	1.28	2	2.25	0.5	0.53	0.4	36.50
Tellinacea	–	–	0.2	1.38	–	–	–	–	0.2	0.23
Glycymeridae	1.5	9.54	1.6	74.70	1	4.33	1	185.75	2.8	103.77
Nuculanidae	1.25	2.34	2	35.77	1	3.63	4.5	14.83	5.2	31.19
Arcidae	–	–	0.8	0.66	3	565.95	0.75	134.88	2.4	4.61
Bryozoa	–	–	–	–	–	–	–	–	0.4	0.25
Holothuria	–	–	–	–	–	–	–	–	0.2	2.07
Ophiuroida	0.25	5.04	–	–	1	9.01	–	–	0.8	14.09
Sum	31.5	65.37	55.8	164.93	88	654.50	93.75	496.02	94	324.61

megafaunal abundance ($r = 0.85$). TOC content ($r = -0.89$), macrofauna abundance ($r = 0.98$) and biomass ($r = 0.84$) were significantly correlated with the mud content. Except for chlorophyll *a*, no further significant correlations were found between megafauna and environmental factors.

Feeding modes: macrofauna. Predatory polychaetes, peracarids and facultative surface deposit feeders or predatory sipunculids occurred in similar ratios in all areas. Facultative subsurface deposit feeding or predatory nematodes and oligochaetes increased towards

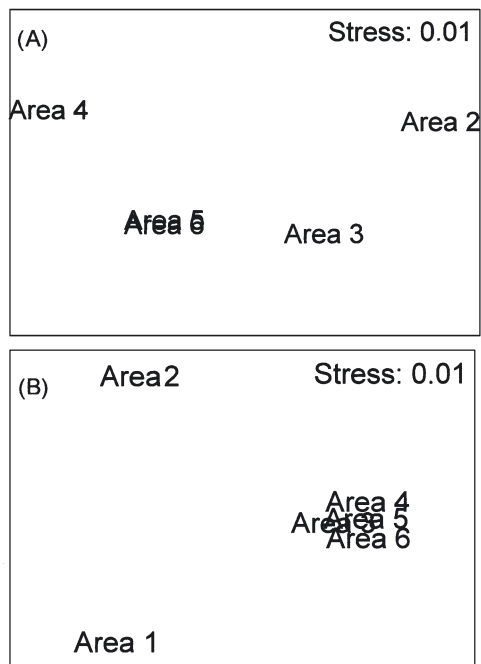


Fig. 5. MDS for (A) macrofauna and (B) megafauna

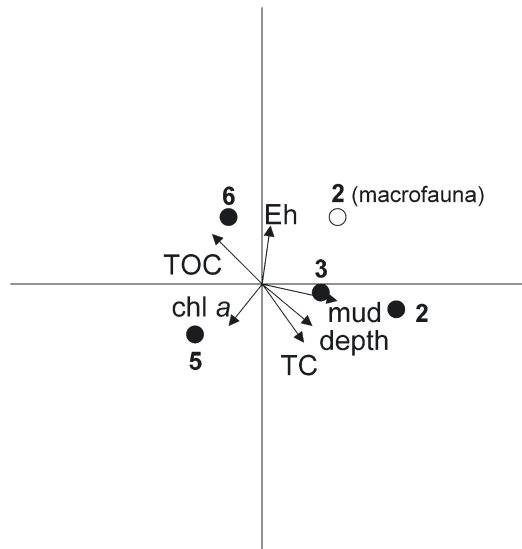


Fig. 6. Triplot of the CCA ordination for macro- and megafauna in Areas 2, 3, 5 and 6 (●); (○) macrofauna in Area 2). Vector lines represent the relationship of significant environmental variables to the ordination axes and their length is proportional to their relative significance

Areas 4 to 6 (Fig. 7A). In Areas 2 and 3, the communities were dominated by surface deposit and interface feeding organisms, such as polychaetes and ophiurids, which feed at the sediment surface or in the benthic boundary layer. Percentages of surface deposit/interface feeders were lowest in Area 4, but also lower in Areas 5 and 6 than in Areas 1 and 2. Organisms which feed mainly in the sediment (subsurface deposit feeders) were less abundant.

Feeding modes: megafauna. In Area 1, the ophiurids foraging as surface deposit feeders as well as predators dominated (Fig. 7B). In Areas 2 and 3, the proportion of organisms feeding as suspension feeder or predator as well as surface deposit feeder increased. In Areas 4 to

6, bivalves feeding as surface or subsurface deposit feeder dominated, followed by surface deposit feeders or predators.

DISCUSSION

The Angola Basin benthic environment reflects a typical deep-sea feature with extremely muddy sediment, containing high amounts of foraminiferans. The positive Eh values are typical for deep sea sediment (Boetius et al. 1995, Sauter et al. 2001) and the North Atlantic Deep Water is oxygen-rich and contains about 5.6 ml oxygen l⁻¹ in 5500 m depth (in Schmiedl et al. 1997). Nevertheless, the Eh values were lower than those measured by Boetius et al. (1995) in the extremely oligotrophic eastern Mediterranean deep sea in summer, where seasonally varying pulses of food supply are not detectable below 1500 m (Danovaro et al. 2000, Kröncke et al. 2003). However, our data indicate higher benthic metabolism in Angola Basin sediments even in winter, especially in the northern areas.

Community structure

Macrofaunal abundance, as well as megafaunal abundance and biomass in the southern Areas 1 and 2, were similar to those found by Vinogradova et al. (1990) in the SW Angola Basin. In general, macro- and megafaunal abundance and biomass at the 6 study sites in the deep Angola Basin were similar to those known for depths >4000 m, such as the Venezuela Basin, Demerara Abyssal Plain, Porcupine Sea Bight, Coral and Salomons Seas, the Goban Spur area (Tietjen 1992, Heip et al. 2001), the Porcupine Abyssal Plain (Galéron et al. 2001) and the southern Arabian deep sea (Witte 2000), but higher than in the NE Atlantic Biotrans station (Pfannkuche 1993), depths >5000 m in the Cape Verde Basin (Rowe & Deming 1985) or in extremely oligotrophic areas >4000 m depth such as the Arctic (Kröncke et al. 2000) and the eastern Mediterranean deep sea (Kröncke et al. 2003). Despite this higher general macrofaunal abundance and biomass, the occurrence of huge numbers of foraminiferans, found especially in Areas 1 to 3 in the Angola Basin, indicates an oligotrophic situation and seasonally fluctuating organic matter supply (Linke et al. 1995, Schmiedl et al. 1997).

The macrofaunal communities were dominated by polychaetes, peracarids (especially isopods) and bivalves, as in other deep sea areas of similar depth (Kröncke 1998, Galéron et al. 2001). Dominant megafaunal groups were ophiurids, bivalves, actinarians and sponges as also described by Vinogradova et al.

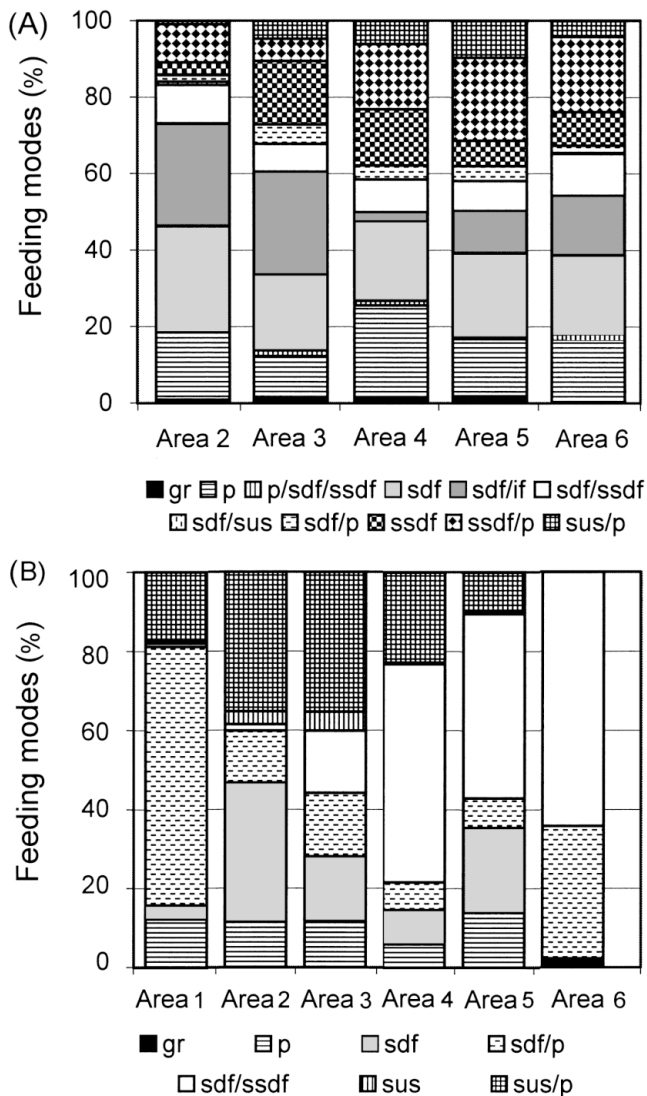


Fig. 7. Relative percentage of different feeding modes for (A) macro- and (B) megafauna. gr: grazer, p: predator, sdf: surface-deposit feeder, if: interface feeder, ssdf: subsurface deposit feeder, sus: suspension feeder

(1990) for the SW Angola Basin. The high number of isopods at the study sites is typical for deep sea areas (Kröncke 1998, Galéron et al. 2001) and is probably due to high proportions of agglutinated foraminiferans in the sediments (Schmiedl et al. 1997), which are a favourite prey item for isopods (Svavarsson et al. 1993, Gudmundsson et al. 2000).

Feeding types and food availability

The feeding modes reveal that most of the macrofauna as well as the megafauna in the Angola Basin forage as (facultative) predators or feed on organic material deposited at the sediment surface as also found in the deep Arctic Ocean or the eastern Mediterranean deep sea (Kröncke 1994, 1998, Tselepidis et al. 2000, Kröncke et al. 2003). Predation is common in oligotrophic seas or in the case of limited food supply (Rosenberg et al. 1996, Riemann-Zürneck 2000, Wieking & Kröncke 2003).

TOC contents in Angola Basin sediments were similar to data from other deep sea regions (Sibuet et al. 1989, Stein et al. 1994, Boetius et al. 1995), but contents from the southern Areas 2 and 3 were 0.2 % lower than at the northernmost Area 6. TOC was used only as general background information on sedimentation of organic matter, since Rowe et al. (1990, 1991), Anderson et al. (1994) and Sauter et al. (2001) showed that organic matter in deep sea sediments is highly refractory and turns over on scales of years and centuries. Micro-organisms are needed to remobilise detrital organic matter for higher trophic levels (Rowe & Deming 1985, Rowe et al. 1991, Kröncke et al. 2000). Also, nematodes living in extreme depths and frequently found in our samples are mainly detritivorous-bacterivorous species which provides evidence for the importance of the microbial loop in the deep benthic system (Boetius & Lochte 1996, Vanreusel et al. 2000).

Food availability is better reflected by phytopigment, and especially chlorophyll *a* contents in sediment, than by TOC content. Phytopigments are an indicator of the quality of settled organic matter (Boon & Duineveld 1996). High contents of chlorophyll *a* indicate fresh organic material. Chlorophyll *a* contents found in offshore Angola Basin sediment are higher than concentrations, if converted, in the coastal deep Angola Basin (Soltwedel 1997), but similar to the deep Arabian Sea (Pfannkuche et al. 2000) and offshore North Sea sediment (Stoeck & Kröncke 2001).

Our pigment analyses gave peaks for chlorophyll *a* and its derivatives in all areas, which indicates freshly settled organic material as found in many deep sea areas (Billett et al. 1983, Gage & Tyler 1991, Pfannkuche 1993). However, a significant correlation be-

tween chlorophyll *a* and megafaunal abundance was found, but not between chlorophyll *a* and macrofaunal abundance. Bivalves, especially of the family Arcidae, increased in Areas 4 to 6, which might be due to higher food availability indicated by higher TOC and chlorophyll *a* contents in sediment. Furthermore, bivalves can switch from suspension- to surface- as well as sub-surface deposit feeding (Wikander 1980, Gage & Tyler 1991) and might be better competitors for food compared with macrofauna or meiofauna. Unselective surface feeding of other megafauna and macrofauna might result in dilution of high quality food particles and prevent significant correlation between fauna and chlorophyll *a* contents. Jumars et al. (1990) mentioned that meiofauna is favoured in the deep sea because of particle selection, but Soltwedel (1997) found no correlation between meiofauna and chlorophyll *a* content in the coastal deep Angola Basin, and nor did Gooday et al. (1996) in the north-eastern Atlantic. Gooday et al. (1996) explained this as outcompetition of meiofauna by foraminifera, which possess extremely efficient food-gathering organelles and are able to raise their levels of metabolic activity, as found by Gooday et al. (1992), Linke (1992), Pfannkuche (1993), Linke et al. (1995), Schmiedl et al. (1997) and Kröncke et al. (2000).

In contrast to the megafauna, the macrofauna was significantly correlated with the TOC content. This correlation was also found by Sibuet et al. (1989) in 7 deep sea areas in the Atlantic Ocean. These authors explained that the flux of particulate organic matter is the first order parameter to control faunal distribution in the deep sea. Carbon is mainly important for basic metabolism (calorimetric needs) and even refractory organic matter seems to be sufficient to fulfil energetic requirements (Tenore 1983, Tenore & Chesney 1985).

Pelago-benthic coupling

In a deep basin like the Angola Basin, with differences in depth of only 60 m between Areas 2 and 6 over a distance of 360 nautical miles, one expects rather stable environmental conditions. However, our environmental data such as TOC, TC, chlorophyll *a* and mud content reveal small but significant differences between the southern and the northern study areas. The low TOC and chlorophyll *a* contents in the southern areas (Areas 2 and 3) coincided with the low macro- and megafauna abundance and biomass, whereas higher nutritional values and faunal parameters were found in the north (Areas 4 to 6). A similar trend was also found for protozoans (K. Hausmann pers. comm.), plathelminthes (A. Faubel pers. comm.), amphipods (H.-G. Andres pers. comm.) and polychaetes (D. Fiege pers. comm.).

The differences in environmental and faunal parameters seem to follow the latitudinal gradient along the study sites, which was also confirmed by the CCA analysis. These differences seem to make a good match with the differences in water masses of the warm South Equatorial Counter Current and the cold Benguela Oceanic Current, which meet in the Angola–Benguela front, crossing the Angola Basin in a north-westerly direction (Peterson & Stramma 1991, Jansen et al. 1996).

North of this front, the Angola Basin is a highly productive region with carbon fixation rates of 90 to 180 g m⁻² yr⁻¹ (van Bennekom & Berger 1984, Berger et al. 1987, Berger 1989), from which only 0.01 to 1% is accumulated in the sea floor (Berger et al. 1989). The high production is supported by the South Equatorial Counter Current, which carries warm water from the north at subsurface depths and which mixes with water masses from the Zaire (Congo) River. This river plume extends about 800 m far from the river mouth and feeds the Angola Basin with nutrients and suspended matter (Eisma & Kalf 1984, Jansen et al. 1984). Bernard et al. (1999) found that the downward settling of the suspended matter in the Angola Basin is much faster than the horizontal transport by currents. Thus, high primary production in the Angola basin due to warm water masses, and nutrient supply from rivers, might lead to higher sedimentation rates and food supply for the benthos north of the frontal system. This scenario seems to be confirmed by the higher TOC and chlorophyll *a* contents and higher abundance and biomass of macro- and megafauna north of the front.

South of the front, the cold Benguela Oceanic Current flows in a north-westerly direction and separates the benthos from the highly productive northern water masses, thus reducing the supply of organic matter for the benthos. This seems to be the reason for the low macro- and megafauna abundance and biomass, as well as TOC contents, at the southernmost areas. On the other hand, the TC content was higher in these areas than in the north, and it was obvious that the sediments contained a higher amount of foraminiferans than the northern sediments, which are indicators for oligotrophic environments and sudden food supply (Gooday et al. 1992, Linke 1992, Pfannkuche 1993, Linke et al. 1995, Schmiedl et al. 1997). This confirms the lower food availability in the southern areas compared with the northern ones.

Although only descriptive, our data give evidence of differences in food supply north and south of the front even in extreme depths of about 5500 m, as found for other deep sea areas of shallower depths of 1000 to 4000 m (Thiel et al. 1987, Sibuet et al. 1989, Witte 2000), since benthic fauna integrates environmental conditions over longer time periods and is thus the most sensitive probe available.

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LITERATURE CITED

- Alva V, Vadon C (1989) Ophiuroids from the western coast of Africa (Namibia and Guinea-Bissau). *Sci Mar* 53(4): 827–845
- Anderson RF, Rowe GT, Kemp PF, Trumbore S, Biscaye PE (1994) Carbon budget for the mid-slope depocenter of the Middle Atlantic Bight. *Deep-Sea Res II* 41(2/3): 669–703
- Berger WH (1989) Global maps of ocean productivity (Appendix). In: Berger WH et al. (eds) *Productivity of the ocean: present and past*. John Wiley & Sons, New York, p 429–455
- Berger WH, Lai K, Wu G (1987) Ocean productivity and organic carbon flux. Part I. Overview and maps of primary production and export production. University of California, San Diego
- Bernard P, Eisma D, van Grieken R (1999) Electron microprobe analysis of suspended matter in the Angola Basin. *J Sea Res* 41:19–33
- Billett DSM, Lampitt RS, Rice AL, Mantoura RFC (1983) Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* 302:520–522
- Boetius A, Lochte K (1996) High proteolytic activities of deep-sea bacteria from oligotrophic polar sediments. *Arch Hydrobiol Spec Issue Adv Limnol* 48:269–276
- Boetius A, Scheibe S, Tselepidis A, Thiel H (1995) Microbial biomass and activities in deep-sea sediments of the eastern Mediterranean: trenches are benthic hotspots. *Deep-Sea Res I* 43(9):1439–1460
- Boon AR, Duineveld GCA (1996) Phytopigments and fatty acids as molecular markers for the quality of near-bottom particulate organic matter in the North Sea. *J Sea Res* 35(4):279–291
- Clarke KR, Warwick M (1994) Change in marine communities: an approach to statistical analysis and interpretation. Natural Environmental Research Council, UK
- Danovaro R, Della Croce N, Dell'Anno A, Fabiano M, Marralle M, Martorano D (2000) Seasonal changes and biochemical composition of the labile organic matter flux in the Cretan Sea. *Progr Oceanogr* 46:259–278
- Dinet A (1973) Distribution quantitative de meiobenthos profond dans la région de la dorsale de Walvis (Sud-Ouest Africain). *Mar Biol* 20:20–26
- Eisma D, Kalf J (1984) Dispersal of Zaire River suspended matter in the estuary and the Angola Basin. *Neth J Sea Res* 17(2–4):385–411
- Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. *Oceanogr Mar Biol Annu Rev* 17:193–284
- Fedorov VV, Karamyshev AK (1991) Trophic structure of benthos on the Walvis Ridge and conditions of its formation. In: Nejman AA (ed) *Biotopic basis of the distribution of commercial and food marine animals*. VNIRO, Moscow, p 6–18
- Gage JD, Tyler PA (1991) Deep-sea biology: a natural history

- of organisms at the deep-sea floor. Cambridge University Press, Cambridge
- Galéron J, Sibuet M, Vanreusel A, Mackenzie K, Gooday AJ, Dinert A, Wolff GA (2001) Temporal patterns among meiofauna and macrofauna taxa related to changes in sediment geochemistry at an abyssal NE Atlantic site. *Prog Ocean* 50:3030–324
- Gooday AJ, Levin LA, Linke P, Heeger T (1992) The role of benthic foraminifera in deep-sea food webs and carbon cycling. In: Rowe GT, Pariente V (eds) *Deep-sea food chains and the global carbon cycle*. Kluwer Academic Publishers, Dordrecht, p 63–91
- Gooday AJ, Pfannkuche O, Lamshead PJD (1997) An apparent lack of response by metazoan meiofauna to phytodetritus deposition in the bathyal north-eastern Atlantic. *J Mar Biol Assoc UK* 76:297–310
- Gudmundsson G, Von Schmalensee M, Svavarsson J (2000) Are foraminifers (Protozoa) important food for small isopods (Crustacea) in the deep sea? *Deep-Sea Res I* 47: 2093–2109
- Hartmann-Schröder G (1996) Annelida, Borstenwürmer, Polychaeta. In: Dahl F (ed): *Die Tierwelt Deutschlands und der angrenzenden Meeressteile*, Vol 58, 2nd edn. Fischer Verlag, Jena, p 668
- Hedges JI, Stern JH (1984) Carbon and nitrogen determinations of carbonate-containing solids. *Limnol Oceanogr* 27: 954–958
- Heip C, Duineveld G, Flach E, Graf G and 11 others (2001) The role of the benthic biota in sedimentary metabolism and sediment-water exchange processes in the Goban Spur area (N.E. Atlantic). *Deep-Sea Res II* 48(14–15): 3223–3243
- Holmes ME, Müller PJ, Schneider RR, Segl M, Pätzold J, Wefer G (1996) Stable nitrogen isotopes in Angola Basin surface sediments. *Mar Geol* 134:1–12
- Jansen JHF, van Weering TCE, Gieles R, van Iperen J (1984) Middle and late quaternary oceanography and climatology of the Zaire-Congo fan and the adjacent eastern Angola Basin. *Neth J Sea Res* 17(2–4):201–249
- Jansen JHF, Ufkes E, Schneider RR (1996) Late quaternary movements of the Angola-Benguela Front, SE Atlantic, and implications for advection in the equatorial ocean. In: Wefer G, Berger WH, Siedler G, Webb DJ (eds) *The South Atlantic*. Springer-Verlag, Berlin, p 553–575
- Jumars PA, Mayer LM, Deming JW, Baross JA, Wheatcroft RA (1990) Deep-sea deposit-feeding strategies suggested by environmental and feeding constraints. *Phil Trans R Soc Lond A* 331:85–101
- Kröncke I (1994) Macrobenthos composition, abundance and biomass in the Arctic Ocean along a transect between Svalbard and the Makarov Basin. *Polar Biol* 14:519–529
- Kröncke I (1998) Macrofauna communities in the Amundsen Basin, at the Morris Jesup Rise and at the Yermak Plateau (Eurasian Arctic Ocean). *Polar Biol* 19:383–392
- Kröncke I, Vanreusel A, Vincx M, Wollenburg J, Mackensen A, Liebezeit G, Behrends B (2000) The different benthic size compartments and their relation with sediment chemistry in the deep Eurasian Arctic Ocean. *Mar Ecol Prog Ser* 199:31–41
- Kröncke I, Türkay M, Fiege D (2003) Macrofauna communities in the eastern Mediterranean deep-sea. *PSZN I:Mar Ecol* 24(3): (in press)
- Larqué L, Maamaatuaiahutapu K, Garçon V (1997) On the intermediate and deep water flows in the South Atlantic Ocean. *J Geophys Res* 102(6):12425–12440
- Lincoln RJ (1979) *British marine Amphipoda: Gammaridea*. Natural History Museum, London
- Linke P (1992) Metabolic adaptations of deep-sea benthic foraminifera to seasonally varying food input. *Mar Ecol Prog Ser* 81:51–63
- Linke P, Altenbach A, Graf G, Heeger T (1995) Response of deep-sea foraminifera to a simulated sedimentation event. *J Foraminifer Res* 25:75–82
- Mackensen A, Schmiedl G, Harloff J, Giese M (1995) Deep-sea foraminifera in the South Atlantic Ocean: ecology and assemblage generation. *Micropalaentology* 41(4): 342–358
- Macpherson E (1991) Biogeography and community structure of the Decapod crustacean fauna off Namibia (southeast Atlantic). *J Crustac Biol* 11(3):401–415
- Monniot C, Monniot F (1976) Quelques ascidies bathyales et abyssales du Sud-Est Atlantique. *Bull Mus Nat Hist Paris* 3(387), *Zool* 269:671–680
- Petersen RG, Stramma L (1991) Upper-level circulation in the South Atlantic Ocean. *Prog Oceanogr* 26(1):1–73
- Pfannkuche O (1993) Benthic response to the sedimentation of particulate matter at the BIOTRANS station, 47°N, 20°W. *Deep-Sea Res* 40:135–149
- Pfannkuche O, Kähler A, Sommer S (2000) Coupling between phytodetritus deposition and the small benthic biota in the Arabian Sea, analyses of biogenic sediment compounds. *Deep-Sea Res II* 47:2805–2833
- Reid JL (1989) On the total geostrophic circulation of the South Atlantic Ocean: flow patterns, tracers, and transport. *Prog Oceanogr* 23:149–244
- Riemann-Zürneck, K. (2000). *Oractis bursifera* sp. nov., an Arctic deep-sea anemone with peculiar invaginations of its oral disc (Cnidaria: Actinaria). *Polar Biol* 23:604–608
- Rosenberg R, Hellman B, Lundberg A (1996) Benthic macrofaunal community structure in the Norwegian trench, deep Skagerrak. *J Sea Res* 35:181–188
- Rowe GT, Deming JW (1985) The role of bacteria in the turnover of organic carbon in deep-sea sediments. *J Mar Res* 43:925–950
- Rowe GT, Sibuet M, Deming J, Tietjen J, Khripunoff A (1990) Organic carbon turnover time in deep-sea benthos. *Prog Oceanogr* 24:141–160
- Rowe G, Sibuet M, Deming J, Khripounoff A, Tietjen J, Macko S, Theroux R (1991) Total sediment biomass and preliminary estimates of organic carbon residence time in deep-sea benthos. *Mar Ecol Prog Ser* 79:99–114
- Sauter E, Schlüter M, Suess E (2001) Organic carbon flux and remineralization in surface sediments from the northern North Atlantic derived from pore-water oxygen microprofiles. *Deep-Sea Res I* 48:529–553
- Schmidt M, Mohrholz V, Schmidt T, John HC and 8 others (2000) Data report of RV 'Poseidon' cruise 250 ANDEX 1999. *Meereswiss Ber, Warnemünde* 40:1–117
- Schmiedl G, Mackensen A (1997) Late quaternary paleoproductivity and deep water circulation in the eastern South Atlantic Ocean: evidence from benthic foraminifera. *Palaeogeogr Palaeoclimatol Palaeoecol* 130:43–80
- Schmiedl G, Mackensen A, Müller PJ (1997) Recent benthic foraminifera from the eastern South Atlantic Ocean: dependence on food supply and water masses. *Mar Micropaleontol* 32:249–287
- Shannon LV, Chapman P (1991) Evidence of Antarctic bottom water in the Angola Basin at 32°S. *Deep-Sea Res* 38(10): 1299–1304
- Sibuet M, Lambert CE, Chesselet R, Laubier L (1989) Density of the major size groups of benthic fauna and trophic input in deep basins of the Atlantic Ocean. *J Mar Res* 47: 851–867
- Soltwedel T (1997) Meiobenthos distribution in the tropical

- East Atlantic: indication for fractionated sedimentation of organic matter to the sea floor? *Mar Biol* 129:747–756
- Soltwedel T, Thiel H (1995) Biogenic sediment compounds in relation to marine meiofaunal abundances. *Int Rev Ges Hydrobiol* 80(2):297–311
- Speer KG, Siedler G, Talley L (1995) The Namib Col Current. *Deep-Sea Res I* 42(11/12):1933–1950
- Stein R, Grobe H, Wahsner M (1994) Organic carbon, carbonate, and clay mineral distributions in eastern central Arctic Ocean surface sediments. *Mar Geol* 119:269–285
- Stoeck T, Kröncke I (2001) Influence of particle mixing on vertical profiles of chlorophyll *a* and bacterial biomass in sediments of the German Bight, Oyster Ground and Dogger Bank (North Sea). *Estuar Coast Shelf Sci* 52:783–795
- Svavarsson J, Gudmundsson G, Brattegard T (1993) Feeding by asellote isopods (Crustacea) on foraminifers (Protozoa) in the deep sea. *Deep-Sea Res I* 40:1225–1239
- Tenore KR (1983) What controls the availability to animals of detritus derived from vascular Plants: organic nitrogen enrichment or caloric availability? *Mar Ecol Prog Ser* 10: 307–309
- Tenore KR, Chesney E (1985) The interaction of rate of food supply and population density upon the bioenergetics of the opportunistic polychaete, *Capitella capitata* (Type I). *Limnol Oceanogr* 30:1188–1195
- Thiel H, Pfannkuche O, Theeg R, Schriever G (1987) Benthic metabolism and standing stock in the central and northern deep Red Sea. *PSZN I: Mar Ecol* 8:1–20
- Tietjen JH (1992) Abundance and biomass of metazoan meiobenthos in the deep sea. In: Rowe GT, Pariente V (eds) *Deep-sea food chains and the global carbon cycle*. Kluwer Academic, Dordrecht, p 45–62
- Tselepidis A, Papadopoulou K-N, Podaras D, Plaiti W, Koutsoubas D (2000) Macrobenthic community structure over the continental margin of Crete (South Aegean Sea, NE Mediterranean). *Prog Oceanogr* 46:401–428
- Türkay M, Allspach A, Bohn J, Cristobo FJ and 6 others (2003) Mega-Epifauna. Meteor Report, Cruise 48 (in press)
- van Bennekom AJ, Berger GW (1984) Hydrography and silica budget of the Angola Basin. *Neth J Sea Res* 17(2–4): 149–200
- Vanreusel A, Clough LM, Jacobsen K, Ambrose W, Jivaluk J, Ryheul V, Herman R, Vincx M (2000) Meiobenthos of the central Arctic Ocean. *Deep-Sea Res I* 147:1855–1879
- Vinogradova NG, Galkin SW, Kamenskaja OE, Levenstein RY, Romanov VN (1990) The distribution of the deep sea bottom fauna in the transoceanic section in the south Atlantic Ocean along 31° 30'. *Academy of Science USSR, Studies of the Institute of Oceanography, Moscow, Vol 126:7–19*
- Wallerstein P, Liebezeit G (1999) Determination of photosynthetic pigments. In Grasshoff K, Kremling K, Ehrhard M (eds) *Methods of seawater analysis*. Wiley-VCH Verlag, Weinheim, p 557–566
- Wefer G, Berger WH, Siedler G, Webb DJ (eds) (1996) *The South Atlantic*. Springer-Verlag, Berlin
- Wieking G, Kröncke I (2003) Benthic communities of the Dogger Bank (central North Sea) in the late 90s: spatial distribution, species composition and trophic structure. *Helgol Mar Res* 57:34–46
- Wikander PB (1980) Biometry and behaviour in *Abra nitida* (Müller) and *A. longicallus* (Scacchi) (Bivalvia, Tellinacea). *Sarsia* 65:255–268
- Witte U (2000) Vertical distribution of metazoan macrofauna within the sediment at 4 sites with contrasting food supply in the deep Arabian Sea. *Deep-Sea Res II* 47: 2979–2997

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