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

A method for comparing within-core alpha diversity values from repeated multicorer samplings, shown for abyssal Harpacticoida (Crustacea: Copepoda) from the Angola Basin

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Abstract

A methodology for comparing repeatedly sampled multicorer stations as to significant differences in alpha diversity of selected cores is presented. This is demonstrated for Harpacticoida of the Angola Basin which were sampled during the DIVA-1 campaign of RV “Meteor” in the year 2000 (M48/1).

Two replicatedly sampled multicorer stations were compared as to their species-level alpha diversity values of all adult Harpacticoida in single cores. This was done by a newly developed procedure: based on a rank-ordered alpha diversity matrix, using each a species richness, evenness, and dominance diversity index, a minimum spanning tree test (MST-test) was performed to test for significant diversity differences between the replicates of stations 325 (depth: 5448 m) and 346 (depth: 5389 m). The Canberra Metric was used as a measure of dissimilarity between multicorer deployments. With this procedure, any choice of combination of diversity indices can be made, according to the desired emphasis on certain aspects of diversity. This freedom of choice, together with the possibilities to test for significant diversity differences and to visualize this test, are desirable features of the presented procedure for diversity comparisons. Testing for diversity differences may be useful in the context of conservational purposes when politicians need clear statements from scientists.

Due to sufficient replicates, for the first time a significant diversity difference between two abyssal (> 2000 m depth) multicorer stations was detectable. Station 346 (eight replicates) was significantly more diverse in harpacticoid species than station 325 (seven replicates). Regional-scale differences in food availability are assumed to be of importance for the different patterns of diversity at stations 325 and 346.

The slope of the line of regression in a species/individuals plot on single-core level was not far from 1 \( (R^2 = 0.990; y = 0.877x) \), indicating that most species were represented by singletons and the rest only by very few specimens.

The data supported scale-dependent differences of harpacticoid diversity in the Angola Basin. Local-scale (between replicates) differences in harpacticoid within-core species diversity were lower than regional-scale (between stations) differences.

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doi:10.1016/j.ode.2004.10.001
At least 134 species of Harpacticoida were found at the two stations, of which the subgroups of Pseudotachidiidae, Argestiidae, Ameiridae, and Ectinosomatidae turned out to be richest in species and individuals. © 2004 Elsevier GmbH. All rights reserved.

**Keywords:** Diversity comparison method; Minimum spanning tree test; Alpha diversity; Productivity; Scale dependency; Deep sea; Harpacticoid copepods; Meiobancha

**Introduction**

The total number of marine species is still unknown. Estimations range from 500,000 species (May 1992; Gray 1996), to 5 million species (Poore and Wilson 1993), to more than 10 million species (Grassle and Maciolek 1992; Lambshead 1993; doubted by Gray 1994 and Gray et al. 1997). Many estimates have been derived from local data rendering extrapolations to global scale at least doubtful (Lambshead and Boucher 2003). Furthermore, some of these estimates rely on macrofauna data only and do not take into account meiofaunal diversity, which in fact is high, at least at small scales. In detail, meiofaunal abundance per unit area is much higher than for macrofauna, leading to a higher meiofauna richness within a particular patch (Snelgrove and Smith 2002); but this does not tell much about the proportions on larger scales. Some publications (e.g. Rex 1983; Stuart et al. 2003) indicate a higher macrofauna diversity at intermediate depths (2000–3000 m), but for meiofauna this has to be evaluated more thoroughly. Whilst meiofaunal densities seemed to decrease with depth in some studies (Vincx et al. 1994: Northeast Atlantic; Vanhove et al. 1995: Weddell Sea), other authors found no simple relationship between these two parameters (Herman and Dahms 1992: Weddell Sea; George (1999) for Harpacticoida only: Magellan Region, high Antarctic). All these somewhat contradictory results and assumptions indicate that marine biodiversity is far from being understood. Above all, more studies on the organismal diversity in the deep sea are needed to improve the situation, not least since this huge habitat constitutes about 50% of the earth’s surface.

For this reason, the DIVA-1 expedition of RV “Meteor” (M48/1) started in July 2000 to investigate the abyss of the Angola Basin for latitudinal diversity gradients. First results of this expedition show that there is indeed quite a considerable diversity in many groups of organisms (Polychaeta, Tanaidacea, Isopoda, Cumacea, Kinorhyncha, Loricifera, Tardigrada) collected from the deep-sea bed (depth about 5400 m) of the Angola Basin (see other contributions to this volume).

A striking example for another diverse taxon from this region are the harpacticoid copepods which make up about 98.7% of all sampled copepods. Thistle (2001) gave an interesting statement as to the overall diversity of Harpacticoida in the deep sea: “harpacticoids are not only successful in the deep sea, they are unusually so when compared to the macrofauna taken as a whole”.

Despite their importance in benthic assemblages, studies on the diversity of copepod communities in the deep sea are still scarce. Here, we present one of very few quantitative investigations on the species level diversity of Harpacticoida of all subgroups sampled from abyssal regions (>2000 m depth). Former studies were those of Coull (1972), who compared diversity and affinities of harpacticoid assemblages from different depths, Montagna and Carey (1978), who investigated Harpacticoida from the Beaufort Sea in the Arctic Ocean, and Thistle (1983a), who compared two deep-sea soft bottom communities as to the time-stability hypothesis as a predictor of diversity.

The scarcity of quantitative studies on species level is somewhat surprising, as comparatively high abundance and diversity make the deep-sea meiofauna (of which Harpacticoida are a very diverse and abundant part) ideally suited to quantitative studies and suggest that this group plays an important role in ecological processes (Vincx et al. 1994). Former qualitative or quantitative studies on abyssal Harpacticoida either concentrated on single or few subgroups of this species rich taxon (e.g. Bodin 1968; Por 1969; Dinet 1974; Becker and Schriever 1979; Becker et al. 1979; Reidenauer and Thistle 1983; Schriever 1983; Thistle and Eckman 1988; Huys and Thistle 1989; Huys 1993; Moura and Pottek 1998; George 1999; George and Schminke 2002), or were restricted to superspecific taxa (e.g. Dinet 1973; Rachot 1975; Thiel 1982; Thiel 1983; Herman and Dahms 1992; Tietjen 1992; Vincx et al. 1994; Vanhove et al. 1995; Vanaverbeke et al. 1997; George and Schminke 2002). The high logistic effort of sampling in the abyss (here defined by depth below 2000 m, according to Friedrich 1965) as well as the difficulty to cope with the task of species identification for all Harpacticoida subgroups resulted in the low number of comprehensive investigations. Consequently, many specialists for single or several harpacticoid subgroups had to combine forces in order to make this study possible.

Although so far most species obtained from the DIVA-1 expedition still remain undescribed and could
at best be identified to the level of working species in some groups, a diversity analysis was nevertheless performable, based on species and individual counts in single multicorer (MUC) cores, leading to core-scale alpha diversity values.

The concept of a subdivision of biological diversity into alpha, beta, and gamma diversity was comprehensively defined by Whittaker (1972). Whereas alpha diversity simply means the diversity of a single sample or a small area (Fisher et al. 1943; Whittaker 1960, 1967), gamma diversity usually means the diversity of combined alpha samples or larger regions. Beta diversity deals with diversity differences between locations and along gradients (Whittaker 1960); it is based on the scattering of species along changing abiotic and biotic environmental factors. This conceptual partitioning of diversity of Whittaker has recently been put on a more operational base (e.g., Crist et al. 2003).

In the present study, harpacticoid alpha diversity values of single cores from replicated samples are compared to those of samples from another area of the Angola Basin, so as to reveal significant diversity differences at core-scale. In further investigations, when the obtained Harpacticoida have at least been identified to level of working species, alpha diversity will be studied at replicate- and station-scale.

It is planned for the future to integrate alpha diversities at several abyssal stations for an estimation of the total harpacticoid gamma diversity of the Angola Basin. This may finally lead to a better understanding of the overall deep-sea biodiversity, since Harpacticoida often rank as one of the species-richest groups of organisms in the deep sea.

Material and methods

Material and sample locations

This study concentrates on two abyssal stations in the Angola Basin that were sampled using a multicorer (Barnett et al. 1984) during the DIVA-1 campaign of the RV “Meteor” M48/1 from July 6 to August 2, 2000 (Fig. 1). Station 325 (19°58.2’S, 002°59.8’E; depth: 5448 m) was located 300 nm southwest of station 346 (16°17.0’S, 005°27.0’E; depth: 5389 m). Food availability and sediment structure differed between these stations. Total organic carbon content (TOC) was higher at station 346 (0.62%) than at station 325 (0.41%). Mud and chlorophyll-α content turned out to be higher at station 325 (98.94%, 1.72 μg/g) compared to station 346 (95.23%, 1.67 μg/g; Kröncke and Türkay 2003).

Both stations were sampled repeatedly (see Table 1 for depth and position of the deployments). At station 325, seven MUC hauls were taken and 5 cores out of 10 from each of the seven replicates were chosen randomly for further investigation. At station 346, eight replicates were taken and treated in the same way. Hence, 75 cores were analysed for the present study. Each core with a diameter of 9.6 cm consisted of the upper 5 cm layer of sediment; the volume of each core amounted to 362 cm³, the surface to 72.4 cm².

The upper 5 cm sediment layers were preserved in 5% formaldehyde solution on board. In the laboratory the fixed samples were washed through a 40-μm mesh sieve with tap water. Meiofauna and organic material were extracted from remaining sand particles by centrifugation with a coloidal silica polymer (Levasil) as flotation...
medium and kaolin to cover the heavier particles (McIntyre and Warwick 1984). The centrifugation was repeated three times at 4000 rpm for 6 min, respectively. After each centrifugation the floating matter was decanted and rinsed with tap water. Copepods were subsequently transferred to glycerin. Afterwards, the adult harpacticoid copepods obtained from stations 325 and 346 were analysed quantitatively at species level for each single core.


**Statistical treatment and analysis of data**

The following procedure of diversity analysis was developed for a comparison of two replicatively sampled stations, when it is desired to consider diversity in terms of a combination of diversity indices. For the diversity comparison in this study, a richness, evenness, and dominance diversity index were chosen. The number of species $S$ per core served as a species richness index. The corresponding evenness index was $S$ divided by $S_{max}$; since the latter term simply equals the number of individuals, $N$, the evenness index is the $S/N$ ratio. Finally, as an index with emphasis on the dominance of species the Hill's number $N_\infty$ (Hill 1973) was chosen. These and other statistical decisions and procedures are discussed in the discussion section of this paper.

Firstly, with the diversity values a matrix was built that served as a basis for similarity analysis and nonmetrical multidimensional scaling (NMDS). This matrix contained three alpha diversity values (one for each chosen index) for each core, adding up to a total of 15 diversity values for each replicate with its 5 cores. For each index the 5 cores of a replicate were put in rank order with respect to their alpha diversity values. The 15 diversity values formed the rows of the matrix; the 15 MUC deployments formed the columns.

A similarity analysis for the deployments followed this procedure. The Canberra Metric was chosen as an adequate measure of dissimilarity (Lance and Williams 1966). After matrix formation and dissimilarity calculation, multidimensional scaling was performed for a graphic impression of the similarities of the deployments. A Shepard diagram was drawn to show the representativity of the NMDS plot.

Finally, to compare stations 325 and 346 for significant diversity differences, a minimum spanning tree test was specified (MST-test; Schleier and van Bernem 1996). A null hypothesis was formulated, stating that these stations were not different as to their core-scale harpacticoid species-level alpha diversities. The MST-test was based on the formerly built dissimilarity matrix. A minimum spanning tree (the shortest tree connecting all replicates in a multidimensional space) was constructed out of the data of the matrix. After tree building, all connections between points (edges) of different stations were removed and a certain number of subtrees was left. If significantly fewer subtrees would be left than expected under the null hypothesis, the two investigated stations would be shown to be significantly different ($\alpha = 0.05$).

A two-dimensional NMDS ordination served as an approximated graphic basis for a drawing of this tree. The MST-test was performed using SPANTREE 1.0 (AG Angewandte Statistik in der Ökosystemforschung Niedersächsisches Wattenmeer and C. v. O.-Universität Oldenburg 1997).

**Results**

**Alpha diversity of all Harpacticoida**

NMDS ordination (Fig. 2) separates the investigated stations 325 and 346 perfectly regarding to their single-core alpha diversity values (Table 2). A stress of 0.01 and the nearly linear Shepard diagram (Fig. 3) indicate
that the NMDS plot is a good representation of the original Canberra dissimilarity matrix (Table 3; matrix is scaled for dissimilarity values between 0 and 1). The local-scale diversity differences within each station are smaller than the regional-scale diversity differences between both stations for nearly all pairwise comparisons of multicorer deployments.

A null hypothesis was specified that stations 325 and 346 do not differ with respect to their core-scale harpacticoid species-level alpha diversities. This null hypothesis was tested with the MST-test. The test statistic was the observed number of trees, tested against an expected number of trees under randomized conditions ($\alpha = 0.05$).

An approximated graphic visualization of the minimum spanning tree within the NMDS plot clearly shows that after removal of all connections between deployments of different stations only two trees are left (Fig. 2). Under randomized conditions 8.47 trees would

### Table 2. Diversity matrix for similarity analysis of the multicorer deployments from stations 325 and 346 (Angola Basin); five randomly selected cores of each haul are rank ordered according to their species number ($S$), species/individuals-ratio ($S/N$), and Hill's number $N_H$.

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have been expected in average. Following, the core-scale species-level alpha diversities of the Harpacticoida are different between stations 325 and 346 on a highly significant level ($p = 0.00031$; computed by SPANTREE 1.0). The null hypothesis has to be rejected.

To be more precise, diversity is much higher at station 346, since almost every core from this station contained more species than any core from station 325. This is confirmed by plotting Harpacticoida species numbers in single cores against corresponding numbers of specimens (Fig. 4). Numbers of species and individuals in single cores are nearly always higher at station 346. Only 3 out of 40 cores from station 346 fall into the range of station 325 in this respect. Drawing a line of regression through all points, a nearly perfect linear relationship can be established ($R^2 = 0.990$). The slope of the line of regression is almost 1 ($y = 0.877x$). The same is true when a regression analysis for the points of each station alone is performed (not shown). For the cores of station 325 the slope of the line of regression is only slightly steeper ($y = 0.935x$; $R^2 = 0.969$) than for station 346 ($y = 0.874x$; $R^2 = 0.964$). Power regression fits similarly well in all cases, but the linear model is chosen here for its higher simplicity. The results point to a generally higher species density at station 346.

An average of about 40 harpacticoid species was found in the cores from station 346, whereas an average of only 10 species was recorded for the cores from station 325. A maximum of 61 species was found in a single core from station 346 (Table 3), stressing the extraordinary high small-scale diversity of Harpacticoida in certain deep-sea localities.

### Alpha diversities of the taxonomical subgroups of Harpacticoida

A total of 2199 adult harpacticoid copepods out of 75 selected cores from stations 325 and 346 were examined in this study. Since an additional 4747 copepods were caught (974 at station 325, and 3773 at station 346), this sums up to a total of 6946 Harpacticoida in the selected cores.

A closer look at the species numbers and abundances of the taxonomic subgroups of Harpacticoida recorded from the Angola Basin during the DIVA-1 campaign shows that the total number of species is not available for every Harpacticoida subgroup (Table 4). For many groups, especially the species-rich ones, it has to rely on species counts per core. For that reason, the maximum species number in one core, of all cores of a station,
serves as a rough measure for the species richness proportions between the subgroups. This measure is chosen here because it provides the least number of species for each subgroup.

The Huntemanniidae Por, 1986, and Idyanthidae data demonstrate, however, that the maximum species count is not necessarily a good estimate for species richness, but at least provides further interesting information, if combined with the total species number (Table 4). For these two taxa, working species have already been recognized at station level. For the Huntemanniidae, the total number of species exceeds by far the single core maximum. It may be suggested that this difference between the two counts is caused by a sparse and more homogeneous distribution of individuals and species. On the other hand, the Idyanthidae species and individuals seem to be distributed less homogeneously. Combining the total species numbers of the better known subgroups with the least number of species of the remaining groups, we are able to calculate a minimum total number of harpacticoid species at stations 325 and 346. At least 52 harpacticoid species were recorded from station 325. A few more individuals are found at station 346, with a total number of 75 species. At least 37 species of harpacticoid copepods were recorded at station 346. In total, at least 134 species of harpacticoid copepods were recorded from the Angola Basin during the DIVA-1 campaign. The real numbers of species in the 25 investigated cores might be two or three times higher than the obtained least number of species.

There is some evidence that Pseudotachidiidae, Argestidae Por, 1986, Ameiridae Monard, 1927, and Ectinosomatidae Sars, 1903, are not only richest in individuals but also in species. The maximum species count for one core was 16 for the Pseudotachidiidae, 15 for the Argestidae, 15 for the Ameiridae, and 11 for the Ectinosomatidae. Each of these subgroups was represented by more than 250 adults in the 25 cores. Each of these subgroups has been recorded only once, but in the 25 cores, the maximum species count of species that have been recorded only twice is 16 (Pseudotachidiidae). The real numbers of species of the remaining subgroups might be two or three times higher than the obtained least number of species. The obtained least number of species is not necessarily a good estimate for species richness, but at least provides further interesting information. If combined with the total species number, the obtained least number of species at station level provides the least number of species for each subgroup. For the Huntemanniidae, the total number of species exceeds by far the single core maximum. It may be suggested that this difference is caused by a sparse and more homogeneous distribution of individuals and species. On the other hand, the Idyanthidae species and individuals seem to be distributed less homogeneously.

In order to compare the abundance of the Harpacticoida subgroups at stations 325 and 346, the different number of replicates at the two stations must be taken into account. As 25 cores were analyzed from station 325, and 30 cores from station 346, the abundances of station 346 had to be multiplied by 0.875 (7/8) for comparability (Table 4). It is quite obvious that in nearly all groups of Harpacticoida, far more specimens were obtained from station 346. Only the Rhizothricidae Por, 1986 were exclusively found at station 325 (one specimen only). For the genus Parameiropsis Becker, 1974 (formerly Ameiridae, but obviously not belonging to this taxon), a few more individuals are found at station 325.

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Table 4. Species numbers and abundances of the taxonomic subgroups of Harpacticoida recorded from the Angola Basin during the DIVA-1 campaign

| Station/parameter | Aegisthidae | Ameiridae | Parameiropsidae | Ancorabolidae | Argestidae | Cangrothamnidae | Canuellidae | Cleothororidae | Dactylopusidae | Ectinosomatidae | Huntemanniidae | Idyanthidae | Minicidae | Neobradyidae | Paramesochridae | Pseudotachidiidae | Rhizothricidae | Rometidae | Tisbidae | Zosimitidae | Harpacticoida |
|------------------|------------|-----------|-----------------|--------------|------------|----------------|------------|--------------|--------------|---------------|--------------|-------------|---------|----------|-------------|----------------|----------------|-------------|----------|--------|--------|----------------|
| M325 N           | 4          | 30        | 15              | 5            | 32         | 18             | 0          | 7            | 0            | 47            | 12           | 20          | 5       | 52       | 16           | 68            | 1           | 0         | 37      | 2       | 371          |
| M325 S           | 2          | 3         | 2               | 1            | 3          | 1              | 0          | 1            | 0            | 4             | 2            | 2           | 2       | 3        | 2             | 5             | 1           | 0         | 3       | 1       | 20            |
| M325 S max/core  | —          | —         | —               | 2            | —          | —              | 0          | 1            | 0            | —             | 7            | —           | —       | —        | 4             | —             | 1           | 0         | 0       | —       | —              |
| M325 S total     | —          | —         | —               | 2            | —          | —              | 0          | 1            | 0            | —             | 7            | —           | —       | —        | 4             | —             | 1           | 0         | 0       | —       | —              |
| M346 N           | 21         | 299       | 10              | 14           | 388        | 57             | 5          | 30           | 1             | 211           | 33           | 59          | 46      | 140      | 66           | 366           | 0           | 2         | 7       | 69      | 4              |
| M346 N*0.875     | 18         | 262       | 9               | 12           | 340        | 50             | 4          | 26           | 1             | 185           | 24           | 52          | 40      | 123      | 58           | 320           | 0           | 2         | 6       | 60      | 4              |
| M346 S max/core  | 3          | 15        | 2               | 1            | 15         | 4              | 1          | 1            | 1             | 11           | 2            | 5           | 4       | 7        | 4             | 16            | 0           | 1         | 2       | 6       | 2              |
| M346 S total     | —          | —         | —               | 2            | —          | —              | 1          | 1            | 1             | 13           | 11-14        | —           | —       | —        | —             | —             | 8           | 0         | 0       | —       | —              |
| Total N          | 25         | 329       | 25              | 19           | 420        | 75             | 5          | 37           | 1             | 258           | 45           | 79          | 51      | 192      | 82           | 434           | 1           | 2         | 7       | 106      | 6              |
| Total S max/core | 3          | 15        | 2               | 1            | 15         | 4              | 1          | 1            | 1             | 11           | 2            | 5           | 4       | 7        | 4             | 16            | 1           | 1         | 2       | 6       | 2              |
| Total S total    | —          | —         | —               | 3            | —          | —              | 1          | 1            | 1             | 17           | 13-20        | —           | 9       | —        | —             | —             | 1           | —         | —       | —       | —              |

M = multicorer station; N = individuals; S = species; S max/core = single core maximum species count; i.s. = incertae sedis; in order to obtain comparable abundance values for stations 325 and 346, abundances for station 346 were corrected for the different number of replicates and multiplied by 0.875 (7/8).
Idyanthidae, Canthocamptidae, Miraciidae, Huntemanniiidae, Cletodidae T. Scott, 1905, Aegisthidae, the genus Parameiropsis, and the Ancorabolidae Sars, 1909, were recorded in medium abundance, Tisbidae, Canuellidae Lang, 1944, Rometidae, Rhizothricidae, and Dactylopusiidae in low abundance.

Comparing the single core maximum species counts for both stations, a similar trend as for the abundance becomes apparent. There is no group except Rhizothricidae for which this count is higher at station 325, but it is often lower there. The same is true for total species numbers where available.

A final important result of the subgroups analysis is that the above shown significant difference in the overall harpacticoid single core diversity between the two stations (see Fig. 2) is obviously not only based on a few species-rich Harpacticoida subgroups. As shown in Table 4, the trend of a higher diversity at station 346 is consistent throughout most subgroups, including many less species-rich taxa as well.

Discussion

Statistical procedure

The available data set is restricted in its scope. As only very few species are known to science and the rest was assigned to working species only for some groups, this evaluation had to concentrate on alpha diversities of Harpacticoida in single cores. No diversity calculation for higher sample units was possible here, since for many subgroups it was not analysed whether species from different cores were identical. Consequently, a special kind of input matrix for the diversity similarity analysis of the multicorer deployments had to be developed that could be calculated from our special kind of species-stations-matrix.

The obtained data also bear some restrictions with respect to statistical analysis. First of all, random sampling may be doubtful with a multicorer. MUC ‘replicates’ may not scatter randomly over the ground, but should be more concentrated in a central area with decreasing probability of deployment to the margins. This has to be kept in mind when doing statistical analyses with the deployments.

Within each deployed MUC, the statistical situation is as follows: According to Hurlbert (1984), the cores of a multicorer are pseudoreplicates. They cannot be treated as real replicates but as parallel samples. As those, it would be desirable to join cores successively as to obtain increasing diversity-per-core-number curves in future. However, this was not possible at the moment due to the fact that only a few working species have been assigned.

The chosen procedure for a comparison of diversities needs further explanation. After a decision was made which aspects of diversity to be emphasized, we made a choice as to which diversity indices served best for our purposes. There is a huge variety of measures with different properties. Classical indices can be divided roughly into richness, evenness, and dominance indices. For most biological data, dominance and evenness measures are not significantly correlated to richness measures (Magurran 1988). A special case are phylogenetically and taxonomically based diversity indices (e.g. taxonomic distinctness measures; Warwick and Clarke 1995, Clarke and Warwick 1998, 2001a). These will be invaluable for measuring deep-sea diversity in the future, when there is a larger data base of recorded and described species to compare with; however, measures like the ‘average taxonomic distinctness’, $\Delta^-$ are not applicable at the momentary stage of Harpacticoida deep-sea biogeography when no faunal lists from recruitment areas exist.

Richness, evenness and dominance indices were chosen in order to combine these aspects of diversity. The number of species $S$ per core served as a species richness index. This simple measure was adequate for our data, since our calculations and comparisons relied on cores of the same diameter and volume. By this, $S$ measured species densities. Not least, the species number had the advantage to be biologically easily interpretable. The species-individuals ratio $S/N$ ($N$ is equal to $S_{\text{max}}$), the corresponding evenness measure to $S$, was taken as an appropriate measure of evenness here. The $S/N$ ratio gave the best resolution for our data compared to other tested evenness indices (Pielou Evenness, Brillouin Evenness). This was due to the structure of our data matrix which (like many data sets obtained from the deep sea) contained low numbers of individuals per species. Finally, the Hill's number $N_\infty$ (Hill 1973), also known as the reciprocal of the Berger–Parker Index (Berger and Parker 1970), served as an index with emphasis on the dominance of species. This index is independent of $S$; it totally relies on the relative abundance of the most dominant species.

Classical diversity indices are sample-size dependent as shown by Soetaert and Heip (1990). Going in the same direction, Warwick (1998) and Warwick and Clarke (2001) pointed out that species richness measures are unsuitable for assessing comparative biodiversity on broad regional scales and hence recommended taxonomic distinctness measures for those purposes. We agree that taxonomic distinctness measures should be of greater importance in future studies. However, we think that our comparison based on classical indices is nevertheless valid because we compare regional diversity on the basis of small-scale diversity, the latter being assessed by samplings of the same size and hence being comparable. However, the volume of each core was by
far too small to get even approximately representative species lists for the stations.

With the 5 randomly chosen cores (3 diversity values each), $5 \times 3$ diversity values per replicate were obtained. It is not appropriate to perform standard statistical analyses like ANOVA, nested ANOVA, or t-test with these values, for the following reasons: (1) The cores of a multicorer are pseudoreplicates (Hurlbert 1984) and not taken randomly out of a MUC-sized locality. This problem even increases when distance decay, spatial dependence, or autocorrelation are to be expected which prevent random sampling nearly anywhere in nature. These do not act on species compositions only, but also on diversity measures derived from such data. (2) Species numbers and abundances as well as diversity indices derived from those counts are discrete data and must be statistically treated in a different way (Sokal and Rohlf 1995). (3) The underlying distribution models are unknown. Many species tend to be patchily distributed at certain unknown scales. For that reason, standard statistical models are not adequate for most studies on species diversity and distribution.

With our chosen statistical procedure some of these shortcomings were avoided, but not all. For example, it was assumed that diversity distance decay would be negligible for the 5 cores of a MUC deployment. This may not have been the case.

With the ranked diversity values, a new kind of input matrix was created that served as a basis for similarity analysis and NMDS. Identical diversity ranks of cores were assumed to be comparable units between replicates. By combining certain diversity indices, the matrix enables a combination of different aspects of diversity.

A similarity analysis for the samples followed this procedure. However, there was one problem: the values of the three indices were of different order. This problem was solved by choosing a dissimilarity index which automatically standardized the values: the Canberra Metric. This dissimilarity measure gave all single row comparisons equal weight and was adequate for our purposes.

After matrix formation and dissimilarity calculation, an NMDS was performed to get a graphic impression of the similarities of the samples. This explorative statistical technique was applied, e.g., to benthic communities by Warwick and Clarke (1991). A stress factor is given in the NMDS plot that indicates how well the original dissimilarities are represented in the plot. Values below 0.1 indicate a good representation (Clarke and Warwick 2001b). A Shepard diagram should always be drawn when NMDS ordination is done. It serves as a graphic impression of the representativity of the NMDS plot and shows outliers. If the values form a straight line, a good representativity of the NMDS plot can be assumed.

No ellipses are drawn to highlight apparently grouped replicates in our NMDS plot (Fig. 2), even though two such groups seem to be clearly defined. One may now wish to draw ellipses around those two apparent groups, but this would not be a correct interpretation of the NMDS plot. In particular, when taking a closer look at the distances between all deployments (Table 3) it may be recognized that two replicates of one station are not always more similar than two deployments of different stations. As rule of thumb for delimiting groups in the NMDS plot, points within a group should be less distant to each other than to the nearest neighbour of another group.

Finally, to compare stations 325 and 346, a test had to be chosen to decide whether or not alpha diversity differences between the replicates of these two stations were significant. It was decided to use a minimum spanning tree test (MST-test), a special kind of randomization test (Friedman and Ralşky 1979). The MST-test has three advantages (Schleier and van Bernem 1996): First of all, one is free in the selection of any adequate similarity measure. Secondly, the test does not rely on a certain distribution model. Then, it works with discrete as well as continuous data. Finally, it does not require random sampling. On account of these properties, Schleier and van Bernem (1996) recommend the MST-test for statistical comparisons of replicated benthos samples. It has to be admitted that the test serves best, if at least 10 replicates are sampled from a station (AG Angewandte Statistik in der Ökosystemforschung Niedersächsisches Wattenmeer and C. v. O.-Universität Statistik Oldenburg 1997). Relying on only seven, respectively eight replicates this study did not meet the optimal requirements of the test. Other randomization tests like ANOSIM (Clarke and Green 1988) would also have been possible, but have the disadvantage that they cannot be visualized in an NMDS plot.

In this study a two-dimensional NMDS plot served as an approximate basis for a graphic impression of the minimum spanning tree. Nevertheless, it should be kept in mind that there are always slight inconsistencies between the NMDS plot which does not show exact dissimilarities between points, and the minimum spanning tree which is defined by mathematically exact dissimilarities. An expression of this is the cross-like tree structure in the upper part of Fig. 2.

Finally, it is questionable whether testing for significant diversity differences makes sense anyway, and what kind of conclusions can be drawn from such a statement. At least the possibility of testing for significant diversity differences would be useful in the context of conservational purposes when politicians need clear statements from scientists for their decisions.
Results of diversity analysis

In our study of the Angola Basin, Pseudotachidiidae, Argestidae, Ameiridae, Ectinosomatidae, and Neobradyidae were the most abundant subgroups of Harpacticoida. These results are in apparent contrast to those of investigations in the Northeast Atlantic, where harpacticoid deep-sea assemblages were dominated by Cletoidea. Diversity differences in the Angola Basin. Local-scale (tens to hundreds of meters) within-station differences in harpacticoid core-scale diversity were lower than regional-scale (hundreds of kilometres) between-stations differences. Variability within the multicorer deployments was not analysed due to statistical reasons (see statistical discussion).

Biodiversity in marine habitats at a variety of different scales ([a] hierarchical levels: genetic, organismal, community level with additional scaling according to body size; [b] spatial scales from single samples to regional and global; [c] temporal scales of change) is also discussed by Warwick (1998). Scale-dependent diversity differences may be based on mechanisms that regulate diversity at different scales (Rex et al. 1993). However, these mechanisms are still obscure. Of special interest in our context is a study of Thistle (1978) who investigated scale-dependency of harpacticoid dispersion patterns in the San Diego Trough (~1220 m depth) in detail and found aggregations of harpacticoid species mainly on meter and centimeter scale; on 100-m scale the number of aggregated species was only slightly greater than by chance. This demonstrates the patchiness of harpacticoid species at smaller scales, increasing the problem of nonrandom sampling with the cores of a multicorer (see statistical discussion).

How can the significant difference in the single core alpha diversities of harpacticoid copepods between stations 325 and 346 be explained when depth-related differences can be excluded (both stations were located in abyssal areas of about the same depth of approximately 5400 m)?

One possible starting point would be the different latitude of the two stations. Latitudinal diversity gradients of various forms have been proposed in literature (e.g., Rex et al. 1993, 2000, 2001; Roy et al. 1998; Culver and Buzas 2000; Crame 2000; Jablonski and Valentine 2000; Lambshead et al. 2000, 2001; Lyons and Willig 2002; Macpherson 2002; Mokievsky and Azovsky 2002; Stuart et al. 2003). Recently, Hillebrand (2004) reviewed 232 studies with a total of 583 latitudinal gradients. He concluded that gradients on regional scales were significantly stronger and steeper than on local scales, and the slopes also varied with sampling grain. Furthermore, Hillebrand stated that the latitudinal gradient of diversity is a highly general spatial pattern at regional scale, with only few exceptions. Nevertheless, gradients were less strong in freshwater than in terrestrial or marine environments.

In summary, the relationship between latitude and diversity is diverse itself and still poorly understood. It is important to keep in mind that latitude on its own has no influence on diversity. Several factors change with latitude (Gage 1996), and it is often difficult to say which one is relevant for a certain taxon or community.

Hillebrand (2004) favours differences in energy acquisition, area, or very basic factors like temperature.
Dynesius and Jansson (2000) and Jansson and Dynesius (2002) observed long-term climatic oscillations such as Milankovitch-cycles to reduce persistent cladogenesis at higher latitudes. Nevertheless, an apparent change of diversity of a certain taxon with latitude usually results from a mix of various more or less complex environmental gradients.

Hillebrand’s (2004) results infer that it would be quite difficult to explain the observed contrasting diversity patterns of station 325 and 346 by latitude alone, since the positions differ by only 4° latitude, which should cause only minor diversity differences.

One factor which often correlates with diversity is productivity in its various measurable components. A unimodal (hump-shaped) productivity-diversity relationship is assumed to be a general pattern of diversity (at least at regional scale) by some authors (Begon et al., 1990; Rosenzweig and Abramsky 1993; Huston and DeAngelis 1994; Rosenzweig 1995). However, Waide et al. (1999) showed that this assumption is not based on results in literature. The authors reviewed approximately 200 published relationships, of which 30% were unimodal, 26% were positively linear, 12% were negatively linear, and 32% were not significant at all. This overall picture consisted of different subpatterns for various taxonomic groups, biomes, and scales. Unimodal relationships were far more common in aquatic than in terrestrial environments. For the latter, positive linear or not significant relationships were predominant. Furthermore, unimodal relationships are more often found in investigations between communities than within communities. However, it has to be kept in mind that the nondominance of unimodal relationships in literature might partly be an artefact of insufficient sampling range.

Deep-sea habitats generally show lower productivity compared to other marine or terrestrial habitats (Grassle 1989; Valiela 1995). Productivity is therefore a limiting factor in deep-sea environments under normal circumstances (e.g., low productivity is thought to be responsible for reduced body size of some macrofaunal organisms (Hessler and Jumars 1974); however, this could not be observed for meiofauna (Shirayama and Horikoshi 1989; observations of co-authors of this publication). Despite former suggestions that deep-sea diversity may have been supported by low productivity in evolutionary time (Valentine 1973; Van Valen 1976), diversity of Harpacticoida within the quite homogeneous low-productive abyssal basins may as well be positively correlated with productivity on a regional scale. A peak or descending part of a possible unimodal productivity–diversity relationship may not be reached within the range of abyssal productivity values (according to the general assumption of Rosenzweig (1995, p. 351): “As productivity rises from very low to moderate levels, diversity also rises”). Regarding macrofauna, however, Glover et al. (2002) found neither a clear unimodal nor linear relationship between productivity (POC flux) and abyssal polychaete diversity.

In addition, a seasonally higher input of detritus through algal blooms (as known for the Benguela upwelling system, Richardson et al. 2003) could cause higher patchiness in some abyssal regions that leads to higher diversity, following the spatial-temporal mosaic-cycle theory (Grassle 1989; Remmert 1991). Seasonally varying deposition of phytodetritus to the deep-sea floor was indeed observed (Rice et al. 1986) with some evidence for reduced phytodetrital fallout at lower latitudes (Rice et al. 1994). Small-scale heterogeneity and thus diversity may also be supported by current-driven resuspension of this seasonally deposited organic material (Rice and Lambshead 1994).

For this study it is important that Krönecke and Türkay (2003) indeed found a gradient in total organic carbon content (TOC) in the investigated area. Station 325 is located within an area of low productivity, with low TOC contents on the sea bed (Krönecke and Türkay 2003) and low long-term phytoplankton contents in the surface water (SeaWIFS project—homepage, NASA 2003). This may have caused lower diversity at this station (which was not only observed for the Harpacticoida but also for most groups of organisms: see other contributions to this volume). At station 346, TOC and long-term chlorophyll-α content in the surface water are considerably higher, which may have caused a higher diversity.

Upwelling and subsequent nutrient transport by the Benguela Coastal Current are assumed to be one reason for a higher TOC content and harpacticoid diversity at station 346. Another possible nutrient source for the area around station 346 is the Kongo River plume interacting with the South Equatorial Counter Current. From an upwelling region off Northwest Africa, it was shown that standing stock of deep-sea macrobenthos communities was related to primary productivity in surface waters (Thiel 1982); meiofaunal densities were high in this region compared to other regions of similar depth, leading Thiel to the assumption that upwelling and high productivity influence this faunal component off Northwest Africa. Already Späck (1951) in his pioneer deep-sea benthos investigation stressed the importance of higher productivity near the Benguela Coastal Current and the Southwest African upwelling region for increased deep-sea macrobenthos density and richness. These studies support our assumption of a relationship between harpacticoid diversity and productivity in the Angola Basin.

In summary, large-scale heterogeneity in food availability is assumed to be an important factor in structuring harpacticoid communities in the abyss of the Angola Basin and possibly also in other deep-sea regions. Studies of Schaff et al. (1992) on macrofauna...
support the thesis that large-scale (100 km) persistent heterogeneity in organic input (organic C flux) influences benthos community structure.

Factors other than productivity may have been important for creating diversity patterns in the Angola Basin (e.g. sediment structure). Deep-sea diversity is influenced by several factors acting on various temporal and spatial scales (Gage 1996). Distribution patterns of macrofaunal organisms may be important for meiofaunal diversity (Thistle 1979, 1983b; Thistle and Eckman 1990; Thistle et al. 1993). Small-scale, biogenic processes were thought to be important in creating a mosaic of microhabitats that allow co-existence of the large numbers of rare species that is often found in deep-sea sediments (Lamont et al. 1995; Gage 1996). However, differences in hydrodynamics may be less important for copepod diversity in some regions (Thistle 1983a).

Discussing productivity, our interpretation reflects just one aspect of diversity. Since only a few square meters of the deep-sea beds worldwide were investigated for meiofauna so far (see Lambshead (1993); only little has changed since then), much more information is needed for a better understanding of overall marine diversity. This study is just another stepping stone.

Acknowledgements

We kindly thank Iris Zaehle for centrifugation of the samples as well as Iris Ohlendorf and Brigitte Hilbig for correcting the English manuscript. Furthermore, we are indebted to many students at the Carl von Ossietzky-Universität, Oldenburg for sorting the meiobienthic material. The participation of KHG and EW at the DIVA-1 expedition in 2000 was funded by the Forschungsinstitut und Naturmuseum Senckenberg and the Deutsche Forschungsgemeinschaft (DFG). Further support by the Deutsche Forschungsgemeinschaft (SCHM 352/30) is gratefully acknowledged by SS.

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