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# Meiobenthos distribution pattern in the tropical East Atlantic: indication for fractionated sedimentation of organic matter to the sea floor?

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**Abstract** To test the extent to which sea surface productivity governs the distribution pattern of benthic organisms, meiobenthic standing stocks were investigated on the shelf, continental margin and the adjacent abyssal plains off the western African coast between Guinea (10°N) and Angola (18°S). The area of investigation is characterized by gradients in surface productivity due to spatially and seasonally varying coastal upwelling. Reflecting the dependency of deep-sea organisms on organic matter input from the euphotic zone, similar gradients ought to be expected within the benthos. Meiofaunal abundances and biomasses (including Foraminifera) from a total of 57 stations along 13 transects across the continental margin showed a fairly close correlation with sediment-bound chloroplastic pigment concentrations, indicating the sedimentation of particulate organic matter from phytoplankton production. However, certain discrepancies in faunal and pigment distribution patterns were found in regions apart from the centres of enhanced primary productivity, i.e. apart from the upwelling centres: whereas pigment concentrations in the sediments were still comparably high, meiofaunal numbers in those peripheral areas were generally lower. It is suggested that smaller/lighter phytodetritial matter, transported over long distances by subsurface currents and exposed to ongoing microbial degradation during its passage, probably does not have the same energy content as the relatively fast-sinking, larger phytodetritus aggregates ("marine snow"), which are found in centres of enhanced primary productivity and support extensive benthic stocks. Thus, meiobenthic abundances in relation to sediment-bound pigment concentrations on the western African continental margin may indicate fractionated sedimentation of organic matter to the sea floor.

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## Introduction

It is commonly accepted that benthic biomass, production and activity depend upon the amount of sedimentary organic matter reaching the ocean floor in subsequent degradation stages after its production in the overlying water layers. Therefore, high benthic standing stocks, as first approximations for benthic production, are to be expected in upwelling areas. The data so far available confirms this expectation (e.g. Thiel 1978, 1982; Pfannkuche et al. 1983).

However, this simple model is altered by a variety of local physical, chemical and biological variables. For instance, upwelling associated with strong winds could result in reduced primary production not equivalent to the actual nutrient transport; a strong drift of water masses and downwelling processes at hydrographic fronts may cause water bodies to sink before nutrients are optimally used. Downwardly directed water movements may also rapidly transfer contained organic matter into deeper layers. Moreover, all (active and passive) sinking processes have horizontal movements due to surface currents and to undercurrents, effecting that organic particles may settle far away from their area of origin.

Similarly, biological processes involved in the transfer of organic matter between primary production and benthic utilization are not the same in all regions because organism feeding habits in relation to food density, the number of trophic stages, short circuits and recycling rates of organic matter in the water column may differ locally. Sinking of organisms and detritus, which generally is a slow process, increases when the organic matter is concentrated into fecal pellets or large phytodetritus aggregates termed "marine snow" (Shanks and Trent 1980; Alldredge and Silver 1988; Lampitt et al. 1993; Alldredge and Jackson 1995). Due to the high organic matter sedimentation in the upwelling centres, oxygen depletion in the sediment and in the overlying water masses may also alter the relationship between organic matter (energy) input and benthic organism densities.

The data presented in the present paper describe for the first time meiobenthos abundances and biomasses in the tropical eastern Atlantic. Moreover, the evaluation of meiobenthic distribution patterns at sites with spatially varying productivity due to varying upwelling intensities permits the assessment of the relationship between benthic organism abundances/biomasses and the quantity and quality of organic matter available.

## Materials and methods

### Area of investigations

A total of 13 transects across the continental margin were sampled between 10°N (off Guinea) and 18°S (off Angola) during R.V. "Meteor" cruise legs 6/5 and 6/6 from mid-January till the end of February 1988 (Fig. 1). Station depths ranged from 30 m on the shelf to 4500 m in the adjacent abyssal plains (Sierra Leone Basin, Guinea Basin and Angola Basin, respectively). In general, four to five stations were sampled along each transect, resulting in a total number of 57 stations (see Table 1). Station depths on each transect were chosen at similar depth horizons, i.e. 50, 700, 1500, 3000 and 4500 m water depth, irrespective of the differing hydrographic and topographic conditions.

Inclination of the western African continental margin between transects 1 and 13 varies from < 1° off Nigeria, Gabon and Angola to > 9° off the Ivory Coast. Large rivers (Congo, Niger) discharge huge water masses into the Gulf of Guinea, e.g. average discharge of the Congo River, the second largest river in the world, is about 40 000 $m^3 s^{-1}$ (Lerman 1980). Nutrient concentrations in the river plumes are high due to direct river influence (especially silicate) and due to river-induced upwelling (mainly nitrate and phosphate) (Van Bennekom et al. 1978). However, primary production in the river plumes is reduced because of the high input of suspended matter clouding the waters (e.g. Congo: 28.9 mg $l^{-1}$; Niger: 23.7 mg $l^{-1}$; see Eisma et al. 1978).

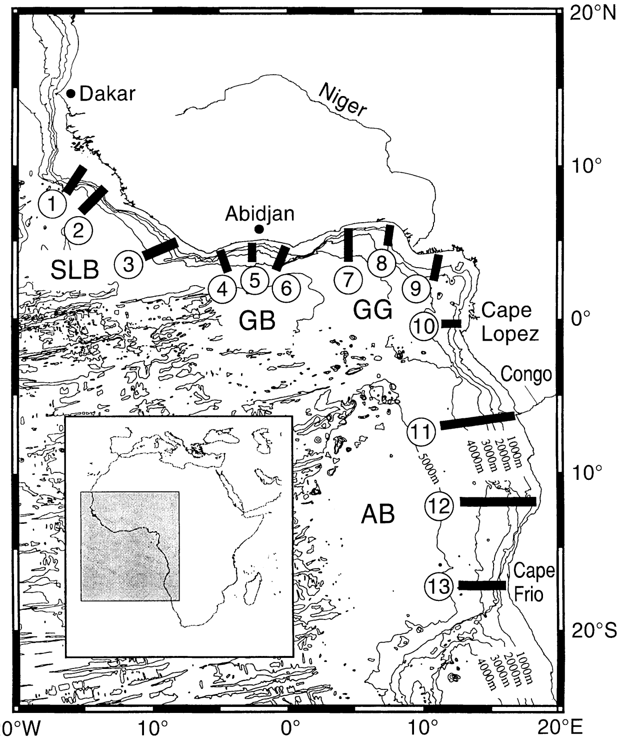

**Fig. 1** Location of 13 transects off the tropical western African coast (*SLB* Sierra Leone Basin; *GB* Guinea Basin; *GG* Gulf of Guinea; *AB* Angola Basin)

### Coastal upwelling off West Africa

Generally, there are two different types of coastal upwelling systems along the western African coast (Voituriez and Herbland 1982): (I) a wind-induced, more-or-less permanent coastal upwelling off subtropical NW Africa (north of Cap Blanc) and off SW Africa (south of Cap Frio) with minor annual variability and, geographically in between, (II) a highly seasonal coastal upwelling off Senegal/Guinea, off the Ivory Coast/Ghana and off Gabon/Congo/Angola (Fig. 2). Excluding the most southerly transect (Fig. 1), which is affected by permanent upwelling off SW Africa, all other transects investigated in this study lay within and between areas of seasonal coastal upwelling.

Voituriez and Herbland (1982) demonstrated the important role of the subsurface eastward Equatorial Undercurrent (EUC) for the coastal upwelling in northern and eastern parts of the Gulf of Guinea, whereas the upwelling off Guinea is influenced by water masses from the northern branch of the Equatorial Countercurrent (NECC; Fig. 2).

The EUC carries relatively cold and nutrient-rich Southern Atlantic Central Water (SACW). In the eastern part of the Gulf of Guinea the EUC splits up into a northern and a southern branch (Fig. 2). The northern part proceeds westwards as the Guinea Undercurrent (Lemasson and Rébert 1973a, b) and mixes with the NECC off the coast of Guinea; the southern part proceeds southwards as the Gabon-Congo Undercurrent (Wascogne 1988). The seasonal cooling of the subthermoclinal waters off the Ivory Coast/Ghana and Gabon/Congo/Angola is related to the advection and vertical spreading of SACW between 500 and 50 m in June to September and, with less intensity, in December to January (Verstraete 1987). Seasonal upwelling off Guinea appears in February by advection of nutrient-rich waters from the NECC (Voituriez and Herbland 1982).

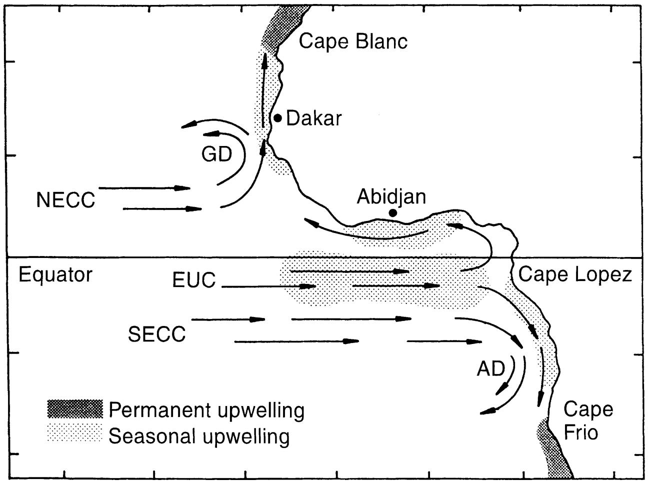

**Fig. 2** Position of the various upwelling areas in the tropical eastern Atlantic Ocean, in relation to the eastward flows in the equatorial current system (redrawn after Voituriez and Herbland 1982) (*EUC* Equatorial Undercurrent; *NECC* North Equatorial Countercurrent; *SECC* South Equatorial Countercurrent; *GD* Guinea Dome; *AD* Angola Dome)

### Sampling and sample processing

Bottom samples were taken using a modified USNEL box corer (BC) (see Fleeger et al. 1988); the area covered by the BC was 0.25 m$^2$. Subsamples for meiobenthic investigations were taken from the cores by inserting small, piston-style corers (plastic disposal syringes; 2 cm inner diameter and 5 cm length). To estimate small-scale variability, three replicates from each BC were analyzed. Subsamples were split into five 1-cm-thick layers, each of which was preserved separately in 4% buffered formalin. Following Dinet et al. (1973) and Thiel (1972, 1983), the meiobenthos is defined herein as a size group of sediment-inhabiting animals passing through a 1000 µm sieve and being retained on a 42 µm sieve.

In the laboratory, sediment samples were washed through a set of sieves with different mesh sizes (500, 150, 100, 65 and 42 µm), stained with Rose Bengal and sorted under a low power stereo microscope (see Pfannkuche and Thiel 1988). Numerical abundances and meiofaunal biomasses (ash-free dry weight, AFDW) were determined for each station. Organisms were identified to major taxa, i.e. Foraminifera, Nematoda, Polychaeta, Harpacticoidea/Nauplii. All other taxa appearing in minor quantities (e.g. Ostracoda, Kinorhyncha, Bivalvia, Gastropoda, Tanaidacea, Tardigrada) were pooled in one category, classified as the "rest". For weight determinations, total meiofaunal organisms of the same taxa per station (three replicates) were rinsed on pre-incinerated and pre-weighed glassfibre filters (Whatman GF/C). Filters and specimens were dried and then incinerated at 500 °C (4 h) for AFDW determinations. The samples were weighed on a ultrabalance to 1 µg accuracy.

The distribution of chloroplastic pigments (chlorophyll *a* and pheopigments) in the upper 5 cm of the sediments was studied to estimate the amount of settled primary organic matter. Chloroplastic pigments were extracted in 90% acetone and measured with a Turner fluorometer according to Yentsch and Menzel (1963) and Holm-Hansen et al. (1965). The method does not discriminate between individual breakdown products, and, as the pigment composition in sediments is not completely understood, the term chloroplastic pigment equivalents (CPE) for the bulk of pigments registered with this method is preferred. CPE values are expressed in micrograms per 5 cm$^3$ as an overall value for the upper 5 cm of the sediment column.

## Results

Table 1 shows station data, information on sediment porosities (water content) and on concentrations of sediment-bound chloroplastic pigments. Mean densities of individual taxa, total meiofaunal abundances (ind/10 cm$^2$) and total meiofaunal biomass (AFDW/10 cm$^2$) per station are listed in Table 2.

### Meiofaunal distribution patterns

Meiofaunal abundances within the sediment columns in general decreased with increasing sediment depth. In the uppermost centimetre, 40 to 51% (mean values from stations on the same water depth horizons; abundances over 5 cm = 100%) of organisms were found; 4 to 8% inhabited the deepest sediment layer investigated (4 to 5 cm). The smoothest gradients were detected in mid-slope depths (1500 m) and on the continental rise (3000 m), probably correlated with the sediment types.

**Table 1** Benthos sampling stations on 13 transects off the tropical western African coast: station data, water content and sediment-bound pigment concentrations (*CPE* chloroplastic pigment equivalents)

| Transect No. | Depth (m) | Location | Water content (%) | CPE (µg/5 cm$^3$) |
|---|---|---|---|---|
| 1 | 37 | 10°05.3′N;16°06.1′W | 17.8 | 6.88 |
| 1 | 646 | 09°30.2′N;16°37.4′W | 59.6 | 5.62 |
| 1 | 1495 | 09°04.7′N;17°00.0′W | 49.2 | 1.61 |
| 1 | 3089 | 08°45.8′N;16°47.9′W | 64.0 | 1.25 |
| 2 | 66 | 08°29.2′N;14°18.6′W | 27.3 | 14.06 |
| 2 | 701 | 08°22.8′N;14°26.4′W | 69.6 | 13.28 |
| 2 | 1500 | 08°19.9′N;14°29.3′W | 69.5 | 3.45 |
| 2 | 3123 | 08°06.5′N;14°43.1′W | 75.7 | 1.15 |
| 2 | 4327 | 07°37.8′N;15°10.1′W | 69.8 | 1.24 |
| 3 | 75 | 04°40.6′N;08°54.1′W | 44.6 | 11.80 |
| 3 | 674 | 04°28.9′N;09°11.7′W | 52.7 | 7.82 |
| 3 | 1483 | 04°17.9′N;09°29.9′W | 75.9 | 1.49 |
| 3 | 3282 | 03°55.7′N;10°37.2′W | 62.0 | 1.04 |
| 3 | 4257 | 03°44.4′N;11°23.4′W | 62.8 | 0.59 |
| 4 | 54 | 04°41.2′N;06°27.3′W | 59.3 | 19.05 |
| 4 | 691 | 04°30.2′N;06°28.2′W | 74.1 | 17.24 |
| 4 | 1505 | 04°26.8′N;06°26.0′W | 73.3 | 7.30 |
| 4 | 3296 | 04°06.5′N;06°16.6′W | 75.6 | 1.51 |
| 4 | 4307 | 03°27.6′N;06°13.2′W | 70.5 | 1.43 |
| 5 | 58 | 05°06.4′N;04°33.9′ W | 53.6 | 11.53 |
| 5 | 698 | 04°59.3′N;04°31.8′W | 68.2 | 15.90 |
| 5 | 1204 | 04°57.0′N;04°33.2′W | 73.0 | 9.99 |
| 5 | 2992 | 04°28.7′N;04°40.3′W | 78.7 | 2.66 |
| 6 | 63 | 04°40.6′N;02°14.8′W | 58.8 | 18.50 |
| 6 | 749 | 04°23.3′N;02°22.0′W | 73.8 | 3.54 |
| 6 | 1500 | 04°09.9′N;02°28.6′W | 75.1 | 2.46 |
| 6 | 3102 | 03°43.6′N;03°03.0′W | 73.6 | 1.56 |
| 7 | 39 | 05°57.8′N;01°08.9′E | 39.3 | 12.75 |
| 7 | 740 | 05°46.7′N;01°09.2′E | 70.4 | 12.94 |
| 7 | 1230 | 05°43.2′N;01°09.6′E | 72.8 | 11.61 |
| 7 | 2739 | 05°21.9′N;01°17.2′E | 57.3 | 4.02 |
| 7 | 4449 | 03°40.1′N;00°44.8′E | 70.9 | 0.95 |
| 8 | 68 | 06°16.4′N;03°44.8′E | 70.0 | 6.30 |
| 8 | 770 | 06°03.3′N;03°38.6′E | 77.0 | 3.22 |
| 8 | 1583 | 06°01.0′N;03°36.5′E | 77.7 | 2.20 |
| 8 | 2860 | 04°48.2′N;03°24.5′E | 71.3 | 0.75 |
| 9 | 31 | 04°05.6′N;06°30.0′E | 38.0 | 8.30 |
| 9 | 698 | 03°32.8′N;06°29.2′E | 74.5 | 6.11 |
| 9 | 1495 | 03°09.3′N;06°17.1′E | 74.5 | 3.67 |
| 9 | 2492 | 02°40.3′N;06°03.3′E | 75.0 | 0.91 |
| 10 | 27 | 00°20.1′S;09°01.0′E | 16.8 | 12.78 |
| 10 | 803 | 00°20.3′S;08°33.0′E | 76.5 | 6.59 |
| 10 | 1619 | 00°20.5′S;08°18.0′E | 77.4 | 1.89 |
| 11 | 30 | 06°06.0′S;12°07.6′E | 20.6 | 17.85 |
| 11 | 682 | 06°17.2′S;11°18.1′E | 73.4 | 11.36 |
| 11 | 1533 | 06°23.8′S;10°56.3′E | 82.2 | 4.45 |
| 11 | 3100 | 06°35.6′S;10°19.1′E | 80.5 | 2.94 |
| 11 | 4474 | 07°25.9′S;07°25.3′E | 79.1 | 0.28 |
| 12 | 73 | 11°48.2′S;13°39.7′E | 36.2 | 16.82 |
| 12 | 1638 | 11°46.6′S;12°50.8′E | 83.7 | 2.57 |
| 12 | 3410 | 11°45.6′S;11°41.7′E | 75.3 | 1.20 |
| 12 | 4530 | 11°43.5′S;08°52.7′E | 66.8 | 0.59 |
| 13 | 75 | 17°10.5′S;11°38.8′E | 59.8 | 23.37 |
| 13 | 551 | 17°10.2′S;11°18.0′E | 24.6 | 22.53 |
| 13 | 1965 | 17°09.7′S;11°00.6′E | 72.6 | 18.02 |
| 13 | 2802 | 17°09.7′S;10°40.9′E | 75.4 | 14.97 |
| 13 | 4601 | 17°10.2′S;08°54.4′E | 26.7 | 2.11 |

Along the transects, meiofaunal abundances generally decreased with increasing water depth (Fig. 3a). However, the steepness of gradients varied considerably in different regions off the western African coast. Steepest gradients appeared along transects reaching the Guinea and Angola Basins. Maximum values over

**Table 2** Meiofauna abundances (ind/10 cm$^2$) and biomass (µg/10 cm$^2$) along the transects (*FORA* Foraminifera; *NEMA* Nematoda; *POLY* Polychaeta; *HARP* Harpacticoidea; *NAUP* Nauplii; *REST* Pooled minor taxa; *missing Foraminifera numbers; – no values)

| Transect No. | Depth (m) | Meiofauna abundance (ind/10 cm$^2$) | | | | | | | Total biomass (µg/10 cm$^2$) |
|---|---|---|---|---|---|---|---|---|---|
| | | FORA | NEMA | POLY | HARP | NAUP | REST | Total | |
| 1 | 37 | – | 143 | 29 | 78 | 106 | 44 | 400* | – |
| 1 | 646 | 80 | 244 | 11 | 43 | 28 | 6 | 411 | 878 |
| 1 | 1495 | 35 | 172 | 12 | 26 | 18 | 14 | 277 | 150 |
| 1 | 3089 | 13 | 177 | 5 | 15 | 7 | 4 | 222 | 83 |
| 2 | 66 | 102 | 271 | 26 | 58 | 43 | 25 | 525 | 752 |
| 2 | 701 | 97 | 350 | 25 | 23 | 12 | 12 | 523 | 1163 |
| 2 | 1500 | 57 | 514 | 13 | 27 | 37 | 13 | 662 | 493 |
| 2 | 3123 | 22 | 206 | 4 | 22 | 11 | 11 | 274 | 89 |
| 2 | 4327 | 30 | 160 | 1 | 32 | 22 | 4 | 250 | 64 |
| 3 | 75 | 78 | 326 | 40 | 51 | 64 | 13 | 563 | 745 |
| 3 | 674 | 57 | 494 | 15 | 54 | 62 | 13 | 685 | 850 |
| 3 | 1483 | 22 | 314 | 4 | 26 | 20 | 13 | 390 | 281 |
| 3 | 3282 | 23 | 220 | 1 | 31 | 21 | 5 | 301 | 560 |
| 3 | 4257 | 23 | 111 | 3 | 13 | 26 | 6 | 182 | 98 |
| 4 | 54 | 675 | 1763 | 46 | 150 | 171 | 71 | 2877 | 1783 |
| 4 | 691 | 104 | 587 | 13 | 82 | 145 | 27 | 959 | 1331 |
| 4 | 1505 | 81 | 635 | 16 | 63 | 64 | 15 | 874 | 860 |
| 4 | 3296 | 40 | 217 | 0 | 26 | 35 | 6 | 324 | 402 |
| 4 | 4307 | 92 | 306 | 3 | 31 | 19 | 6 | 456 | 398 |
| 5 | 58 | 888 | 1225 | 66 | 158 | 162 | 59 | 2558 | 589 |
| 5 | 698 | 410 | 854 | 21 | 79 | 137 | 62 | 1564 | 446 |
| 5 | 1204 | 139 | 372 | 62 | 108 | 135 | 9 | 826 | 638 |
| 5 | 2992 | 178 | 371 | 3 | 49 | 52 | 23 | 676 | 425 |
| 6 | 63 | 470 | 1535 | 78 | 130 | 176 | 39 | 2430 | 1060 |
| 6 | 749 | 256 | 606 | 10 | 59 | 81 | 12 | 1023 | 208 |
| 6 | 1500 | 113 | 455 | 13 | 82 | 69 | 16 | 747 | 185 |
| 6 | 3102 | 103 | 504 | 9 | 62 | 31 | 9 | 716 | 257 |
| 7 | 39 | 645 | 1108 | 88 | 105 | 137 | 86 | 2168 | 1476 |
| 7 | 740 | 250 | 869 | 23 | 104 | 92 | 30 | 1367 | 1120 |
| 7 | 1230 | 248 | 818 | 17 | 107 | 134 | 36 | 1359 | 445 |
| 7 | 2739 | 153 | 392 | 5 | 52 | 41 | 14 | 658 | 329 |
| 7 | 4449 | 96 | 165 | 5 | 21 | 25 | 5 | 317 | 483 |
| 8 | 68 | 472 | 1235 | 64 | 66 | 145 | 46 | 2027 | 676 |
| 8 | 770 | 229 | 344 | 20 | 79 | 67 | 27 | 767 | 704 |
| 8 | 1583 | 86 | 381 | 11 | 37 | 32 | 10 | 555 | 257 |
| 8 | 2860 | 66 | 176 | 3 | 46 | 33 | 10 | 334 | 301 |
| 9 | 31 | 187 | 728 | 74 | 73 | 181 | 52 | 1296 | 667 |
| 9 | 698 | 177 | 300 | 5 | 41 | 45 | 14 | 583 | 93 |
| 9 | 1495 | 142 | 383 | 12 | 54 | 65 | 8 | 663 | 204 |
| 9 | 2492 | 112 | 204 | 6 | 22 | 15 | 6 | 365 | 1412 |
| 10 | 27 | 102 | 358 | 41 | 73 | 126 | 44 | 746 | 504 |
| 10 | 803 | 144 | 248 | 10 | 58 | 42 | 16 | 521 | 223 |
| 10 | 1619 | 293 | 196 | 14 | 19 | 26 | 15 | 570 | 859 |
| 11 | 30 | 152 | 305 | 26 | 38 | 64 | 22 | 607 | 734 |
| 11 | 682 | 118 | 283 | 13 | 19 | 39 | 4 | 478 | 406 |
| 11 | 1533 | 20 | 305 | 9 | 35 | 20 | 9 | 398 | 117 |
| 11 | 3100 | 104 | 449 | 2 | 27 | 38 | 13 | 632 | 190 |
| 11 | 4474 | 118 | 323 | 3 | 18 | 7 | 7 | 476 | 107 |
| 12 | 73 | 759 | 994 | 55 | 42 | 77 | 27 | 1954 | 926 |
| 12 | 1638 | 398 | 705 | 11 | 114 | 146 | 24 | 1398 | 417 |
| 12 | 3410 | 184 | 557 | 2 | 51 | 76 | 14 | 884 | 271 |
| 12 | 4530 | 236 | 425 | 1 | 27 | 39 | 6 | 733 | 248 |
| 13 | 75 | 785 | 2217 | 8 | 509 | 105 | 37 | 3660 | 603 |
| 13 | 551 | 409 | 240 | 23 | 57 | 38 | 21 | 788 | 825 |
| 13 | 1965 | 274 | 717 | 18 | 18 | 23 | 13 | 1063 | 213 |
| 13 | 2802 | 343 | 547 | 6 | 33 | 39 | 10 | 978 | 984 |
| 13 | 4601 | 130 | 376 | 3 | 16 | 16 | 0 | 541 | 239 |

5 cm sediment depth on the shelf ranged from 525 to 3660 ind/10 cm$^2$ and from 182 to 733 ind/10 cm$^2$ at the deepest stations of the transects (4500 m). An isoline plot for total meiofaunal abundances on the western African continental margin between 10°N and 18°S (Fig. 4) demonstrates that densities strongly increased from transects off Guinea/Liberia to transects off the Ivory Coast/Ghana/Togo. Comparatively low numbers were found off Gabon and the Congo estuary, again rising drastically to highest values along transects off

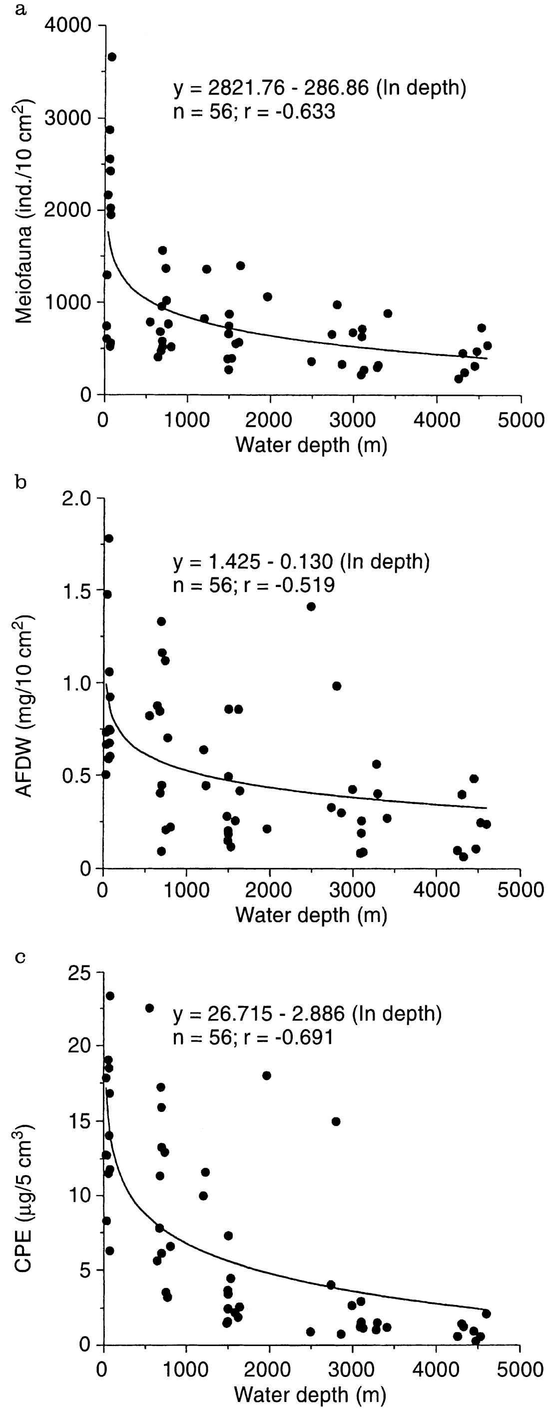

**Fig. 3** Relationship between water depth and **a** meiofaunal abundances (ind/10 cm$^2$), **b** meiofaunal biomasses (mg/10 cm$^2$) as well as **c** sediment-bound pigment concentrations (µg/5 cm$^3$) on the western African continental margin between 10°N and 18°S

Angola/Namibia. Isoline plots for individual taxa (not illustrated) in general show the same trends. Thus, taxonomic composition at the various stations was relatively constant and exhibited no clear regional shifts.

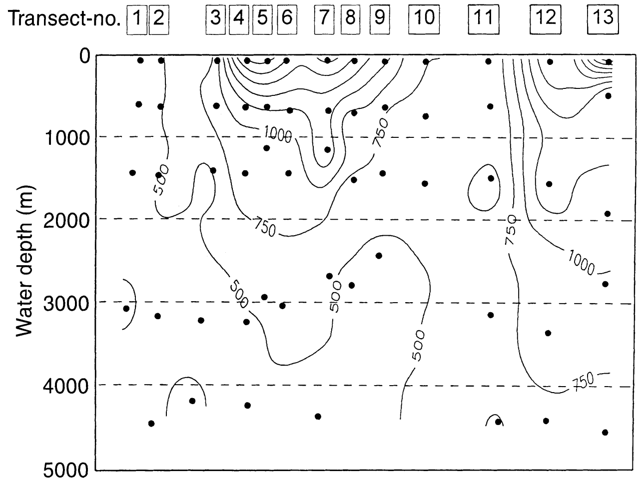

**Fig. 4** Distribution pattern of meiofauna abundances (ind/10 cm$^2$) on the western African continental margin (50 to 4500 m water depth) between 10°N and 18°S

Generally, nematodes were the most dominant taxon. Mean relative abundances were about 53 to 54% on the shelf (50 m) and the upper slope (700 m) and about 63 to 65% on deeper water depth horizons (1500, 3000, 4500 m). Foraminiferans were second in dominance, with mean relative abundances of about 23 to 24% at shallower stations (50, 700 m), ≈18% at mid-slope (1500 m) and continental rise stations (3000 m) and again increasing relative abundances (≈22%) at the abyssal stations. Relative abundance of total other taxa (mainly harpacticoids and nauplii) was 20 to 22% from shelf to mid-slope stations, slowly decreasing with increasing water depth to 15% on the abyssal plains (Fig. 5). A more detailed investigation of the so-called "rest" taxa exhibited that certain groups (e.g. ostracods, kinorhynchs) appeared over the whole depth range,

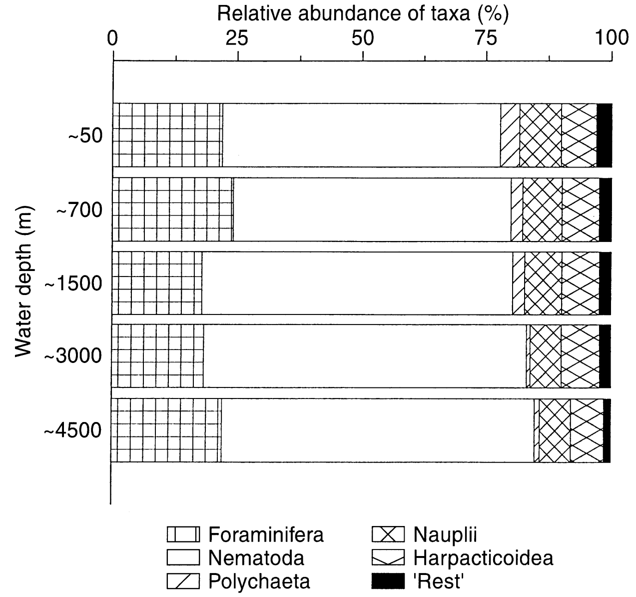

**Fig. 5** Relative abundance (%) of meiofauna taxa on different water depth horizons off the tropical western African coast

**Table 3** Relative occurrence of "Rest" taxa (+, present at <50% of stations from the same water depth horizon; + +, present at >50% of stations from the same water depth horizon)

| Taxon | Depth (m) | | | | |
|---|---|---|---|---|---|
| | ~50 | ~700 | ~1500 | ~3000 | ~4500 |
| Hydroidea | + | | | + | + |
| Bryozoa | + | + | + | | |
| Sipunculida | + | + | + | + | |
| Turbellaria | + | + | + | | |
| Gastrotricha | + | | + | + | + |
| Kinorhyncha | + + | + + | + + | + + | + + |
| Solenogastres | + | + | + | | |
| Gastropoda | + + | + | + | + | |
| Bivalvia | + + | + + | + + | + | + |
| Scaphopoda | + | + | + | | |
| Tardigrada | + | + | + | + | + |
| Acarina | + | | | + | |
| Ostracoda | + + | + + | + + | + + | + + |
| Amphipoda | + | + | | | |
| Cumacea | + | + | + | | |
| Tanaidacea | + | + | + | + | + |
| Isopoda | + | + | + | + | |
| Ophiuroidea | + | | | | |

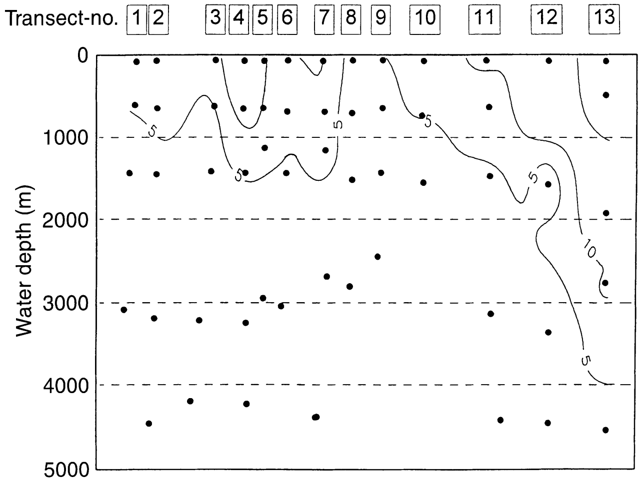

Fig. 6 Distribution pattern of sediment-bound pigment concentrations (µg/5 cm$^3$) on the western African continental margin between 10°N and 18°S

whereas other taxa (e.g. amphipods, isopods, scaphopods) were found exclusively in shallower water depths (Table 3).

Total meiofaunal biomasses (AFDW) in general declined with water depth (Fig. 3b), following the changes in abundances. A higher variability of AFDW on the shelf and upper slope is probably attributable to more frequently occurring larger organisms (>150 µm), such as polychaetes, ostracods, bivalves and cumaceans. Generally, because of their diminutive individual size and weight, biomass determinations of meiofauna organisms are flawed by methodological imponderabilities. Within this study, meiofauna biomass values were only regarded as rough estimates.

## Sediment-bound chloroplastic pigment equivalents

Concentrations of CPE in the sediments in general decreased with bathymetric depth (Fig. 3c). High values of maximum 23.37 µg/5 cm$^3$ were measured on the shelf, decreasing to minimum values of 0.28 µg/5 cm$^3$ at the deepest stations of the transects. Sometimes enhanced concentrations could be found at stations in 700 m water depth. Within the sediment column, CPE concentrations generally decreased with sediment depth; highest values were always found in the top centimetre.

An isoline plot for sediment-bound chloroplastic pigments on the continental margin off the western African coast (Fig. 6) exhibits comparably low values on transects reaching the northern part of the Sierra Leone Basin (transects 1 to 3) and in the inner Gulf of Guinea (transects 8 to 10); significantly higher values were found between 10°W and 1°E (transects 4 to 7) and especially between 5°S and 18°S (transects 11 to 13).

## Correlations between CPE values and meiofaunal abundances

Isoline plots of meiofaunal abundances and sediment-bound chloroplastic pigments on the western African continental margin showed fairly similar patterns. This suggests a close relationship between organic matter input from phytoplankton sedimentation and organism densities in the benthal (Fig. 7) and a tight pelago-benthic coupling. Nevertheless, transects 1 to 3 as well as 10 and 11 deviate from the overall trend, especially at the shallower stations above 1500 m water depth (Fig. 8).

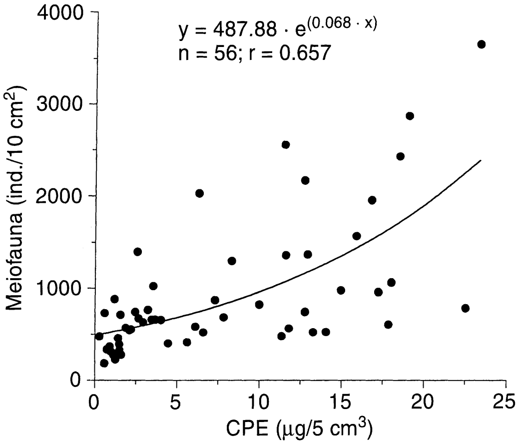

Fig. 7 Relationship between meiofaunal abundances (ind/10 cm$^2$) and sediment-bound pigment concentrations (µg/5 cm$^3$) on the western African continental margin between 10°N and 18°S

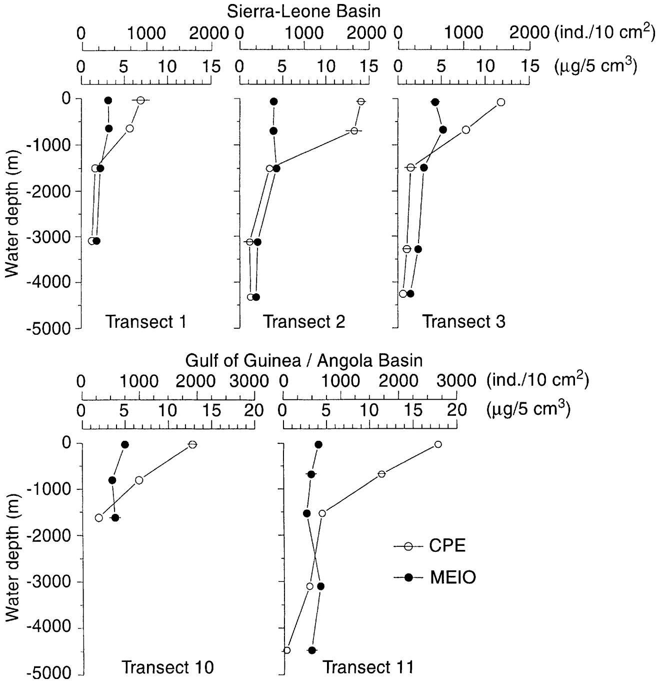

**Fig. 8** Meiofaunal abundances (ind/10 cm$^2$) and sediment-bound pigment concentrations (µg/5 cm$^3$) on transects reaching the Sierra Leone Basin as well as the inner Gulf of Guinea and the northern part of Angola Basin (standard deviations often indistinguishable from data points)

## Discussion and conclusions

Except for benthic assemblages around hydrothermal vents and cold seeps, the deep-sea benthic ecosystem is driven by energy produced in surface waters. The energy content of settling organic matter generally decreases with water depth due to degradation processes within the water column (Suess 1980; Walsh et al. 1981; Martin et al. 1984). Consequently, benthic standing stocks decrease with increasing water depth (see Gage and Tyler 1991) or, more generally, "distance from the (energy) source" (DeBovée et al. 1990).

Enhanced densities of benthic animals are to be expected in areas of increased surface production, e.g. in open ocean and especially in coastal upwelling regions. Along continental margins the sedimentary regime is complicated by a web of interacting hydrographical factors such as tides, internal waves, along-slope counter currents and down-slope detritus flows (Mittelstaedt 1976; Fahrbach and Meincke 1978), directly influencing population densities of benthic organisms (Thiel 1978, 1982, 1983). Moreover, due to the high organic matter sedimentation in upwelling areas, oxygen depletion in the sediment and in the overlying water masses may alter the relationship between organic matter (energy) input and benthic organism densities (see Tarazona et al. 1988a, b). For instance, the upwelling zone off Namibia is characterized by reduced benthic standing stocks between 50 and 200 m water depth, comprising a zone of extremely low oxygen concentrations (Calvert and Price 1971 in Pfannkuche et al. 1983). Analogous reduced benthic biomass was found in an oxygen-minimum layer varying between 150 and 500 m depth off Peru and Chile (Gallardo 1976, 1977 in Pfannkuche et al. 1983). Similar conditions ought to be expected on the western African continental margin between Guinea and Angola. Within this study, the relevant depth range was probably not covered with sampling stations, resulting in more-or-less regular gradients and values generally decreasing with increasing water depths. The extent of organic matter input to the sea floor may also be less or not sufficient enough to produce oxygen-minimum or high $H_2S$ concentrations.

### Sampling strategy

The main goal of investigations during R.V. "Meteor" expedition legs 6/5 and 6/6 to the tropical eastern Atlantic was to study large-scale distribution patterns of foraminiferans and also metazoan meiofauna off the western African coast. Coull et al. (1977) demonstrated that one box corer sample could be sufficient to estimate meiofauna abundances for a certain sampling site, whereas patchiness of meiofauna is predominantly a small-scale phenomenon within the area covered by the box corer (Bernstein and Meador 1979; Eckmann and Thistle 1988; Thistle 1988). The sampling strategy has to be regarded as a compromise between local accuracy and the geographical extension of the area of investigation.

### Meiobenthos in the tropical eastern Atlantic

Meiobenthos densities and biomasses generally showed a close correlation to regionally varying upwelling intensities in the areas of investigation. Relatively high values ($>2000$ ind/10 cm$^2$ on the shelf and significantly increased values at slope stations) were found along transects towards the Guinea Basin and the southern part of the Angola Basin, whereas comparatively low numbers ($<2000$ ind/10 cm$^2$ on the shelf, slowly decreasing downslope) appeared on transects reaching the Sierra Leone Basin, the inner Gulf of Guinea and the northern part of the Angola Basin.

Due to varying methods used in meiobenthic investigations (different mesh sizes of sieves and sediment depths investigated) a comparison of meiobenthic data from different locations is a challenge, e.g. standardization of mesh sizes is urgently required. However, a comparison of meiofaunal numbers from the tropical western African continental margin with meiofaunal data from the literature (Table 4) showed that highest values from the centres of upwelling off the Ivory Coast/Ghana and Angola were on the same order as abundances identified by Thiel (1982) and Pfannkuche et al.

**Table 4** Metazoan meiobenthic standing stocks (ind/10 cm$^2$) on continental margins in various climatic regions. Abundances including Foraminifera in *parentheses*

| Location [Mesh size; sed. depth] | Water depth (m) | | | | | | Source |
|---|---|---|---|---|---|---|---|
| | < 500 | 500–1000 | 1000–2000 | 2000–3000 | 3000–4000 | > 4000 | |
| Nansen Basin<br>[> 42 µm; 9 cm] | 1143–4339<br>(7164–16295) | 1330<br>(2840) | –<br>– | 1358<br>(1528) | 291<br>(441) | –<br>– | Pfannkuche and Thiel (1987) |
| NE Atlantic<br>[> 42 µm; 5 cm] | 2604<br>– | 1593–1963<br>– | 828–943<br>– | 744–900<br>– | 663<br>– | 315–528<br>– | Pfannkuche (1985) |
| NW Africa, 35°N<br>[> 42 µm; 5 cm] | –<br>(1778–2656) | –<br>(1175–1465) | –<br>(620–631) | –<br>(550–570) | –<br>(557) | –<br>– | Pfannkuche et al. (1983) |
| NW Africa, 21°N<br>[> 42 µm; 4 cm] | –<br>(1850) | –<br>(2600) | –<br>(1000) | –<br>– | –<br>(1150) | –<br>– | Thiel (1982) |
| NW Indian Ocean<br>[> 40 µm; 4 cm] | 178–698<br>– | 305–712<br>– | 61<br>– | 61–229<br>– | –<br>– | 11–63<br>– | Romano and Dinet (1981) |
| NW Atlantic<br>[> 44 µm; 10 cm] | 357–1174<br>(389–1196) | 154–166<br>(173–424) | 98–121<br>(447–715) | 41–64<br>(238–425) | –<br>– | –<br>– | Tietjen (1971) |
| E Atlantic<br>[> 42 µm; 5 cm] | 400–2875<br>(525–3660) | 331–1154<br>(411–1564) | 242–1111<br>(277–1398) | 253–635<br>(334–978) | 209–700<br>(222–884) | 159–497<br>(182–733) | Present study |

(1983) in the region of permanent upwelling off NW Africa between 21°N and 35°N. Similar high values were also found by Pfannkuche (1985) in the Porcupine Seabight, NE Atlantic. Meiofaunal densities from a polar region (Pfannkuche and Thiel 1987) even exceeded these numbers, especially when foraminiferans were taken into account. The extremely high meiofaunal densities in (seasonally ice-covered) polar regions might be the result of adaptations to low and oscillating food levels and particularly to the low maintenance energy requirement associated with the low ambient temperature (Brey and Clarke 1993). Low meiofaunal densities along transects towards the Sierra Leone Basin, the inner Gulf of Guinea and the northern part of the Angola Basin were comparable to those found, e.g. by Tietjen (1971) in the NW Atlantic and Romano and Dinet (1981) in the NW Indian Ocean.

## Meiofaunal abundances in relation to organic matter input

Distribution patterns of meiofaunal abundances and sediment-bound pigment concentrations off the western African coast generally showed broad similarities, stressing the overall close relationship between food (energy) availability and benthic standing stocks. However, in contrast to meiofaunal numbers, relatively high pigment values could be found to the west (transects 1 to 3) and to the north (transects 10 and 11) of the centres of upwelling and enhanced primary production off the Ivory Coast/Ghana and Congo/Angola, predominantly at stations above 1500 m (Fig. 8). It is suggested that this discrepancy might be caused by the dislocation of smaller/lighter (phyto-)detritial particles during their passage to the sea floor by coastal currents. Meiofaunal numbers probably do not follow the increased pigment concentrations off Guinea/Liberia and Gabon/Congo because this phytodetritus apparently has been transported over long distances and does not have the same energy content as relatively fast and/or vertically sinking larger phytodetritus aggregates in the centres of enhanced primary production.

Sinking phytodetrital aggregates (“marine snow”) are heavily colonized by numerous microorganisms in concentrations 2 to 5 orders of magnitude higher than in the surrounding water (Prezelin and Alldredge 1983). Enhanced microbial enzymatic activity within these aggregates (Smith et al. 1992) suggests that easily degradable compounds of algal material should be largely utilized/respired. Subsequently resulting smaller and lighter phytodetritus flocks, consisting of more refractile compounds (including partly degraded chloroplastic pigments), may be transported by currents over long distances and reach the sea floor far away from their origin.

Indications for a lateral, current-driven, along-slope transport of planktonic organisms off the western African coast were given by Weikert (1984) for calanoid nauplii and cladocerans (*Penilia avirostris*) as well as by John et al. 1981 for lancelet larvea (*Branchiostoma senegalense*). The same dislocation mechanism could be considered for phytoplankton and any kind of particulate detritus. Off the African coast between 0° and 15°W this along-slope transfer of settling particles is probably mediated by the westward flowing Guinea Undercurrent (Lemasson and Rébert 1973a, b). Off Congo/Angola the current system is extremely complicated by the huge discharge of water masses by the Congo River, and there is no common opinion on the relative importance of the Equatorial Undercurrent and waters from the Benguela Current. However, it seems quite possible that the various domes, fronts and thermal crests described for this region are nothing but sections through a subsurface tongue of the Benguela Current, possibly extenting north to 3°S (Van Bennekom and Berger 1984). Dislocation of (phyto-)detritus could be caused by a coastal branch of the Benguela Current and the Congo River outflow.

In general, one can consider other possible reasons for the identified discrepancies between the potential organic matter input from the euphotic zone and meiobenthic standing stocks in distinct regions off the western African coast. Increased sediment-bound pigment concentrations along transects 1 to 3 and 10 to 11 could be the result of a most recent seasonal input of phytodetrital material to the sea floor. If sampling was carried out immediately following such a sedimentation event, meiofauna assemblages might not have had enough time to respond to it. However, pigment analyses showed no shift towards higher concentrations of intact chlorophyll *a* within the bulk of chloroplastic pigments (CPE) in the areas of transects 1 to 3 and 10 to 11, confirming that there was no recent input of "fresh" phytodetritus to the sea floor. The identified discrepancies between meiobenthic standing stocks and pigment concentrations within sediments in distinct areas off the western African coast may also be explained by predator–prey interactions regulating meiobenthic stock sizes. Such a "top down" control of living and detrital carbon reservoirs (Rowe 1996) might also be important in the areas investigated within the present study. Unfortunately, there are no macro- and megafaunal data available to check this.

Therefore, with the given data, it is hypothezised that low meiobenthic abundances in relation to relatively high sediment-bound pigment concentrations in certain regions on the western African continental margin may indicate fractionated sedimentation of organic matter to the sea floor.

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