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# Large-scale diversity and biogeography of benthic copepods in European waters

Gritta Veit-Köhler · Marleen De Troch · Mateja Grego · Tania Nara Bezerra ·
Wendy Bonne · Guy De Smet · Christina Folkers · Kai Horst George · Chen Guotong ·
Rudy Herman · Rony Huys · Nikolaos Lampadariou · Jürgen Laudien · Pedro Martínez Arbizu ·
Armin Rose · Michaela Schratzberger · Sybille Seifried · Paul Somerfield · Jan Vanaverbeke ·
Edward Vanden Berghe · Magda Vincx · Borut Vriser · Leen Vandepitte

**Abstract** A large-scale database concerning benthic copepods from the Arctic, Baltic Sea, North Sea, British Isles, Adriatic Sea and Crete was compiled to assess species richness, biodiversity, communities, ecological range size and biogeographical patterns. The Adriatic showed the highest evenness and the most species-rich communities. Assemblages from the North Sea, British Isles, Baltic and Crete had a lower evenness. The British Isles were characterised by impoverished communities. The ecological specificity of copepod species showed two diverging trends: higher specificity of species in more diverse assemblages was observed in the Adriatic, North Sea and Baltic. A uniformly high species specificity disregarding sample diversity was found on Crete and in the British Isles. Benthic copepod communities showed distinct

G. Veit-Köhler (✉) · C. Folkers · K. H. George ·
P. Martínez Arbizu · A. Rose
DZMB, Senckenberg Research Institute, Südstrand 44,
26382 Wilhelmshaven, Germany
e-mail: gveit-koehler@senckenberg.de

M. De Troch · T. N. Bezerra · W. Bonne · G. De Smet ·
C. Guotong · J. Vanaverbeke · M. Vincx
Marine Biology, Biology Department, Ghent University,
Krijgslaan 281–S8, 9000 Ghent, Belgium
e-mail: marleen.detroch@UGent.be

M. Grego · B. Vriser
Marine Biology Station Piran, National Institute of Biology,
Fornace 41, 6330 Piran, Slovenia
e-mail: Mateja.Grego@mbss.org

R. Herman
Vlaamse Overheid, Departement Economie,
Wetenschap en Innovatie, Ellips building,
Koning Albert II-laan 35, 1030 Brussels, Belgium

R. Huys
Natural History Museum, Cromwell Road,
SW7 5BD London, UK

N. Lampadariou
Hellenic Centre for Marine Research, Institute of Oceanography,
P.O. Box 2214, 71003 Iraklion, Crete, Greece

J. Laudien
Alfred-Wegener-Institute for Polar and Marine Research,
P.O. Box 120161, 27515 Bremerhaven, Germany

M. Schratzberger
Centre for Environment, Fisheries and Aquaculture Science,
Pakefield Road, Lowestoft NR 33 0HT, UK

S. Seifried
Faculty 5, Institute of Biology and Environmental Sciences,
AG Zoosystematics, University of Oldenburg,
26111 Oldenburg, Germany

P. Somerfield
Plymouth Marine Laboratory, Prospect Place,
West Hoe, Plymouth PL1 3DH, UK

E. Vanden Berghe · L. Vandepitte
Flanders Marine Institute, Wandelaarkaai 7,
8400 Oostende, Belgium

*Present Address:*
E. Vanden Berghe
Institute of Marine and Coastal Sciences, Rutgers University,
71 Dudley Road, New Brunswick, NJ 08901, USA

patterns that clearly fit the predefined geographical regions. Communities were distinguishable and $\beta$-diversity was found to be high around Europe, indicating a high species turnover on the scale of this investigation. The British Isles and the North Sea were found to be faunistic links to the Baltic and the Arctic.

## Introduction

Meiofauna diversity and community studies have been carried out in many regions and different habitats across European waters. Most of them were single spot studies or at least geographically limited (see references in: Chertoprud et al. 2007; Vandepitte et al. 2009). Comprehensive and complete datasets, including raw data necessary for extensive interregional comparisons, were difficult to obtain. Apart from species lists, published material often contains only transformed information on individual densities (mean values, etc.). In most of the cases no complete information based on single samples or species-station matrices has been published. In addition, a huge amount of data is "hidden" in doctoral theses, some of them only published in "grey" literature that is not easy to access. However, a first large-scale comparison of European harpacticoid copepod assemblages was presented by Chertoprud et al. (2007).

In the course of the MANUELA project "Meiobenthic and Nematode Biodiversity: Unravelling Ecological and Latitudinal Aspects" in the framework of the MarBEF Network of Excellence "Marine Biodiversity and Ecosystem Functioning" an extensive database on meiofauna studies in European waters was compiled (Vandepitte et al. 2009). The aim was to carry out joint analysis of this information source on patterns of meiobenthic diversity and community composition.

Chertoprud et al. (2007) carried out a large-scale study on the community structure of Harpacticoida (Copepoda, Crustacea) from intertidal and shallow-water zones of European seas. Our study, however, is based on completely different data from the MANUELA database. Thus, it can be used as an independent approach to test their hypothesis. Furthermore, we carried out a broad array of analyses to investigate diversity, community composition, ecological specificity and biogeography of benthic copepods in European waters (Fig. 1) and related them to geographical and ecological factors as well as to historical geological facts.

## Materials and methods

Altogether 15 field study datasets, including 234 stations, 1,042 samples and 9,929 distribution records from European marine waters, were extracted from the integrated MS Access MANUELA database (Vandepitte et al. 2009). The records contain abundance data for benthic copepod species. Additional information on sampling gear, sample surface, latitude and longitude, water depth and environmental factors is available.

A priori assumptions and database clearance

In this study, data were analysed at the species level. As there are still inadequately (Seifried and Veit-Köhler 2010) and undescribed benthic copepod species in European waters, data providers have assigned working species names to the individuals in question. We treated the working species of different studies as different species.

Stations from impacted and/or disturbed sites belonging to the experimental part of colonisation studies were excluded from the analysis. According to Schratzberger et al. (2009), a high level of disturbance has to be assumed for 13 stations of the study $Hc$ (detailed introduction to studies below) and two stations of the study $pl$, which have therefore been removed. Colonisation studies were carried out at two sites: we excluded 68 stations from the study $mt$ and six samples from the study $ds$. As benthic copepods react to heavy metal contamination (Somerfield et al. 1994b), the $pa$ study stations Restronguet and Mylor were excluded. Another five stations were removed from the $pc$ study due to their location in or close to a sewage disposal site (Moore and Somerfield 1997).

In the study $u14$, the surface water from the used box corer was treated as a separate sample by the data provider. Since there were mainly pelagic species in these six samples, they were omitted from further analysis.

Finally, all samples that reported only one individual were cleared from the extracted data table: four samples from the study $c1$, four samples from $u17$ and 21 samples from $u18$.

The 15 cleared field studies contained 144 stations, 735 samples and 7,631 distribution records (Fig. 1). Maps were created with the free software 4.5.1 GMT "Generic Mapping Tools" (http://gmt.soest.hawaii.edu).

Studies were grouped for geographical regions as follows:

*Region: Arctic*

*ds—Arctic Meiofauna Succession* (*Veit-Köhler* et al. 2008; *data provider: SS*)
Marine, diver-operated push corer, 20 m depth
This experimental study in glacial Kongsfjorden (Spitsbergen) investigated the long-term colonisation capacities of Arctic soft-bottom meiofauna from 2003 to 2005. Harpacticoid copepods were reported in detail together with abiotic data (sediment characteristics).
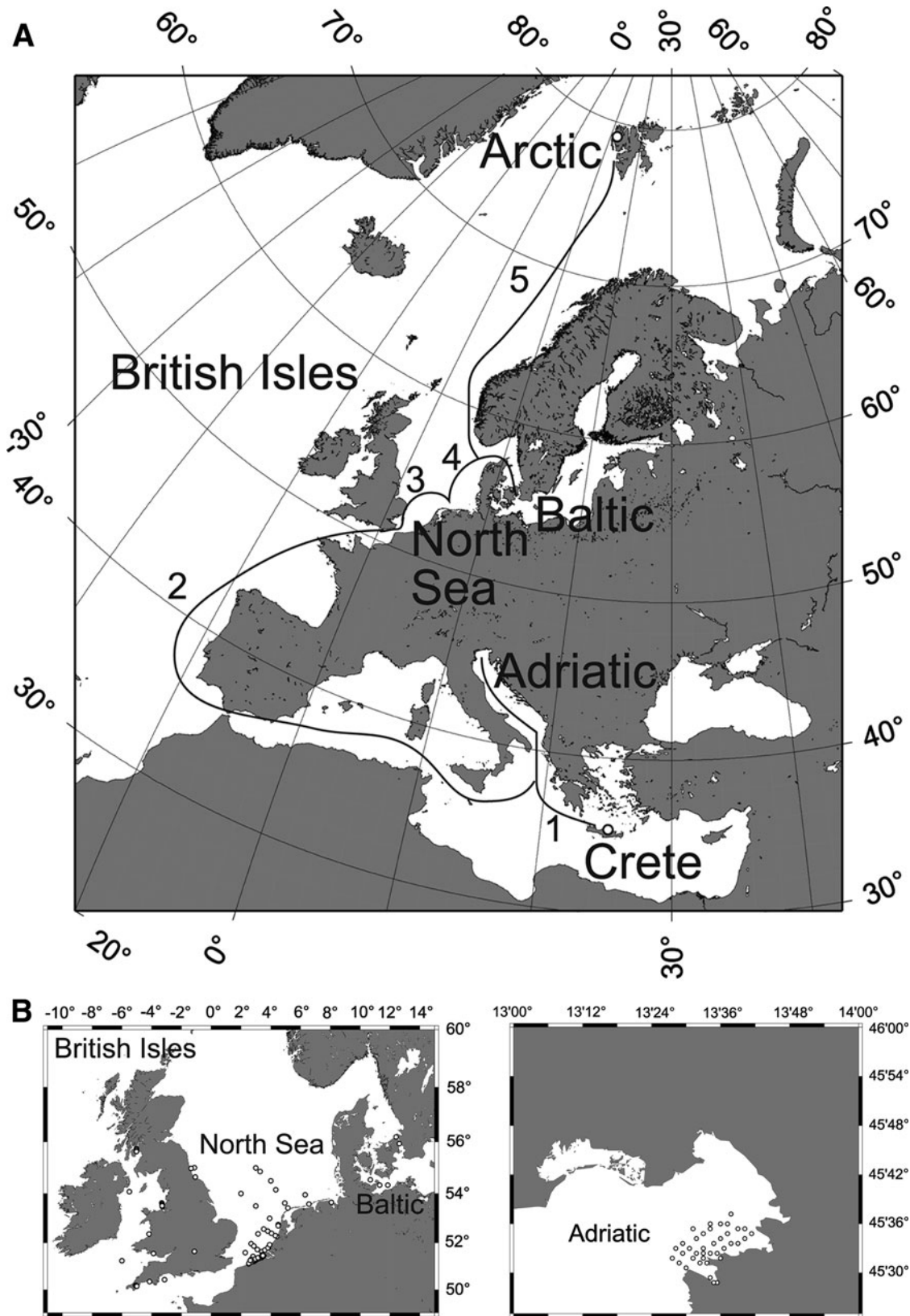
**Fig. 1  a** Map of Europe with indication of sampling locations for Crete and the Arctic and distances between the six predefined regions; distances: 1, approx. 1,700 km; 2, approx. 5,700 km; 3, approx. 600 km; 4, approx. 800 km; 5, approx. 3,000 km. **b** Detailed maps of the sampling locations of the regions British Isles, North Sea, Baltic Sea and Adriatic

Data used: 1 station (Brandal), 2 samples (of 8), 31 records (of 140)

*Region: Baltic*

*dw—Western Baltic Sea Copepods* (*Folkers and George* 2010)
Marine, mini-corer, 20.5–24.2 m depth
Harpacticoid copepod communities were studied in terms of species composition and diversity on a north to south gradient in the western Baltic area.
Data used: 5 stations, 5 samples, 59 records

*Region: North Sea*

*dh—Harpacticoida species and meiofauna major taxa from Hooksiel* (*Rose and Seifried* 2006)
Marine, push corer, 0 m depth (intertidal)
A quantitative small-scale snapshot investigation on harpacticoid species of an intertidal sand flat in Jade Bay (North Sea) was conducted on 31 March 2004, including an assessment of spatial scale dependence of the harpacticoid diversity and information on the sediment.
Data used: 1 station (Hooksiel), 60 samples, 472 records

*u13—Copepoda from the Middelkerkebank, North Sea* (*Bonne* 2003)
Marine, Reineck box corer, 8–22 m depth
This dataset focuses on the copepod density, diversity and community structure in relation to sediment characteristics and depth of a sandbank (Middelkerkebank) in the North Sea.
Data used: 7 stations, 20 samples, 245 records

*u14—Bentho-pelagic coupling in the North Sea: Copepoda* (*Bonne* 2003)
Marine, Reineck box corer, 13–24 m depth
Abundance data of benthic copepod species were investigated for two stations on two sandbanks (Kwintebank, Gootebank) on the Belgian Continental Shelf. This dataset concentrates on the temporal fluctuations of the vertical distribution of harpacticoid copepods in the sediment and differences between epibenthic and endobenthic interstitial copepod species.
Data used: 2 stations, 24 samples (of 30), 337 records (of 345)

*u17—Copepoda of the Dutch Continental Shelf, spring 1993* (*data providers: RH and GDS*)
Marine, Reineck box corer, depth unknown
Densities and species composition of copepod communities on the Dutch Continental Shelf were determined. Data represent the third springtime sampling campaign of meiofauna on the Dutch Continental Shelf.
Data used: 23 stations (located at Egmond, Noordwijk, Rottum, Terschelling, Voordelta, Walcheren), 41 samples (of 45), 602 records (of 606)

*u18—Copepods from the Southern Bight of the North Sea* (*Herman* 1989)
Marine, Reineck box corer, Van Veen grab, 7–13.1 m depth
Meiobenthic communities (special emphasis on copepod species composition) of the Southern Bight of the North Sea and their relationship with environmental parameters were described.
Data used: 19 stations, 159 samples (of 180), 972 records (of 993)

*u19—Copepods from a sublittoral sandy station in the North Sea* (*data provider: RH*)
Marine, Reineck box corer, 7 m depth
For one year, meiofauna samples were collected at a sublittoral sandy station of the North Sea with special focus on the temporal and spatial distribution of the meiofauna and harpacticoid copepod species.
Data used: 1 station, 52 samples, 438 records

*uc—The meiobenthos of the Southern Bight of the North Sea* (*Guotong* 1987)
Marine, 8–41 m depth
This dataset contains information on the meiobenthic communities and sediment characteristics of six different stations in the Southern Bight of the North Sea.
Data used: 6 stations, 12 samples, 177 records

*Region: British Isles*

*c1—Structure of sublittoral nematode assemblages around the UK coast* (*Schratzberger* et al. 2000)
Marine, multicorer, 8–95 m depth
Meiobenthos was sampled at several stations around the UK coast in May–June 1997 and May–June 1998. The response of species assemblages to both anthropogenic impacts and natural environmental factors was tested. Other available data include environmental variables and sediment granulometry.
Data used: 12 stations (Burbo Bight, Cardigan Bay, Celtic Deep, Dundrum Bay, Lyme Bay, off Humber, off Plymouth, off Thames, off Tyne, Swansea Bay, Tees inshore, Tyne inshore), 42 samples (of 46), 604 records (of 608)

*pa—Nematoda and Copepoda from the Fal estuary* (*Somerfield* et al. 1994a, b; *Somerfield and Clarke* 1995)
Brackish water, push corer, 0 m depth (intertidal)
The effects of long-term contamination by heavy metals and the short-term effects of a spill of mine waters on the meiofaunal communities of an intertidal mudflat were tested in the Fal estuary system. The database contains information on nematode and copepod abundance and environmental data from five creeks.
Data used: 3 stations (of 5; Percuil, Pill Creek, St. Just), 30 samples (of 45), 283 records (of 428)

*pc—Meiofauna from the Firth of Clyde, Scotland* (*Moore and Somerfield* 1997)

Marine, Craib corer, 136 m depth

The meiofauna of the Firth of Clyde was sampled to examine changes in community structure along a classical gradient of organic enrichment and to compare the responses of the different meiofaunal groups. The database contains information on the meiofauna along a transect through Garroch Head disposal site, and the response of the meiofaunal community to sewage sludge disposal in the Firth of Clyde.

Data used: 8 stations (of 13), 8 samples (of 13), 116 records (of 135)

*pl—Liverpool Bay Nematoda and Copepoda, UK* (*Somerfield* et al. 1995; *Somerfield and Clarke* 1995)

Marine, Craib corer, Day grab, 10 m depth

Changes in meiofauna community structures were investigated along an estuarine pollution gradient through a dredging disposal site. The observed changes were related to the measured environmental variables.

Data used: 5 stations (of 7), 40 samples (of 54), 208 records (of 252)

*Region: Adriatic*

*mt—Meiofauna of the Gulf of Trieste-Slovenia* (*Marcotte and Coull* 1974; *Vriser* 1983, 1996a, b, 2000a, b; *data provider: MG*)

Marine, gravity corer, diver-operated corer, 1–31 m depth

This database contains information on 23 years (1972–1995) of meiofaunal research in the Slovenian part of the Gulf of Trieste (North Adriatic), including samples from coastal transects (1–15 m deep), offshore waters, a long-term study at a single location in the central part of the Gulf of Trieste, a recolonisation study and numerous other studies. The database contains abundance data on major meiofauna taxa and harpacticoid copepod species.

Data used: 47 stations (of 115), 232 samples (of 430), 2,948 records (of 4,736)

*Region: Crete*

*hc—Heraklion Harbour Meiobenthos* (*Lampadariou* et al. 1997)

Marine, Craib corer, 5–22 m depth

Meiofaunal community responses to anthropogenic disturbance were tested in Heraklion harbour (Crete, Greece, Eastern Mediterranean). The dataset contains data on the community structure of nematodes and copepods at seventeen stations in relation to environmental variables.

Data used: 4 stations (of 17), 8 samples (of 33), 139 records (of 295)

**Data analysis**

Diversity analysis and prediction of diversity

The number of expected species (ES10–ES200) was calculated per sample and plotted as mean value per region versus number of individuals (rarefaction curves). As the coherent rarefaction method can be sensitive to sampling intensity (Lambshead et al. 1983), we provide additional K-dominance curves (cumulative relative abundance versus number of species) for reliable interpretation of diversity. Analyses were performed using the PRIMER6 software (Plymouth Marine Laboratory; Clarke and Gorley 2006) and Microsoft Office Excel 2007.

Multiple linear models were constructed to detect relationships between variables, such as number of individuals, sampled surface area and water depth, on the one hand, and number of species as a diversity measure, on the other hand (Draper and Smith 1981). The full interaction models contain different combinations (terms) of the variables because it is probable that variables influence each other in a distinct way. The number of species may be dependent on the number of individuals, which itself can be connected to the sampled area or to water depth.

Models were run using the SAS statistical software package JMP 5.0.1. Note that in this study an "adjusted" variation coefficient $r^2$ is calculated using the mean squares instead of the sum of squares in order to make models with different numbers of parameters more comparable.

$$Y = a_0 + a_1 \times X_1 + a_2 \times X_2 + a_3 \times X_3 + a_5 \times X_1 \times X_2 + a_6 \times X_1 \times X_3 + a_7 \times X_2 \times X_3 + a_8 \times X_1 \times X_2 \times X_3$$

where $Y$ is 'No. of species', $X_1$ to $X_3$ refer to the variables 'No. of individuals', 'Water depth [m]', and 'Sampling area [cm$^2$]', $a_0$ is the intercept, and $a_1$ to $a_8$ are the resulting parameter estimates of the model. For reasons of clarity original data were not transformed.

Ecological range size

The ecological range size of a copepod species was defined as the number of samples in which a species was found (De Troch et al. 2001). It can be regarded as the (local) area occupied by that species.

The average ecological range size was then calculated as follows:

Average ecological range size per species

$$= \frac{\sum \text{Species range sizes per sample}}{\sum \text{Species per sample}}$$

with

Species range size = number of samples in

which a species is found

Here, average ecological range size was used to evaluate ecological specificity of benthic copepod species and genera in relation to sample diversity and geographical region. Specificity explains whether a species is a generalist (large range size) or a specialist (narrow range size).

All 735 samples of the cleared database were taken into account when calculating the species range size. The analysis was carried out on the complete dataset (with working species) and on the reduced dataset (excluding working species). In order to test for the influence of sampling effort on average ecological range size results, a third analysis was run: a random selection of 95 samples of each of the highly sampled regions Adriatic, North Sea and British Isles was tested separately.

### Species shared between regions and β-diversity

Number and identity of species shared between regions were obtained using the statistical software R. At the base of the species-sample matrix the data were pooled to a species-region matrix. Numbers of individuals were then converted to presence/absence data from which the shared species and number of species per region were extracted.

Approximate distances by water between regions are given based on map measurements (Fig. 1a). According to Magurran (2004), a cluster analysis (group average linking) based on a similarity matrix (Sørensen coefficient) was carried out as a measure of β-diversity between the six different regions. For this analysis sample data of described species were summed per region.

### Community analysis

A similarity analysis based on sample species composition was carried out. In view of differences in sampling effort and sample size of the 15 studies included, the Sørensen coefficient was chosen as the similarity index. It is identical to the Bray-Curtis coefficient, but it explores similarities between presence/absence data (Clarke and Warwick 1994). A non-metric two-dimensional plot (MDS) was produced to visualise the results. In order to check the effect of the use of working species, this analysis was carried out twice: first for the complete species-station matrix (including working species) and a second time for a reduced species-station matrix after removal of all working species.

The significance of the similarity of copepod species composition was tested by means of one-way ANOSIM. Three factors were introduced: *Study* (15 studies), *Region* (Arctic, Baltic, North Sea, British Isles, Adriatic, Crete) and *Depth* (0–5, 5–10, 10–20, 20–50, 50–100, >100 m).

The intertidal is a habitat with extreme environmental conditions that clearly differ from the more uniform subtidal. Therefore, an additional similarity analysis and ANOSIM was run for a reduced dataset where the two intertidal studies *dh* (North Sea) and *pa* (British Isles) were removed from the database.

Intraregional similarity between single studies was tested for the North Sea and the British Isles.

Analyses were performed using the PRIMER6 software (Plymouth Marine Laboratory; Clarke and Gorley 2006).

## Results

In total, 735 samples from 144 stations representing 15 European field studies provided 155 genera and 613 species (including 332 working species) of benthic Copepoda.

For the different regions the total number of species and number of working species detected were as follows: Arctic, 22 species in 2 samples (including 8 working species, 36.4%); Baltic, 36 species in 5 samples (13 working species, 36.1%); British Isles, 153 species in 120 samples (58 working species, 37.9%); North Sea, 345 species in 368 samples (188 working species, 54.5%); Adriatic, 112 species in 232 samples (32 working species, 28.5%); and Crete, 43 species in 8 samples (33 working species, 76.7%).

### Diversity analysis

Rarefaction curves (Fig. 2a) and K-dominance plots (Fig. 2b) document the sample diversity of the different regions.

The Adriatic was the region with the most diverse samples. The number of expected species in the Adriatic increased steeply with the number of individuals (Fig. 2a). The North Sea, Crete and Baltic samples showed medial increases in the number of expected species, and samples from the British Isles reach the maximum number of species earliest (Fig. 2a). The Arctic was characterised by a steady rise in species numbers with the number of individuals, which was only limited by the number of individuals present in the samples (Fig. 2a).

The Adriatic was the region with the highest evenness and thus the shallowest rise in cumulative relative abundance (Fig. 2b). North Sea, British Isles, Baltic and Crete samples were characterised by higher relative abundances of the dominant species. The Arctic was found in an intermediate position (Fig. 2b).

### Prediction of diversity

Multiple linear models predicting diversity were constructed for the three regions with the highest number of
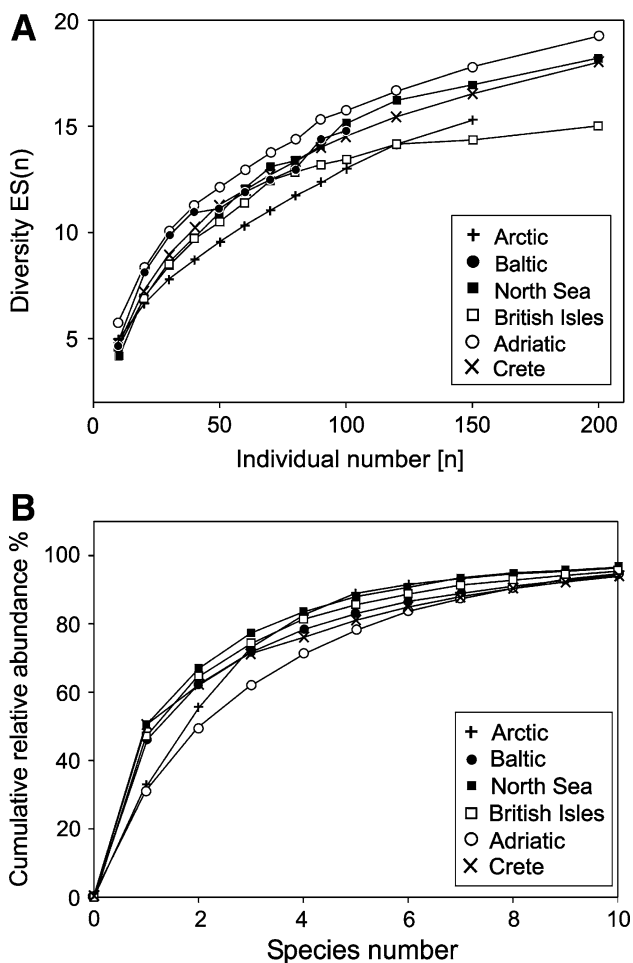
**Fig. 2 a** Sample diversity expressed as number of expected species ES(n) per individual number (rarefaction curves) and **b** Cumulative relative individual numbers per species number (K-dominance curves of mean values) for six European regions

**Table 1** Prediction of benthic copepod species number in the North Sea by a multiple linear model based on individual number, sampling depth [m] and sampled area [cm$^2$] ($r^2 = 0.148$)

| Source | df | Sum of squares | Mean square | F ratio | P |
|---|---|---|---|---|---|
| Analysis of variance | | | | | |
| Model | 7 | 1862.373 | 266.053 | 9.0744 | <0.0001 |
| Error | 319 | 9352.844 | 29.319 | | |
| Total | 326 | 11215.217 | | | |
| Term | | Estimate | SE | t Ratio | P |
| Parameter estimates | | | | | |
| Intercept | | 38.491961 | 25.25973 | 1.52 | 0.1285 |
| Individual number | | 0.0074087 | 0.011854 | 0.63 | 0.5324 |
| Sample area | | −3.478008 | 2.488085 | −1.40 | 0.1631 |
| Water depth | | 0.3974044 | 0.066368 | 5.99 | <0.0001 |
| Individuals × depth | | 0.0042664 | 0.001364 | 3.13 | 0.0019 |
| Individuals × area | | −0.067095 | 0.042255 | −1.59 | 0.1133 |
| Depth × area | | 0.086834 | 0.359779 | 0.24 | 0.8094 |
| Individuals × depth × area | | −0.000711 | 0.005757 | −0.12 | 0.9018 |

samples (North Sea, British Isles, Adriatic). The value of $r^2$ (with $0 < r^2 < 1$) shows the percentage of variation explained by the equation. Therefore, $r^2$ can be used as a measure of the quality of the prediction (Draper and Smith 1981).

For the North Sea no significant prediction formula could be calculated ($r^2_{adj} = 0.148$, Table 1). For the British Isles ($r^2_{adj} = 0.788$) and the Adriatic ($r^2_{adj} = 0.774$) highly significant models can be used for predicting the number of species (Tables 2, 3). To estimate the number of species present in a sample water depth (North Sea), the number of individuals (British Isles, Adriatic) and the interaction of the number of individuals with the sampled area (Adriatic) were the most significant factors in the three tested regions.

Ecological range size

There is a decreasing trend in the average ecological range size in samples with increasing species diversity in the Adriatic, the North Sea and the Baltic, pointing to an inverse relation between specificity and diversity (Fig. 3a). In samples from the British Isles and Crete, specificity did not change considerably with diversity. The average ecological range size of species in these regions stayed the same or increased slightly with the number of species present in a sample.

Overall, the lowest specificity was detected in samples from the Adriatic (Fig. 3a, b; Table 4). Species from this region show the highest ecological range size, which suggests that they occupy large areas in the Adriatic or elsewhere. The Adriatic region is followed by the North Sea, the Baltic, the British Isles and Crete (in this order, Fig. 3a) where higher species specificities and thus lower average ecological range sizes were observed. A random selection of 95 samples of each of the highly sampled regions (Adriatic, North Sea, British Isles) confirmed the particular situation of the Adriatic (Fig. 3b).

After removal of working species, the results for the investigated regions were only slightly different in the maximum number of species per sample and the inclination of the slopes of the fitted lines. Intercepts, trends and position of regions were nearly identical.

At the genus level (Fig. 3c; Table 4), all regions showed a decreasing trend in average ecological range size with increasing genus diversity. The results of all regions are closer together in this case. The highest specificity (lowest trend line on Fig. 3c) was found in samples with low genus diversity from Crete. In samples with high genus numbers the Adriatic shows the lowest specificity (highest trend line on the right side of Fig. 3c).

**Table 2** Prediction of benthic copepod species number in the British Isles by a multiple linear model based on individual number, sampling depth [m] and sampled area [cm$^2$] ($r^2 = 0.788$)

| Source | df | Sum of squares | Mean square | F ratio | P |
|---|---|---|---|---|---|
| Analysis of variance | | | | | |
| Model | 7 | 4569.8556 | 652.837 | 64.0184 | <0.0001 |
| Error | 112 | 1142.1361 | 10.198 | | |
| Total | 119 | 5711.9917 | | | |

| Term | Estimate | Std error | t Ratio | P |
|---|---|---|---|---|
| Parameter estimates | | | | |
| Intercept | −3.428453 | 2.103412 | −1.63 | 0.1059 |
| Individual number | 0.0699803 | 0.016215 | 4.32 | <0.0001 |
| Sample area | 0.4142152 | 0.18223 | 2.27 | 0.0249 |
| Water depth | −0.001127 | 0.05284 | −0.02 | 0.9830 |
| Individuals × depth | 0.0000237 | 0.000666 | 0.04 | 0.9717 |
| Individuals × area | 0.0014928 | 0.002515 | 0.59 | 0.5540 |
| Depth × area | 0.0033725 | 0.006465 | 0.52 | 0.6030 |
| Individuals × depth × area | −0.000086 | 0.000087 | −0.98 | 0.3269 |

**Table 3** Prediction of benthic copepod species number in the Adriatic by a multiple linear model based on individual number, sampling depth [m] and sampled area [cm$^2$] ($r^2 = 0.774$)

| Source | df | Sum of squares | Mean square | F ratio | P |
|---|---|---|---|---|---|
| Analysis of variance | | | | | |
| Model | 7 | 7749.2634 | 1107.04 | 114.3378 | <0.0001 |
| Error | 224 | 2168.8055 | 9.68 | | |
| Total | 231 | 9918.0690 | | | |

| Term | Estimate | SE | t Ratio | P |
|---|---|---|---|---|
| Parameter estimates | | | | |
| Intercept | 2.7755816 | 2.189961 | 1.27 | 0.2063 |
| Individual number | 0.0491694 | 0.003682 | 13.36 | <0.0001 |
| Sample area | 0.1719601 | 0.046623 | 3.69 | 0.0003 |
| Water depth | 0.180336 | 0.08938 | 2.02 | 0.0448 |
| Individuals × depth | 0.0038353 | 0.001007 | 3.81 | 0.0002 |
| Individuals × area | −0.002023 | 0.000256 | −7.89 | <0.0001 |
| Depth × area | −0.000143 | 0.006733 | −0.02 | 0.9831 |
| Individuals × depth × area | −0.000219 | 0.000067 | −3.25 | 0.0013 |

Species shared between regions and β-diversity

The results for approximate distances by water between the different regions are given in Fig. 1a. In combination with Tables 5, 6, 7 they furnish an overview of the geographical ranges widespread species cover.

Overall, 216 out of the 281 described species in the database were restricted to only one region, 40 species
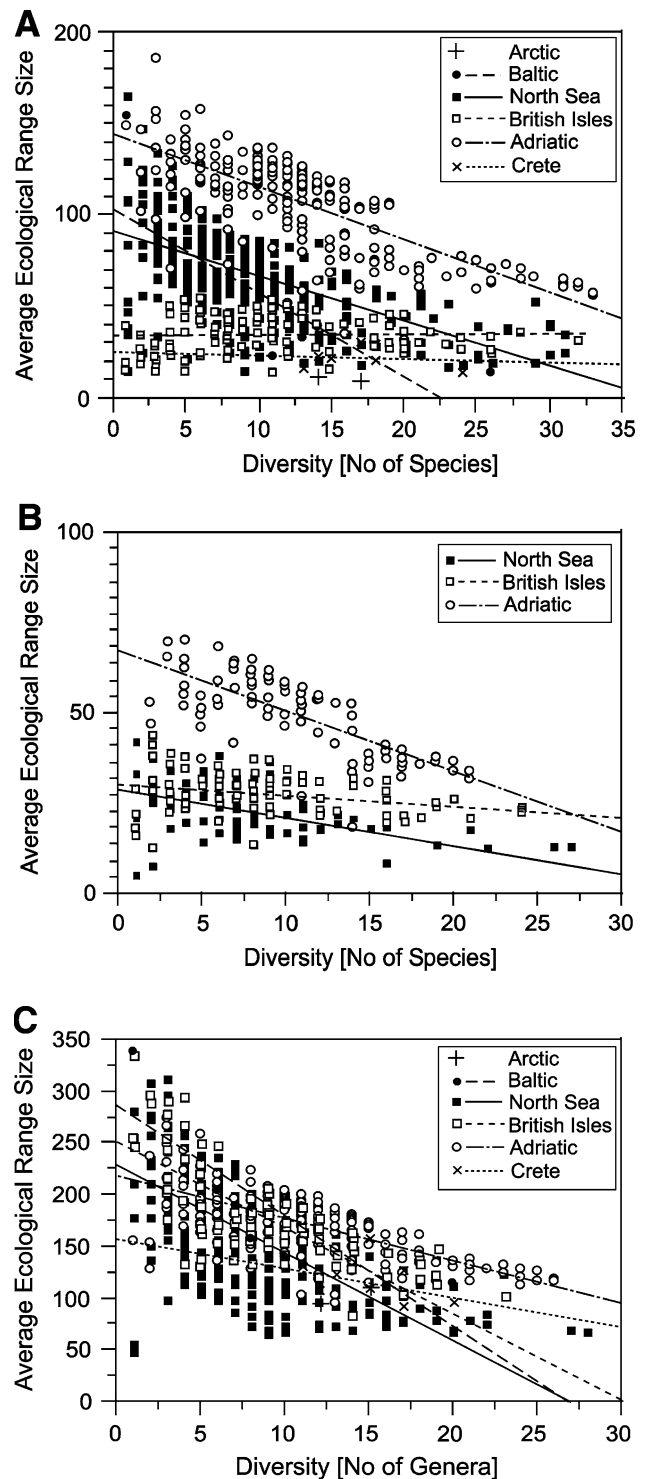


**Fig. 3** Average ecological range size of benthic copepod communities in samples from six geographical regions versus sample diversity. **a** Species level; **b** random selection of 95 samples per presented region; **c** genus level. Results for regressions (**a** + **c**) given in Table 4

occurred in two different regions and 18 species were reported from three regions (Tables 5, 6). Only six species were shared by four regions and one species (*Cletodes*

**Table 4** Regressions between average ecological range size (AERS) of a sample and number of benthic copepod species or genera (S) in that sample in five European regions

| Region | AERS $= a + b[S]$ | | | | |
|---|---|---|---|---|---|
| | Intercept ($a$) | Slope ($b$) | $r^2$ | $n$ | $P$ |
| Species level | | | | | |
| Baltic | 104.358 | −4.568 | 0.505 | 5 | >0.10 ns |
| North Sea | 92.540 | −2.486 | 0.377 | 368 | <0.0001 |
| British Isles | 34.617 | 0.061 | 0.002 | 120 | >0.50 ns |
| Adriatic | 144.329 | −2.895 | 0.514 | 232 | <0.0001 |
| Crete | 26.828 | −0.210 | 0.016 | 8 | >0.50 ns |
| Genus level | | | | | |
| Baltic | 287.510 | −10.622 | 0.699 | 5 | >0.05 ns |
| North Sea | 229.630 | −8.429 | 0.447 | 368 | <0.0001 |
| British Isles | 251.721 | −8.293 | 0.589 | 120 | <0.0001 |
| Adriatic | 218.191 | −4.063 | 0.468 | 232 | <0.0001 |
| Crete | 158.779 | −2.841 | 0.154 | 8 | >0.20 ns |

Data presented in Fig. 3

*limicola*) was present in five out of six regions (Table 7). There were no species reported that were found in all six regions.

The Baltic had 78% of the described species (18 out of 23) in common with other regions. This was the highest ratio of wider-spread species in comparison with the other regions. Despite the large distance between the sampling regions, 10 out of 14 described Arctic species (71%) were found to be trans-regional. The centrally located North Sea had only 45 species out of 157 (29%) in common with one or more regions. The British Isles (49 of 95 species shared, 52%) and the Adriatic (34 of 80 species shared, 42%) showed medial percentages of supra-regionally spread species. The remotely located island of Crete had seven out of ten described species (70%) in common with one or more regions.

Nevertheless, β-diversity between regions around Europe is high. This can be deduced from the cluster analysis (Fig. 4) where the positions of the nodes of the dendrogram indicate very low similarities between the different regions and/or clusters of regions. The highest similarity (and thus the lowest β-diversity) was observed between the Baltic and the British Isles at 28.81%. The greatest step towards higher β-diversity was found between the cluster Baltic/British Isles and the Adriatic (20.74% similarity with Baltic/British Isles). The North Sea, Adriatic, Baltic and British Isles clustered at a similarity level of 17.53%. Another wide step was observed between this group and Crete, which were similar only for 9.55%. The Arctic showed the lowest similarity with the other regions.

Community analysis

The MDS ordination (Fig. 5) indicated that the copepod communities of the six European regions were distinguishable with some overlap. This was confirmed by a one-way ANOSIM for the factor *Region* (Table 8, complete data; $R = 0.54$, $P\% = 0.1$). Samples from the North Sea (Fig. 5; grey symbols), and the Adriatic (black squares with grey border) formed clearly separated aggregations, while the British Isles (open symbols with black border) as well as the Baltic communities were more scattered over parts of the MDS. Crete and the Arctic were found as separate clusters in the middle of the plot. The Adriatic samples formed the densest cluster of the three regions with the highest sampling effort, indicating very homogenous communities. A nearly identical pattern was observed when the analysis was carried out a second time after exclusion of the working species.

Highly specialised intertidal copepod communities seemed to share more species over larger distances than the communities of the subtidal. The samples of the two intertidal studies *dh* (North Sea) and *pa* (British Isles) were found to cluster in the lower part of the MDS plot (Fig. 5, positions indicated by arrows). The *pa* study was completely separate from the rest of the British samples (plotted in the upper part of the MDS). In the North Sea samples the *dh* study grouped separately from the rest. When the (intertidal) studies *dh* and *pa* were removed from the database, ANOSIM detected a more marked separation of the different regions (Table 8, reduced data; $R = 0.689$, $P\% = 0.1$).

However, grouping samples by the factor *Study* yielded the highest rates for Global $R$ and indicated that the different studies were well separated from each other (Table 8; $R > 0.8$). Factor *Depth* as well showed certain grouping tendencies, but only to a minor extent in comparison with the other two factors.

Within regions Global $R$ can reach comparable or higher values than between regions (Table 9). The seven studies from the North Sea are overlapping, but different with a Global $R$ of 0.496 ($P\% = 0.1$). The four studies around the British Isles are nearly completely separated (Global $R = 0.909$, $P\% = 0.1$).

The more detailed pairwise ANOSIM tests for the complete database for the factor *Region* revealed different degrees of separation (Table 10). The $R$ values showed a marked difference between the Arctic and the Baltic ($R = 0.855$) although the significance was quite low due to the low sampling effort in the two regions ($P\% = 4.8$). There was a complete separation between the samples from Crete and the faraway regions Arctic and Baltic as well as the geographically closer Adriatic. This seems to be astonishing as Crete shared 7 of its 10 described species

**Table 5** List of benthic copepod species shared between two European regions

| | Arctic | Baltic | North Sea | British Isles | Adriatic | Crete |
|---|---|---|---|---|---|---|
| *Acrenhydrosoma perplexum* | | | | ▬ | ▬ | |
| *Alteutha interrupta* | | | ▬ | ▬ | | |
| *Amphiascoides dispar* | | ▬ | | ▬ | | |
| *Amphiascoides subdebilis* | | | ▬ | ▬ | | |
| *Amphiascus varians* | | | ▬ | | ▬ | |
| *Asellopsis intermedia* | | | ▬ | ▬ | | |
| *Brianola stebleri* | | | | | ▬ | ▬ |
| *Bulbamphiascus inermis* | | | | | ▬ | ▬ |
| *Cletodes pusillus* | | | | ▬ | | |
| *Cyclopinoides littoralis* | | | ▬ | | | |
| *Dactylopodella flava* | | | ▬ | | ▬ | |
| *Dactylopusia tisboides* | | | ▬ | | | |
| *Dactylopusia vuIgaris* | ▬ | | ▬ | | | |
| *Diosaccus tenuicornis* | | | ▬ | | ▬ | |
| *Stongylacron buchholzi* | | | | ▬ | | |
| *Enhydrosoma gariene* | | | ▬ | ▬ | | |
| *Enhydrosoma sarsi* | | ▬ | | | | |
| *Euterpina acutifrons* | | | ▬ | | ▬ | |
| *Halectinosoma gothiceps* | ▬ | | ▬ | | | |
| *Heteropsyllus major* | | | | ▬ | | |
| *Longipedia scotti* | | ▬ | | ▬ | | |
| *Mesochra lilljeborgi* | | | ▬ | ▬ | | |
| *Microarthridion fallax* | | | ▬ | ▬ | | |
| *Microarthridion littorale* | | | ▬ | ▬ | | |
| *Nannopus palustris* | | | ▬ | ▬ | | |
| *Normanella mucronata* | | | ▬ | | ▬ | |
| *Paramphiascella hyperborea* | ▬ | | | | | |
| *Paronychocamptus curticaudatus* | | | ▬ | ▬ | | |
| *Platychelipus littoralis* | | | ▬ | ▬ | | |
| *Proameira signata* | ▬ | | | | | |
| *Rhizothrix curvata* | | | | ▬ | ▬ | |
| *Robertgurneya rostrata* | | | | ▬ | ▬ | |
| *Robertsonia tenuis* | ▬ | | ▬ | | | |
| *Stenhelia Delavalia normani* | | | ▬ | | ▬ | |
| *Stenhelia  Delavalia palustris* | | | ▬ | ▬ | | |
| *Tachidiella minuta* | | | ▬ | ▬ | | |
| *Tachidius discipes* | | | ▬ | ▬ | | |
| *Thompsonula hyaenae* | | | ▬ | ▬ | | |
| *Tisbe furcata* | | | ▬ | ▬ | | |
| *Typhlamphiascus confusus* | | | | ▬ | ▬ | |

with the Adriatic, though it has to be kept in mind that only 23% of the species found in Heraklion harbour were described. The separation between Crete and the Adriatic persisted even after excluding working species from the analysis. This might be a consequence of the greater homogeneity within the Crete samples. ANOSIM is known to react sensitively to this kind of difference (Anderson 2001). Samples from the North Sea and the British Isles were overlapping with all regions except for the Adriatic samples. The Adriatic itself was clearly separated from all other regions with highly significant pairwise $R$ values of $0.588 \leq R \leq 0.972$.

For the factor *Depth* an inhomogeneous pattern of pairwise results was observed (Table 10). The highest $R$ values and thus the clearest separations were observed for the pairwise tests between the groups 50–100 and >100 m ($R = 0.924$; $P\% = 0.1$), 0–5 and 50–100 m ($R = 0.789$; $P\% = 0.1$), and 0–5 and >100 m ($R = 0.803$; $P\% = 0.1$). Within the two separately tested regions (Table 9) the factor *Depth* plays a nearly as important role as the factor *Study*. The communities in the different depth categories in the North Sea were overlapping (Global $R = 0.43$, $P\% = 0.1$) while for the British Isles the communities were well separated (Global $R = 0.776$, $P\% = 0.1$).

## Discussion

Diversity and predictability

The Adriatic was the region with the highest evenness and showed the most species-rich and diverse communities

**Table 6** List of benthic copepod species shared between three European regions

| | Arctic | Baltic | North Sea | British Isles | Adriatic | Crete |
|---|---|---|---|---|---|---|
| *Ameira parvula* | | | X | X | X | |
| *Amphiascoides debilis* | X | | X | X | | |
| *Amphiascus tenuiremis* | | X | X | X | | |
| *Bradya typica* | X | | X | | X | |
| *Bulbamphiascus imus* | | | X | X | X | |
| *Canuella furcigera* | | | X | | X | X |
| *Canuella perplexa* | | | X | X | X | |
| *Enhydrosoma curticauda* | X | X | | X | X | |
| *Haloschizopera junodi* | | X | X | X | X | |
| *Heteropsyllus curticaudatus* | | | X | X | X | |
| *Laophonte cornuta* | | | X | X | X | X |
| *Longipedia coronata* | | X | | X | X | |
| *Longipedia helgolandica* | | X | X | X | | |
| *Mesochra pygmaea* | | X | | X | X | |
| *Microsetella norvegica* | X | | | X | X | |
| *Proameira simplex* | | X | X | X | X | |
| *Sarsameira parva* | | X | X | X | X | |
| *Stenhelia Delavalia reflexa* | | X | | X | X | |

**Table 7** List of benthic copepod species shared between four (grey bars) and five (black bars) European regions

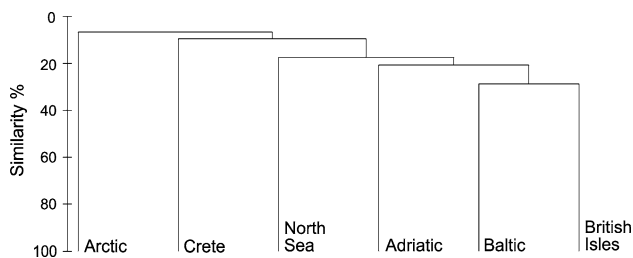| | Arctic | Baltic | North Sea | British Isles | Adriatic | Crete |
|---|---|---|---|---|---|---|
| *Cletodes longicaudatus* | | X | X | X | X | |
| *Cletodes tenuipes* | | X | X | X | | X |
| *Danielssenia typica* | X | X | X | X | | |
| *Enhydrosoma longifurcatum* | | X | X | X | X | |
| *Enhydrosoma propinquum* | | X | X | X | | X |
| *Laophonte longicaudata* | | X | X | X | X | |
| *Cletodes limicola* | | ■ | ■ | ■ | ■ | ■ |



**Fig. 4** Dendrogram of the cluster analysis of the Sørensen similarity (group average linking) of benthic copepod community data (described species) from six European marine regions

found in single samples compared to all investigated regions. Dominant species in the Adriatic were less individual-rich than in other regions. The high species diversity in the Adriatic samples may be explained by the small-scale ecological situation (food spectra, microhabitats) in the variety of inshore and offshore macrohabitats sampled (Vriser 1983, 1996a, b, 2000a, b; Orlando-Bonaca and Lipej 2005). Other factors like inter-specific competition might additionally contribute to these findings.

In the North Sea, the British Isles, the Baltic Sea and Crete dominant species showed higher individual densities than in other regions. Communities thus had a lower evenness than the ones from the Adriatic samples. In general, the variety of habitats sampled from the British Isles was comparable to the situation in the Adriatic (see below). However, the individual densities in communities from single habitats in the British Isles were not as evenly distributed as in the Adriatic. Moreover, the British Isles were characterised by impoverished communities with lower maximum species numbers.

Individual densities play a crucial role for the number of species in a sample. Our findings indicate that the number of species may additionally depend on water depth or the interaction of individual density with the sampled surface area. This means that the effect of the number of individuals on species richness can change with the sampled area, at least in the Adriatic.

Species specificity

The observations and trends on average species range sizes in samples and their relation to sample diversity were
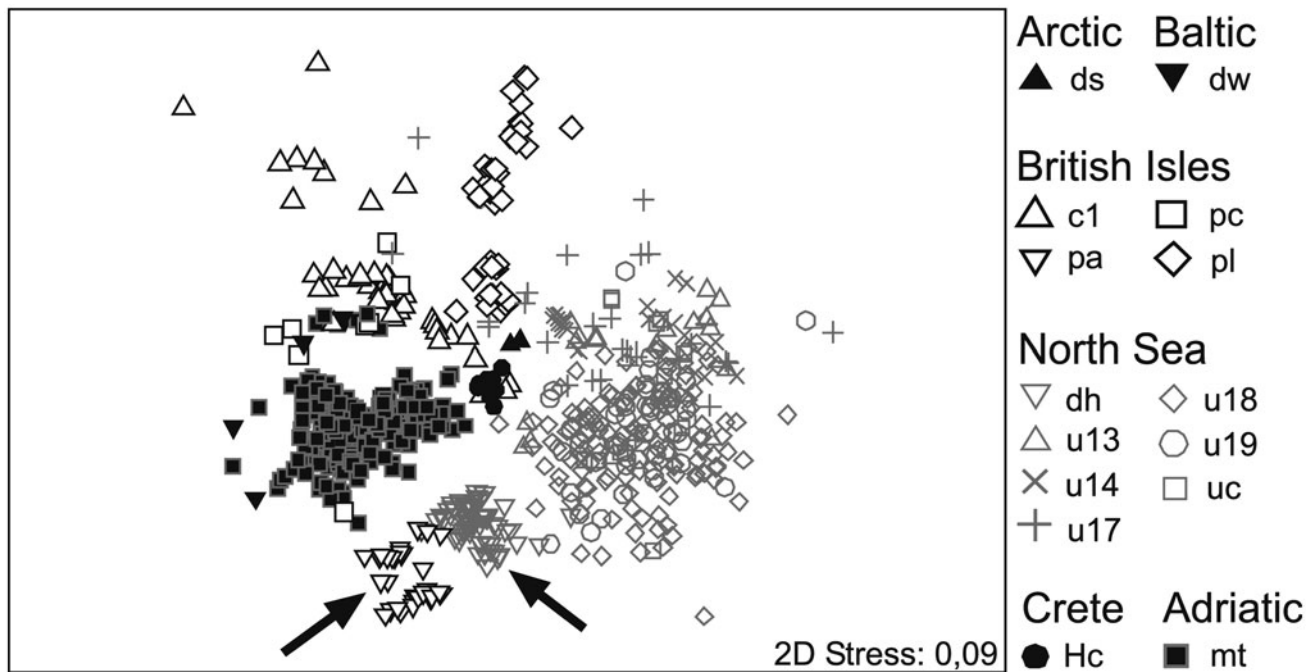
**Fig. 5** MDS of the Sørensen similarity of benthic copepod community data (species level) of 15 studies from six European marine regions. Arrows indicate the isolated position of the two intertidal studies *dh* and *pa*

**Table 8** Copepod community analysis based on species data in single samples: results of the ANOSIM of the Sørensen similarity for the factors *Study*, *Region* and *Depth* for the complete and the reduced database (without the intertidal datasets *dh* and *pa*)

|  | Global $R$ | $P\%$ |
| --- | --- | --- |
| **Complete data** | | |
| Study | 0.816** | 0.1 |
| Region | 0.54* | 0.1 |
| Depth | 0.508* | 0.1 |
| **Reduced data** | | |
| Study | 0.801** | 0.1 |
| Region | 0.689* | 0.1 |
| Depth | 0.461 | 0.1 |

Asterisks indicate state of separation [* groups overlapping but clearly different, ** groups well separated; after Clarke and Gorley (2001)]

**Table 9** Copepod community analysis based on species data in single samples: results of the ANOSIM of the Sørensen similarity for single regions (North Sea, 7 studies; British Isles, 4 studies) based on the factors *Study* and *Depth*

|  | Global $R$ | $P\%$ |
| --- | --- | --- |
| **North Sea** | | |
| Study | 0.496* | 0.1 |
| Depth | 0.43 | 0.1 |
| **British Isles** | | |
| Study | 0.909** | 0.1 |
| Depth | 0.776** | 0.1 |

Asterisks indicate state of separation [* groups overlapping but clearly different, ** groups well separated; after Clarke and Gorley (2001)]

independent of the number of working species used for a region. A cross-check analysis after exclusion of all working species showed only negligible differences in the slopes of the fitted lines for the investigated regions compared to the analysis of the complete dataset. A possible explanation for this finding is that working species were mainly assigned for rare species that did not contribute decisively to ecological range size calculation. This is plausible as undescribed copepod species tend to be the more rare ones.

The high number of samples processed for the Adriatic region (with the use of constant working species by a single investigator) could lead to overestimated ecological range sizes. Consequently, this means that average ecological range sizes should be very low in the North Sea (7 studies, 6 authors, 54.6% working species) because the same species could have been counted several times as different working species. However, this is not the case. In the British Isles we deal with an intermediate value of 37.9% working species (four studies, of four different author groups), but here we find the lowest average ecological range sizes and not in the North Sea.

**Table 10** Copepod community analysis based on species data in single samples: results of the pairwise tests of ANOSIM of the Sørensen similarity for the factors *Region* and *Depth* for the complete database

| Region | Baltic | North Sea | British Isles | Adriatic | Crete |
|---|---|---|---|---|---|
| Arctic | 0.855 (4.8)** | 0.41 (0.1) | 0.226 (0.7) | 0.972 (0.1)** | 1 (2.2)** |
| Baltic | | 0.476 (0.1) | 0.155 (0.4) | 0.88 (0.1)** | 0.968 (0.3)** |
| North Sea | | | 0.406 (0.1) | 0.588 (0.1)* | 0.382 (0.1) |
| British Isles | | | | 0.782 (0.1)** | 0.192 (0.1) |
| Adriatic | | | | | 0.931 (0.1)** |
| **Depth (m)** | **5–10** | **10–20** | **20–50** | **50–100** | **>100** |
| 0–5 | 0.452 (0.1) | 0.496 (0.1)* | 0.693 (0.1)* | 0.789 (0.1)** | 0.803 (0.1)** |
| 5–10 | | 0.08 (0.1) | 0.627 (0.1)* | 0.292 (0.1) | 0.428 (0.1) |
| 10–20 | | | 0.592 (0.1)* | 0.278 (0.1) | 0.364 (0.1) |
| 20–50 | | | | 0.599 (0.1)* | 0.588 (0.1)* |
| 50–100 | | | | | 0.924 (0.1)** |

*R* statistic and corresponding *P*%-levels (in brackets) are indicated. Asterisks indicate state of separation [* groups overlapping but clearly different, ** groups well separated; after Clarke and Gorley (2001)]

Average ecological range size as a measure for ecological specificity in benthic copepod species showed two diverging trends in the analysed datasets. There are geographical regions (Adriatic, North Sea, Baltic) where the average ecological range size decreased with increasing sample diversity. This decreasing trend points to the higher specificity of species in more diverse assemblages compared to species in less diverse areas (Schlacher et al. 1998; De Troch et al. 2001). Overall, the Adriatic shows the highest number of generalist species. This result is independent of sampling effort or of the use of working species. A possible explanation for this may be the adaptation of generalist species to the challenging ecological situation found in this shallow gulf with its pronounced seasonal cycles during the year due to great variations in water temperature, stratification and irradiance (Malačič and Petelin 2001). The study area is situated in the eastern part of the north Adriatic which has mesotrophic or oligotrophic conditions (Mozetič et al. 2009; Flander Putrle and Malej 2003; Turk et al. 2007). However, occasional phytoplankton blooms, mucilages and hypoxic to anoxic bottom events destabilise the benthic community (Stachowitsch 1986, 1991; Turk et al. 2007). The geographical area sampled in the Adriatic was not as large as in the North Sea and the British Isles. Therefore, a certain influence at the ecological range size should be taken into account. Nevertheless, a high percentage of described species (42%) from the Adriatic has been reported from other regions as well.

A second trend with a uniformly high specificity of the species disregarding sample diversity was found in two regions (Crete and the British Isles). One explanation may be that these two regions are inhabited by more specialised species, or by species that are precisely endemic to one region. The second is partly true for Crete. Only 23% of the species of Heraklion harbour were described species, but sampling effort in Crete was relatively low (see below). For the British Isles, however, there seem to be other reasons for the uniform species specificity. The comparably stable level of average ecological range size could partly be explained by the variety of habitats that were included in the British Isles dataset, ranging from brackish intertidal mud flats and sublittoral coast stations to a firth environment. This diversity of habitats found in the British Isles might be the main explanation for the constant level of species specificity that was independent of sample diversity. The North Sea datasets, on the other hand, comprised intertidal sand flats, sandbanks and sublittoral shelf stations from the Southern Bight. These habitats are more uniform than the ones studied from the British Isles, and North Sea samples show a distinct slope in species range sizes with more generalist species in the less diverse samples.

Benthic copepod communities

The benthic copepod communities analysed in this study showed distinct patterns which clearly fit the geographical regions that were predefined. Communities were distinguishable and β-diversity was found to be high around Europe, indicating a high species turnover on this scale of investigation.

The Arctic and the Baltic (western part) communities were clearly distinguishable. Although there were very high percentages of widespread species found in both regions, they had only two species in common. Their separated geographical positions contributed to these results. However, continuous connections between the investigated Arctic fjord system (Kongsfjorden, Spitsbergen) and the central European water masses are realised via the Norwegian Atlantic current (Svendsen et al. 2002). Although benthic copepods do not have pelagic larvae and many species have only reduced swimming abilities (Thistle and Sedlacek 2004), a possible way of dispersal is resuspension by benthic storms (Thistle 1988) followed by passive transport by currents. The fact that benthic copepod species can overcome thousands of kilometres of deep-sea

environment, including abyssal plains and ridge systems, was recently presented by Gheerardyn and Veit-Köhler (2009). The western Baltic, on the other hand, is regularly provided with an influx of North Sea water masses. However, the separation of the Arctic and the Baltic region has to be confirmed by further studies since the sampling effort for these two regions was relatively low.

The communities of the British Isles were very similar to or even non-separable from the copepod assemblages of all other regions, with the exception of the Adriatic. The open geographical position and the constant exchange with the North Sea and even connections to the Arctic did lead to the establishment of interconnected communities in the British Isles. The British Isles, and to a lesser extend the North Sea, can be regarded as faunistic links between the separated Arctic communities on one side and the Baltic ones on the other. Our findings indicate a transitional position of the British Isles.

Within the three regions with the highest sampling effort, the British Isles showed the largest proportion of trans-regional species. This can additionally be explained by the wide variety of habitats investigated around the British Isles (including the subtidal, mudflats and a firth environment). The North Sea habitats, on the other hand, were mainly Southern Bight sites from the subtidal, an intertidal sand flat and sandbanks. However, the highest number of described species was reported from there. This can partly be explained by the number of included samples, which was highest for the North Sea. A high sampling effort may be responsible for detection of more rare species than in other less intensively sampled regions. Consequently, the North Sea showed a low percentage of widespread species. However, the absolute number of species the North Sea shared with other regions nearly equalled that of the British Isles.

For the British Isles and the North Sea, intraregional community analyses were carried out. The different studies around the British Isles were completely separated from each other, which may be attributed to the great variety of different habitat types included (see above). The North Sea studies were found to be overlapping in the intraregional test, a fact that is due to the more uniform structure of the investigated sites.

A special situation was found at intertidal sampling sites. Communities from the North Sea intertidal (German Wadden Sea sand flat) equalled those of a brackish water intertidal mudflat in the southeast British Isles (England, Fal estuary). Apparently, the extreme environmental conditions present in the intertidal lead to a specialised copepod community that is more stable over larger distances than the subtidal communities.

The situation of the copepod communities of the two southernmost regions, the Adriatic and Crete, can be

explained by the geological history of the Mediterranean (Bianchi and Morri 2000). The authors distinguish marine faunal elements by their biogeographical backgrounds. Among others, the categories are as follows: temperate Atlantic-Mediterranean fauna, cosmopolitan/panoceanic fauna, species from the subtropical Atlantic with interglacial remnants, species from the boreal Atlantic with ice-age remnants, eastern Atlantic migrants and endemic elements (Bianchi and Morri 2000). From this diverse scenario, cosmopolitan fauna and ice-age remnants are the most probable explanations that the Crete communities—despite the geographical distance—were not separable from those from the North Sea and especially the British Isles. However, ANOSIM almost completely separated Crete from the Adriatic (independent of working species), which may be explained by the low sampling effort and the very homogeneous communities in Crete since Crete shared all its interregional species with the Adriatic. The Adriatic is a semi-enclosed shallow shelf area that has been completely dry during the last glacial period (Hofrichter 2002). Here a benthic copepod community has evolved that—despite the fact that it shared still 42% of its species with the other European regions—is unique and adapted to the challenging environmental conditions. Environmental and geological conditions, prevailing currents (Hofrichter 2002) and the complex geological history of the Mediterranean (Bianchi and Morri 2000) seem to be the major explanations for this situation.

Comparison to other large-scale studies

Chertoprud and Garlitska (2007) compiled an extensive dataset of harpacticoid species from Russian seas. Their work was based on a large number of different ecological, taxonomic and biogeographical studies. They compared species composition for the different regions, but did not take densities into account. Their total list of the harpacticoid fauna included 527 species and 168 genera. More than half of the species represented were restricted to one region. In the present study we found an even higher percentage (77%): 216 of the 281 described species were "endemic" to a region. Chertoprud and Garlitska (2007) report a gradual reduction of species richness from the subtropical and temperate latitudinal belts to the Arctic zone. This is in line with a study by Kuklinski et al. (2006), who found inverse correlations between latitude and all measures of richness and biodiversity in the faunas of cobbles in intertidal boulder fields. Our data, on the other hand, show a species richness hot spot in the North Sea with a gradual decline in species numbers towards the north and south. Although the high sampling effort in the North Sea should be considered, regional differences in ecological characteristics, such as productivity and habitat

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suitability, have to be considered as factors influencing species richness.

In general, from their Russian study Chertoprud and Garlitska (2007) find common climatic and hydrographical features to be more important than geographical connection or isolation of regions for the similarity of harpacticoid faunas. Nevertheless, the general importance of ecological factors seems to decrease and that of historical factors seems to increase from local to regional scales (Caruso et al. 2005). Our results support these ideas: on the one hand, the benthic copepod communities of the Adriatic and Crete are completely separated despite their geographical closeness. The present ecological conditions and the differing geological history of both parts of the Mediterranean may explain this. On the other hand, the communities of Crete are closely related to the North Sea and the British Isles. This cannot be explained by the climatic conditions, but only by historical factors.

Chertoprud et al. (2007) were the first to carry out a large-scale study on intertidal and shallow European waters. They stated that the quantitative characteristics of benthic copepod populations are not important for taxocoenosis identification because of their high variability in space and time. Accordingly, and because of the differences in sample size, we also used the Sørensen index for community analysis.

Chertoprud et al. (2007) were able to show that the geographical variability of harpacticoid assemblages was low and that intraregional and biotopical variations were often greater than their geographical (interregional) variability. Sediment characteristics and hydrodynamic processes were the main factors controlling the composition of species and life forms. They found that ANOSIM of the species composition in intraregional and interregional comparisons resulted in Global $R = 0.56$ and thus confirmed a significant geographical variability in European waters. However, their $R$ values, slightly higher than 0.5, indicate that groups (though different) are still overlapping (Clarke and Gorley 2001). With our completely differing database we came to the same conclusion because we obtained the same Global $R$ value for the interregional test (factor *Region*). When we ran the test at study level (factor *Study* for the complete database), by contrast, the differences were much more pronounced and showed that studies were very well separated. This is not in line with the findings of Chertoprud et al. (2007), who reported the same moderate Global $R$ (0.56) for interregional and intraregional analysis at species level. On the other hand, Chertoprud et al. (2007) found comparable results of high intraregional variability with a different statistical analysis for the North Sea and attributed this to the variety of macrobiotopes sampled in the included studies. Our tests for single studies on a regional scale showed marked

differences in separation level: In the North Sea single studies were still overlapping while for the British Isles they were completely separated. On an intraregional scale the topography of the coastline, grain size situation and differences in salinity ranges seem to be responsible for the variability of the taxonomic structure of benthic copepod communities (Chertoprud et al. 2007). The variety of habitats sampled in the British Isles in the present study was much larger than in the North Sea. These possible sources of differences have to be taken into account when drawing conclusions from large-scale studies with combined datasets.

## Conclusions

Patterns of species richness, biodiversity, communities, ecological range size and biogeography are quite distinct between the Arctic, the Baltic, the North Sea, the British Isles, the Adriatic and Crete. The Adriatic showed the highest evenness and the most species-rich communities, which can be explained by the great variety of microhabitats sampled. Assemblages from the North Sea, British Isles, Baltic and Crete had a lower evenness, indicating the dominance of few species. The British Isles had impoverished communities with the lowest maximum numbers of expected species. Correlations between species richness and copepod densities with influences of water depth and sampled surface area were found for the North Sea, the British Isles and the Adriatic respectively. Two diverging trends were detected for the ecological specificity of copepod species. In the Adriatic, the North Sea and the Baltic, higher specificity of species in more diverse assemblages was observed. Overall, the Adriatic showed the highest number of generalist species, a fact that could be explained by the challenging ecological situation found in this shallow gulf. A uniform species specificity disregarding sample diversity was found in Crete and the British Isles. In the case of Crete this could partly be explained by the existence of more undescribed species while in the British Isles the variety of macrohabitats supported more specialised species. The benthic copepod communities analysed in this study showed distinct patterns that clearly fit the predefined geographical regions. The communities of the British Isles were very similar to or even non-separable from the copepod assemblages of all other regions, with the exception of the Adriatic. The British Isles and the North Sea were found to be faunistic links to the Baltic and the Arctic. The open geographical position, the constant exchange with the North Sea and connections to the Arctic lead to the establishment of interconnected communities in the British Isles. Intertidal communities from the North Sea equalled those of the British Isles, indicating that the

extreme environmental conditions present in the intertidal favoured a specialised copepod community that is more stable over larger distances than the studied subtidal communities. Our data show a species richness hot spot in the North Sea with a gradual decline in species numbers towards the north and south. Despite the high sampling effort, regional differences in historical factors and ecological characteristics, such as productivity and habitat suitability, strongly influence species richness.

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