



RESULTS OF THE DIVA-1 EXPEDITION OF RV “METEOR” (CRUISE M48/1)

Diversity of peracarid crustaceans (Malacostraca) from the abyssal plain of the Angola Basin

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Abstract

During the expedition DIVERsity of the abyssal Atlantic benthos (DIVA-1) with RV “Meteor” in July 2000, samples were taken at seven stations by means of an epibenthic sledge north of the Walvis Ridge in the Angola Basin off Namibia in 5125–5415 m depth. Two hundred and forty one species of Peracarida are identified from the material so far. Dominant elements of the peracarid fauna were Isopoda, which were most abundant and diverse, 100 species were identified from 1326 individuals, followed by Tanaidacea with 50 species and 194 individuals, and Cumacea with 45 species and 479 individuals. Amphipoda were less frequent with 39 species and 150 individuals, Mysidacea were rarest yielding only 7 species and 34 individuals. The fauna is characterized by 118 rare species, most of them occurring only with single specimens at one station. Only 123 species occur at more than one station and only two species of the Eurycopinae (Isopoda) at all stations. The few species which are already known are either cosmopolitan or typical for the Atlantic Ocean, while elements known from the Southern Ocean are rare indicating that the Walvis Ridge is an effective distribution barrier for deep-sea organisms.

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Introduction

In general, the species composition of abyssal deep-sea communities is poorly known in comparison with shelf and upper slope environments (Gage and Tyler 1991), their response to biotic and abiotic parameters, speciation processes and the regionalization of the fauna even less. It is, at present impossible to predict how many macroinvertebrates live in the deep sea even though many samples have been taken during deep-sea

expeditions in the past (Gage and Tyler 1991; Grassle and Maciolek 1992) because specimens have been identified rarely to species level and it remains unknown how large the areas colonized by single species are on average. It is also not known whether hot spots of species diversity exist, or whether or how regional faunas can be delimited. Even though ecologists prefer to stress the analysis of processes, a profound knowledge of animal communities requires data on their composition at species level, and for the protection of biodiversity it is necessary to know the geographical distribution of specific communities. The series of

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DIVERSITY of the abyssal Atlantic benthos (DIVA) expeditions was designed to collect high-quality data on the diversity and composition of deep-sea communities and to compensate for the outlined shortcomings. During DIVA-1 a group of systematists collected samples from the Angola Basin from RV “Meteor”, which are currently being described taxonomically. First observations on the composition and diversity of the peracarid fauna are presented.

Before the DIVA-1 expedition (Kröncke and Türkay 2003), the Angola Basin was essentially unknown in terms of benthic biodiversity. Only some details of the megafauna have been studied in the southwestern Angola Basin (Vinogradova et al. 1990), and the meiofauna was only known from coastal regions (Mackensen and Schmiedl 1995; Soltwedel and Thiel 1995; Schmiedl et al. 1997; Soltwedel 1997) and from the Walvis Ridge. Kudinova-Pasternak (1993) reported one tanaidacean (*Neotanais affinis*) from this region, however, she only determined the large animals (Blazewicz-Paskowycz pers. comm.). Bamber (2000) published a list of peracarids with one new species of Isopoda and five species of Tanaidacea from that area.

Study area

The Angola Basin (~5°S to 25°S and 5°W to 8°E) off the Namibian and Angolan coast north of the Walvis Ridge reaches a depth of about 5500 m. The transect of DIVA-1 (16–22°S and ±3°E) lies in the southeastern region of the Angola Basin in depths ranging from 5125 to 5415 m. The water column at this location is strongly stratified, as different water masses enter the area. The physical oceanography of the study area has been described by Dietrich et al. (1975), Reid (1996), Shannon and Nelson (1996), and Wefer et al. (1996).

The North Atlantic Deep Water (NADW) is the most important water mass for the life in the Angola Basin. The major portion of the NADW reaches the Angola Basin through the Romanche-Fracture-Zone (0°N, 20°W) in the Mid-Atlantic Ridge and flows to the southwest in the basin (Warren and Speer 1991; Siedler et al. 1996). The Antarctic Bottom Water (AABW; –2 °C to –1 °C and 34.6–34.7psu), well known from the western part of the South Atlantic, was not detected in the Angola Basin either by DIVA-1 or by previous expeditions.

The Walvis Ridge acts as a barrier to the equatorward flow of the AABW (Shannon and Nelson 1996). It rises up from the seafloor to 1000 m below sea surface, with few deep gaps between 3500 and 3000 m (Dietrich and Ulrich 1968). The Antarctic Intermediate Water (AAIW) can flow easily over the Walvis Ridge into the Angola Basin, but the AABW can only pass through the gaps of the ridge into the southern Angola Basin

(Shannon and Chapman 1991; Tomczak and Godfrey 1994; Dieckmann et al. 1996; Bearman 2001). During DIVA-1 a salinity of 34.8 psu and a temperature of 2.48 °C near the sea bottom was found (Kröncke and Türkay 2003), therefore we can state that the Angola Basin is characterized by the NADW. This hydrographic pattern is important for the study of possible sources of faunal elements.

The study area is in general oligotrophic (Wefer et al. 1996), but there is some evidence that the nutrient availability on the African slope and the higher production also influence the deep-sea in areas closer to the continent. Data on biogenic sediment compounds on the continental slope are found in Soltwedel and Thiel (1995). Fischer and Wefer (1996) reported a high influx of lithogenic and biogenic opal fluxes off Namibia, and an exponential decrease of the organic carbon fluxes with depth was strongest at the Walvis Ridge. The decrease in organic matter fluxes with increasing distance from the coast is also reflected in the abundance and species composition of benthic Foraminifera (Schmiedl et al. 1997).

It is now possible for the first time to present data on the biodiversity of Peracarida in the Angola Basin. The aim of the present study is to describe the composition of the regional peracarid fauna along the transect. Further details besides the taxon list of the Peracarida sampled with the epibenthic sledge at the stations in the Angola Basin are available in the electronic supplement. Species names, descriptions of new species, species distribution along the transect, analysis of their origin and distribution will be published separately by the taxonomists that are currently working with the material (see also references of already published data).

Material and methods

During the expedition DIVA-1 with RV “Meteor” (M48-1) in July 2000, samples were taken at seven stations north of the Walvis Ridge on the abyssal plain of the Angola Basin along a transect of approximately 700 km. For station data and haul lengths see Table 1. The collecting gear used for the samples described herein was an epibenthic sledge (N. Brenke, submitted; modified after Brandt and Barthel 1995). It possessed an epinet and a supranet of 500 µm mesh, both equipped with a cod end of 300 µm. A total area of 27,765 m² was covered by the samples.

We noted that during hauling of the sledge in heavy sea part of the samples was washed out. The reduced catches concern stations 320 and 338. Owing to this problem the relevant stations must be excluded.

On deck samples were sieved (300 µm mesh) gently with precooled seawater and then immediately

Table 1. EBS Stations of the DIVA-1 expedition with RV “Meteor” in the Angola Basin

EBS stations	Date	Position start	Depth (m)	Position end	Depth (m)	Trawled distance (m)
318	09.07.00	22°20.0'S 003°18.3'E	5125	22°20.2'S 003°18.4'E	5144	3146.9
320	10.07.00	22°19.9'S 003°17.8'E	5127	22°20.0'S 003°17.9'E	5126	2445.9
338	22.07.00	18°19.4'S 004°39.7'E	5397	18°20.8'S 004°38.6'E	5398	5781.5
340	22.07.00	18°18.3'S 004°41.3'E	5395	18°19.4'S 004°41.9'E	5395	3984.6
344	25.07.00	17°06.2'S 004°41.7'E	5415	17°07.5'S 004°42.3'E	5415	5372.9
348	28.07.00	16°18.1'S 005°27.2'E	5390	16°19.3'S 005°27.2'E	5387	4261.5
350	29.07.00	16°14.3'S 005°26.8'E	5389	16°14.9'S 005°26.7'E	5389	2769.6

transferred into 80% ethanol kept at -10°C for later DNA extraction. Specimens were partly sorted on board or later in the laboratory at Bochum University.

Peracarids were sorted and distinguished to species level. Since species names are only known for a fraction of the material, species were provisionally numbered and characterized until complete description. The distribution and structure of distinct benthic assemblages was examined by multivariate analysis (PRIMER software package after Clarke and Warwick 2001; Kruskal and Wish 1983; Wilkinson et al. 1983; Clarke and Ainsworth 1993). Classification and ordination procedures were used to compare faunal composition of Peracarida between stations. The faunistic resemblance between stations was measured by the quantitative Bray–Curtis similarities (Bray and Curtis 1957).

Species diversity was defined as the number of species per station (Hurlbert 1971). Diversity (H') after Shannon and Weaver (1949) and evenness (J') after Pielou (1966) were calculated and are presented in Table 3.

Results

Peracarida were (with polychaetes, copepods and bivalves) a dominant taxon of the macrobenthos, constituting 21.8% of the specimens. 2183 peracarid specimens comprising at least 241 species were sampled at the seven stations along the Angola Basin transect. Isopoda were the most abundant and diverse peracarid taxon with 100 species and 1326 individuals. It is possible that this species number will increase in the future after further taxonomic study. 60% of all peracarid specimens sampled are isopods. Tanaidacea were the second most speciose order with 50 species, but less abundant (194 individuals) than the Cumacea, which occurred with 479 individuals comprising 45 species. Amphipoda were less frequent with only 150 individuals and 39 species, and Mysidacea were rarest, 7 species being identified from 34 individuals. Generic names and raw numbers of specimens are found in the preliminary species list included as electronic supple-

ment. This list comprises 227 species which could be attributed to a peracarid family.

In total 1326 specimens of Isopoda comprising 15 families were identified (due to damage, not all specimens could be identified to species level). With the exception of a few larvae of parasitic species, all isopods belonged to a single taxon, the Janiroidea (suborder Asellota, 99% of the Isopoda sampled in the Angola Basin), a taxon of highly specialized deep-sea genera. The isopod family Desmosomatidae was most diverse with at least 37 species from 240 individuals, followed by the Munnopsididae (mainly Eurycopinae and Ilyarachninae), with more than 500 specimens of at least 22 species in the Angola Basin, the Haplomiscidae with 15 species from 114 specimens, the Ischnomesidae with only 47 specimens and 15 species identified, the Macrostylidae with 38 specimens and 6 species, and the Nannoniscidae with 25 individuals and 4 species. The new species of Nannoniscidae and Macrostylidae have already been described (Brandt 2002, 2004). Dendroitiidae, Acanthaspidiidae, and Haplomunnidae were rare, Munnidae were only represented with a single specimen. Families which do occur in the deep Antarctic benthos, like the Serolidae and the Arcturidae, were absent. Many of the species sampled were new to science (see electronic supplement). Of those species already known some have a wide distribution, with records off Greenland, Iceland, or the tropical western Atlantic. Distribution maps will be published in the taxonomic studies that are currently being prepared. It is obvious that these findings will have consequences for the estimation of global diversity. However, better data are needed from other ocean basins to consider the species turnover.

The second most important taxon in terms of numbers of specimens was the Cumacea. Of nine known families at least 45 species were identified. The most speciose families in the region were Diastylidae (17 species), Nannastacidae (12 species) and Leuconidae (8 species). Within these families, the most speciose genera were *Makrokyllindrus* Stebbing, 1912 (Diastylidae, 13 species) and *Leucon* Kröyer, 1864 (Leuconidae, 6 species). Two species of the genus *Styloptocuma* Băcescu

and Muradian, 1974 (Nannastacidae) were dominant within the Cumacea at four stations and had a high presence (86% of all samples) in the area. Species of the genera *Platycuma* Calman, 1905, *Campylaspis* Sars, 1865 (Nannastacidae) and *Hemilamprops* Sars, 1883 (Lampropidae) were almost as abundant as those of *Styloptocuma* Băcescu and Muradian, 1974. The only known species is *Leucon homorhynchus* Bishop, 1981. Descriptions of a new genus and species of the family Diastylidae have been published (*Divacuma tuerkayi* Mühlenhardt-Siegel, 2003).

We found 10 families of Tanaidacea. Leptognathiidae was represented by 45 individuals from 11 species, Anarthruridae by 37 individuals (9 species) Agathotanaididae by 31 individuals (2 species), Pseudotanaididae by 48 individuals (11 species), Nototanaididae by 16 individuals (8 species), Colletteidae by 2 individuals (2 species), Tanaellidae by 8 individuals (2 species), Neotanaididae by 3 individuals (1 species), Leviapseudidae by 1 individual (1 species), and Apeudidae only occurred as 3 individuals, representing 3 species. The most abundant suborder is the Tanaidomorpha which comprised 96% of the tanaidacean fauna. Up to now 2 new genera and 7 new species of the DIVA-1 Tanaidacea have been described (see appendix; Guerrero-Kommritz 2003a, b; Guerrero-Kommritz and Heard 2003; Guerrero-Kommritz and Błażewicz-Paskowycz 2004).

Eleven families of the Amphipoda were sampled in the Angola Basin. The Pardaliscidae were most diverse with 9 species from 7 genera, followed by the Oedicerotidae and the Phoxocephalidae which both occurred with 6 species. Amphilochidae, Calliopiidae, Stegocephalidae and Stenothoidae were rarest and only represented by a single species.

From the 34 specimens of the Mysidacea, 7 species of the family Mysidae could be distinguished.

Hundred and eighteen species of peracarids are considered to be very rare. Most of them occurred only with a single specimen at one station. Only about 50% of all Peracarida sampled (123 species) occur at more than one station and only two species of the Eurycopinae (Isopoda) at all stations. The few species which are already known are either cosmopolitan or typical for the Atlantic Ocean, while elements known from the Southern Ocean are rare.

Diversity of all orders of Peracarida is presented in Table 2 and Fig. 1. While evenness (J') is similar at all stations (slightly higher at stations 248 and 350), diversity (H') is highest at stations 340 and 344, slightly lower at the northernmost stations 348 and 350 and lowest at the southernmost station 318 (Table 3). Species richness is lower at station 350 than at stations 340, 344, and 348. As already mentioned in the previous chapter (material and methods), the catches from stations 320 and 338 cannot be considered due to losses in heavy

Table 2. Peracarid species/individuals per EBS-station in the Angola Basin (A = Amphipoda; C = Cumacea; I = Isopoda; M = Mysidacea; T = Tanaidacea)

Station/taxa	A sp	C sp	I sp	M sp	T sp
318	3/3	8/21	17/87	2/3	8/9
320	1/1	2/2	10/13	2/2	2/2
338	—	14/23	22/78	—	7/7
340	10/32	21/92	40/289	—	29/68
344	10/18	23/80	42/227	2/10	22/50
348	10/30	24/138	42/306	5/10	21/39
350	11/24	19/125	33/326	3/9	12/17

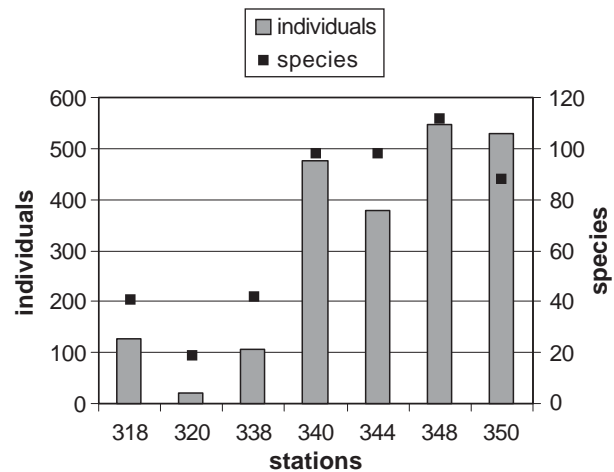


Fig. 1. Numbers of peracarid individuals and species at EBS stations taken in the Angola Basin during DIVA-1.

Table 3. Diversity indices for five EBS stations from the DIVA-1 expedition

EBS station	S	d	J'	H'
318	50	12.47	0.88	3.44
340	107	21.91	0.87	4.08
344	105	23.58	0.89	4.12
348	121	23.88	0.83	3.99
350	100	18.72	0.82	3.76

S = total species number; $d = (S - 1) / \text{Log}(N)$, species richness after Margalef (1983); $J' = H' / \text{Log}(S)$, Pielou's evenness (Pielou, 1966); $H' = \text{SUM}(\text{Pi} \times \text{Log}(\text{Pi}))$, diversity after Shannon & Wiener (Shannon and Weaver, 1949).

weather, but the samples from station 318 are technically comparable to 340–350.

Classification and ordination procedures were used to compare the faunal composition of the Peracarida between stations. A cluster analysis and multidimensional scaling of the peracarid species composition calculated for 1000 m trawled distance at the different stations revealed the closest similarities in species

composition between the two northernmost stations 348 and 350, the northern stations 340 and 344 were also similar. Station 318, in the south, was most different.

These five stations were not sufficient to sample all or most of the rare species of the Peracarida in the Angola Basin, as most species were rare, and with every additional sample more new rare species appeared.

Discussion

The general composition of the macrofauna in the EBS samples with dominant taxa like polychaetes, peracarids, copepods and bivalves is similar to other deep-sea areas of comparable depths (e.g., Galeron et al. 2001). Most of the peracarids of the Angola Basin belong to new species, they are currently being described, some are already published (Bamber 2000; Brandt 2001, 2002, 2004; Guerrero-Kommritz et al. 2002; Malyutina et al. 2001; Mühlenhardt-Siegel 2003; Schmid et al. 2002). However, as long as the taxonomic work is not finished, several important subjects outlined in the introduction cannot be addressed. A precise identification and documentation of the common species of the area is necessary in order to analyze the regionalization of the fauna, its relation to other areas of the Atlantic, and to study the influence of historical and ecological processes on the pattern of the peracarid composition. We therefore advocate a better international coordination of deep-sea sampling programmes and a comprehensive taxonomic evaluation of the samples, which are the only means to get comparable data.

The fact that the deep sea is rich in species is not questioned any more. Sanders (1969, 1979) and Zenkevitch and Birstein (1960) were among the first that reported on the high species diversity in the deep sea and discussed the origin and age of its fauna, and most deep-sea species seem to be rare (Wilson 1998). Today, more precise quantitative analyses have been undertaken like for Asellota from the Bay of Biscay (Chardy 1979), or for Peracarida from the European Northern Seas (e.g. Brandt 1997). However, complete species lists documenting the composition of the most important benthic macrofaunal taxa are rarely published, as for example, for a single area off the east coast of the USA (Hilbig 1994). Therefore, large-scale analyses of the distribution of faunal elements are not possible today.

According to the landmark study of Grassle and Maciolek (1992), the world's deep-sea fauna might harbor 10 million species of macrofauna. This estimation was based on an extrapolation from quantitative studies of box corer samples from off the east coast of the USA and assuming a high rate of appearance of new species per 100 km distance or per square kilometer.

However, for this calculation an important parameter could not be considered on the basis of empirical data, namely the species turnover over larger distances, simply because such data are not available. Even though the EBS samples of DIVA-1 are not quantitative (to get precise data on densities), they are adequate to document the presence of rare species (due to the large area sampled). During DIVA-1, seven epibenthic sledge stations could be obtained, these cover a total area of 27,765 m². This area is equivalent to almost 277,650 van Veen grab samples (0.1 m² each) or 111,060 USNEL box corer samples (0.25 m²). We do consider those species which occur with only a single individual in an area of 27,765 m² to be rare. After an addition of precise taxonomic data from other ocean basins, we will know in future how many species are really endemic and what portion of a local fauna is cosmopolitan.

For the time being, the fact that many species of the DIVA-1 samples are new to science and that little information is available from other areas makes it impossible to compare the peracarid community patterns from the deep Angola Basin with those from other Atlantic areas on species level. However, general patterns of a low abundance and diversity of deep-sea Amphipoda and a high diversity and abundance of Cumacea, Tanaidacea, and especially Isopoda were already reported earlier for deep-sea Peracarida (e.g., Dahl 1954). In the abyssal Angola Basin, Isopoda were also the most abundant and diverse taxon. This high number of isopods is also typical for other deep-sea areas (Gage 1997; Gage and Tyler 1991; Galeron et al. 2001; Hessler 1970; Hessler and Thistle 1975; Hilbig 1994; Kröncke 1998; Menzies 1962). Tanaidacea were also very speciose in the area investigated (compare species list in the electronic supplement). Cumacea comprised almost as many species as Tanaidacea, but more individuals. High numbers of Cumacea are also reported for the deep sea of the European Northern Seas (Brandt 1997). Amphipoda and Mysidacea were rare, as documented for other deep-sea areas (e.g., Dahl 1954).

Menzies (1962) reported 176 isopod species for a series of 116 samples scattered over the abyssal Atlantic Ocean (with no isopod from the Angola Basin). That we could collect 100 species from seven stations in the abyssal Angola Basin alone could either mean that the fauna of this deep-sea basin is extremely diverse, or that the EBS is extraordinarily efficient if compared to formerly used trawled gears.

Most isopod crustaceans of the deep North Atlantic belong to the suborder Asellota (Svavarsson et al. 1990; Svavarsson 1997; Wilson 1998), while in contrast, Southern Ocean isopod faunas and adjacent regions show a higher percentage of isopods of other suborders (e.g., Barnard 1962; Kussakin 1967, 1973; Kussakin and Vasina 1994, 1995; Baltzer et al. 2000). The fact that

these elements are absent from the samples from the Angola Basin is an indication of the isolation of its fauna from the subpolar and South African deep fauna. The Walvis Ridge obviously seems to be an effective distribution barrier in the south of the Angola Basin. We must therefore assume that closest relatives are found in more northern neighbouring abyssal plains. This is probable because the hydrographic regime of the region should contribute to a southward transport of bottom fauna. Systematic comparisons and phylogenetic analyses with material from the hitherto unsampled areas of the tropical western Atlantic are required to confirm this distribution pattern.

In general, the diversity of peracarids is highest on stations 340, 344, 348, and 350, the northeastern stations, while on the southernmost station 318 diversity is significantly lower. As already explained, only station 318 can be compared with the northern stations, while the results of 320 and 338 are artifacts. Stations 348 and 350 were closest geographically, what may be the reason for the high similarity in peracarid species composition. However, diversity (H') is slightly lower at these northernmost stations than at stations 340 and 344, but lies in the same range, whereas H' is lowest at station 318. Evenness is similar at all stations, but slightly higher in the north at stations 348 and 350 (Table 3). Differences between the southernmost station and the more northern ones may reflect the effect of higher concentration of food. Total organic carbon, macrofaunal abundance and biomass were lower at the southern stations than at the northern ones in box corer samples (344, 348, 350) (Kröncke and Türkay 2003). These differences can be attributed to the proximity of the northern stations to the productive upwelling area near the coast that implies a higher food-supply to the benthos (Dieckmann et al. 1996; Warren and Speer 1991; Kröncke and Türkay 2003).

The taxonomy of the new species which occur more frequently in the samples will be important for several other analyses: we need more details about the number of putative endemics, precise data on the simultaneous occurrence of species that otherwise were found far away from the Angola Basin and data on closest relatives to understand the origin, history, and uniqueness of the local faunas.

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