Sublittoral and bathyal Harpacticoida (Crustacea: Copepoda) of the Magellan region. Composition, distribution and species diversity of selected major taxa*

KAI HORST GEORGE

AG Zoosystematik und Morphologie, Institut für Biologie, Fakultät 5, Carl von Ossietzky-Universität, D-26111 Oldenburg, Germany.
Present address: Forschungsinstitut Senckenberg, Abteilung Deutsches Zentrum für Marine Biodiversitätsforschung DZMB, Südstrand 44, D-26382 Wilhelmshaven, Germany. E-mail: kgeorge@senckenberg.de

SUMMARY: Two expeditions, undertaken in 1994 and 1996, provided quantitatively sampled material of sublittoral and bathyal meiobenthos from the Paso Ancho of the Straits of Magellan, the Beagle Channel, and the Patagonian continental slope (Chile). To investigate whether these distinct geographic areas might also be characterised by different harpacticoid assemblages, qualitative and quantitative analyses of Copepoda Harpacticoida were carried out. At supraspecific level 25 harpacticoid families were found, as well as several species that could not yet be assigned to any major harpacticoid taxon. Due to the high amount of collected Harpacticoida, detailed investigations at species level had to be restricted to six taxa, namely the Ancorabolidae, Argestidae, Cletodidae, Diosaccinae, Paramesochridae, and Paranannopinae. The corresponding specimens were assigned to 122 species in 52 genera. More than 80% of them are new to science. Qualitative comparisons of both species composition and species distribution allow the three areas to be distinguished in terms of species richness. However, statistical analyses confirm these results only partly. Similarity analyses applying non-metrical multidimensional scaling, as well as diversity analyses using the rarefaction method, suggest that the observed differences in distribution and diversity patterns are due to small-scale, local conditions, which may overlay possible large-scale ones.

Keywords: meiobenthos, similarity analysis, Harpacticoida, Chile, Straits of Magellan, Beagle Channel.

RESUMEN: HARPACTICOÍDEOS SUBLITORALES Y BATIALES (CRUSTACEA, COPEPODA) DE LA REGIÓN MAGALLÁNICA. COMPOSICIÓN, DISTRIBUCIÓN Y DIVERSIDAD ESPECÍFICA DE TAXONES MAYORES SELECCIONADOS. – Durante dos expediciones realizadas en 1994 y en 1996, se colectó una gran cantidad de material meiobentónico del sublitoral y bathyal en el Paso Ancho del Estrecho de Magallanes, del Canal Beagle y del talud continental patagónico (Chile). Posteriormente, se realizaron análisis cualitativos y cuantitativos de los copépodos harpacticoides para verificar si estas diferentes áreas geográficas también se distinguen con respecto a la fauna harpacticoida. A nivel supra-específico, se determinaron 25 familias diferentes, más varias especies desconocidas que no pudieron ser asignadas a ningún taxon harpacticoides. Debido al gran número de harpacticoides colectados, una evaluación a nivel de especies debió ser restringida a los representantes de solo seis familias, en particular a los Ancorabolidae, Argestidae, Cletodidae, Diosaccinae, Paramesochridae y Paranannopinae. Los especímenes respectivos corresponden a 122 especies que pertenecen a 52 géneros. Más del 80% de ellas puede ser considerado como nuevo para la ciencia. Un análisis cualitativo de la composición y distribución de especies permite diferenciar entre las tres áreas geográficas. Los análisis estadísticos de los datos cuantitativos confirmaron, sin embargo, este resultado sólo parcialmente. Sendos análisis de similaridad usando nMDS y de diversidad aplicando el método de “Rarefaction” indican que las diferencias observadas se deben principalmente a condiciones locales y de pequeña escala, las cuales posiblemente se superponen con condiciones de escala mayor.

Palabras clave: meiobentos, análisis de similaridad, Harpacticoida, Chile, Estrecho de Magallanes, Canal Beagle.

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INTRODUCTION

The disintegration of Gondwana and the related distribution of Gondwanan floral and faunal elements form the basis of biogeographical comparisons within the southern hemisphere. Since the early sixties, several biogeographic investigations have been carried out, focusing exclusively on macrofauna (e.g. Knox, 1960; 1963; 1977; Knox and Lowry, 1977; Lipps and Hickman, 1982; Brattstrøm and Johanssen, 1983; Brandt, 1992; Sieg, 1992; Winkler, 1994). In particular, the supposed high affinity between Antarctica and South America, as the two Gondwanan fragments that were last separated, calls for studies on the origin and spreading of recent Antarctic and Magellan flora and fauna and for potential correlation with latitudinal gradients in species diversity (Crame, 1994; Arntz, 1997, 1999). A number of recent investigations concentrated on different macrofaunal groups (e.g. Arntz and Gorny, 1996; Fahrbach and Gerdes, 1997 (macrofaunal major groups); Brandt, 1991; 1992; Winkler, 1994 (Isopoda); Linse, 1997 (Mollusca)), and were followed some years later by the first studies on meiofauna (Chen et al., 1999; George, 1999; George and Schminke, 1999).

Faunistic investigations dealing with Harpacticoida from deeper waters (>100 m to ~1,000 m) at species level are rare (cf. George 1999). The present contribution is the first one to detect, describe and compare harpacticoid assemblages from deeper waters of different Magellan areas at species level, as a basis for future comparisons with corresponding Antarctic sublittoral and bathyal assemblages. Comparable investigations in general are rare. The detailed investigation of harpacticoid taxa had to be restricted to six families, which is justified by the enormous amounts of specimens and species found in the Magellan region.

MATERIAL AND METHODS

Sampling areas

The investigated material originates from two international sampling expeditions to the southern tip of South America:

The 1994 “Magellan Campaign” of RV “Victor Hensen” (17.10.-20.11.1994; Arntz and Gorny, 1996) provided quantitative sublittoral meiobenthic material of this region for the first time. In total, 62 hauls at just as many stations were taken with a Minicorer (MIC) in the Paso Ancho of the Straits of Magellan, as well as from the channels Magdalena, Cockburn, Brecknock, Ballenero and Beagle (Fig. 1), 17 of which provided sufficient material for further quantitative analyses. The MIC, which resembles a small Multiple corer (MUC) as developed by Barnett et al. (1984), samples up to four cores per haul simultaneously.

The 1996 expedition ANT XIII/4 of RV “Polarstern” in May, 1996 (Fahrbach and Gerdes, 1997) provided material from the Patagonian continental slope (Fig. 1). The MUC was used to sample 8 stations, 3 of which were useful for further analyses.

Sampling localities

For the analyses, material from 20 stations was available (Fig. 1, Table 1). Their distribution over the areas is as follows (depth ranges (m) in brackets):

- Straits of Magellan (79-550):
  - 9 stations at 5 localities
  - 24 MIC cores
- Beagle Channel (100-346):
  - 8 stations at 7 localities
  - 24 MIC cores
- Patagonian continental slope (101-1,168):
  - 3 stations at 3 localities
  - 21 MUC cores

Treatment of samples

The material was immediately fixed in 5% formaldehyde. For the posterior treatment of sam-
samples and abiotic conditions, see Chen et al. (1999). Sedimentological data are summarised in Table 1. Species determination was realised using a Wild Heerbrugg M5 stereo microscope, a Leitz Dialux EB 22 phase contrast microscope, and a Leica DM LB interference contrast microscope, both equipped with a 100x objective. Taxa determination was done using identification keys (Lang, 1948; Wells, 1976-1985; Huys et al., 1996) and original literature. Abbreviations used in the text: BC = Beagle Channel, MR = Magellan region, SM = Straits of Magellan, PCS = Patagonian continental slope.

Selection of major harpacticoid taxa

Due to the high amounts of collected Harpacticoidea, for detailed analyses at species level a restriction of the material was necessary. Ancorabolidae Sars, 1909, Argestidae sensu Por, 1986, Cletodidae sensu Por, 1986, Diosaccinae Sars, 1906, Paramechridae Lang, 1944, and Paranannopinae sensu Por, 1986 were selected because of the taxonomical expertise of the author in particular for these groups. However, as shown by George (1999), they reflect very well the overall abundance data and distribution patterns in the study area.

Similarity analysis

For a similarity analysis, non-metrical multidimensional scaling (nMDS) was applied using Cosine Similarity (Pfeifer et al., 1996):

$$\cos(\mathbf{o}_x, \mathbf{o}_y) = \frac{\sum_{i=1}^{N} x_i y_i}{\sqrt{\sum_{i=1}^{N} x_i^2} \sqrt{\sum_{i=1}^{N} y_i^2}}$$

where $\mathbf{o}_x$ and $\mathbf{o}_y$ are considered as n-dimensional vectors $\mathbf{x} = [x_1, x_2, ..., x_N]^T$ as well as $\mathbf{y} = [y_1, y_2, ..., y_N]^T$. Consequently, the Cosine Similarity then corresponds to $\cos \alpha$ between vectors $\mathbf{x}$ and $\mathbf{y}$ within a multidimensional ecological space. The dimensions are represented by the attributes, i.e. the species at each station. Comparison between two vectors (here: stations) considers both the single and common presence of species. This means that neither single nor common absences are taken into account. To avoid any original data manipulation, no transformation was carried out.

RESULTS

Composition of Harpacticoidea at family level

With 91.9%, Harpacticoidea clearly dominated the benthic copepod fauna (George, 1999). In total, 25 supraspecific harpacticoid taxa were determined, comprising a number of 5,493 adult individuals (Table 2). Ten families (40%) showed a distribution within the whole study area. Furthermore, both SM and PCS present exclusive taxa at family level (Adenopleurellidae and Harpacticidae in SM, Peltidiidae, Superornatiremidae and Tegastidae in PCS), while BC cannot be characterised by any
exclusive family (Table 2). It shares common taxa with at least one of the remaining areas, which indicates its possible role as a transitional area, connecting the northern and eastern Magellan region.

Six families can be considered as generally dominating the harpacticoid community in the study area: Ameiridae, Cletodidae, Diosaccinae, Ectinosomatidae, Paranannopinae and Paramezochridae. However, each geographic area shows at least minor differences in taxa composition, illustrated in Figure 2. Dominating taxa in the SM are Ectinosomatidae (31.4%) and Diosaccinae (24.8%), followed by three families exceeding 5% of relative abundance. Together, the five dominating taxa exceed 77% of the relative abundance, whereas the remaining 13 families collected in this area reach almost 23%.

Distribution of genera

The Harpacticoida dealt with are distributed over 52 genera (Table 3). Compared with the results at family level, the number of taxa showing a distribution within the whole investigation area (Table 3) is lower due to the fact that more families had to be considered. The number of families contributing to the distribution within the whole investigation area (Table 3) is lower due to the fact that more families had to be considered.
decreases. Only 9 genera (17%) were collected at SM, BC, and PCS. The number of taxa shared by SM and BC is 15 (28.8%), which is almost twice the common genera between SM and PCS (7 taxa = 13.5%). PCS and BC show no genus in common (Table 3). However, in contrast to the results at family level, each geographical area can be characterised by a certain number of exclusive genera. SM encloses 5, BC 7, and PCS 9 taxa. As shown in Figure 3, only a few genera seem to dominate each geographic area.

The differences between the areas increase remarkably at this taxonomic level. Whereas SM and BC shows at least two abundant genera (Cletodes and Stenhelia), PCS shows quite a different taxa composition. Between SM and BC there are also noteworthy differences. BC is characterised by a relatively high portion of genera (~38%) not reaching 5% of relative abundance, versus three dominant genera, with Enhydrosoma (39.7%) as the most abundant one. On the other hand, SM seems to present a generally higher variety, comprising five dominant genera (with Haloschizopera (23.4%) showing highest values) versus 31 taxa with a relative abundance below 5%. Finally, PCS is clearly dominated by Amphiascus, Kliopsyllus, Paramesochra.

Table 3. – List of harpacticoid genera and their distribution within the Magellan region.

| No. | Genus/area | SM | BC | PCS |
|-----|------------|----|----|-----|
| 1   | Fultonia   | +  | +  | +  |
| 2   | Cletodes   | +  | +  | +  |
| 3   | Amphiascus | +  | +  | +  |
| 4   | Bulbamphiascus | + | +  | +  |
| 5   | Haloschizopera | + | +  | +  |
| 6   | Robertigurnea | + | +  | +  |
| 7   | Stenhelia  | +  | +  | +  |
| 8   | Typhlamphiascus | + | +  | +  |
| 9   | Paradaniellensia | + | +  | +  |
| 10  | Argestidae sp. 1 | + | +  | +  |
| 11  | Argestidae sp. 2 | + | +  | +  |
| 12  | Argestidae sp. 3 | + | +  | +  |
| 13  | Euryclitodes (O.) | + | +  | +  |
| 14  | Mesocletodes | + | +  | +  |
| 15  | Acrenydromosa | + | +  | +  |
| 16  | Enhydrosoma | +  | +  | +  |
| 17  | Stylicletodes | + | +  | +  |
| 18  | Amphiascoides | + | +  | +  |
| 19  | Diosaccinae sp. 3 | + | +  | +  |
| 20  | Carolincola | + | +  | +  |
| 21  | Jonesiella | + | +  | +  |
| 22  | Paranannopus | + | +  | +  |
| 23  | Paramesochra | + | +  | +  |
| 24  | Pseudomesochra | + | +  | +  |
| 25  | Luophilodontes | + | +  | +  |
| 26  | Diosaccinae sp. 1 | + | +  | +  |
| 27  | Paramesochridae | + | +  | +  |
| 28  | Kliopsyllus | +  | +  | +  |
| 29  | Leptopsyllus | + | +  | +  |
| 30  | Paramesochra | + | +  | +  |
| 31  | Scottopsyllus | + | +  | +  |
| 32  | Dendropsyllus | +  | +  | +  |
| 33  | Argestidae sp. 8 | + | +  | +  |
| 34  | Diosaccinae sp. 2 | + | +  | +  |
| 35  | Diosaccinae sp. 6 | + | +  | +  |
| 36  | Paranannopinae sp. 1 | + | +  | +  |
| 37  | Argestidae sp. 7 | + | +  | +  |
| 38  | Argestidae sp. 4 | + | +  | +  |
| 39  | Argestidae sp. 5 | + | +  | +  |
| 40  | Argestidae sp. 6 | + | +  | +  |
| 41  | Diosaccinae sp. 4 | + | +  | +  |
| 42  | Diosaccinae sp. 5 | + | +  | +  |
| 43  | Paranannopinae sp. 2 | + | +  | +  |
| 44  | Argestidae sp. 7 | + | +  | +  |
| 45  | Diosaccinae sp. 7 | + | +  | +  |
| 46  | Diosaccinae sp. 8 | + | +  | +  |
| 47  | Schizopera | +  | +  | +  |
| 48  | Paranannopinae sp. 1 | + | +  | +  |
| 49  | Paranannopinae sp. 2 | + | +  | +  |
| 50  | Paranannopinae sp. 3 | + | +  | +  |
| 51  | Diantheriodella | + | +  | +  |
| 52  | Rossopsyllus | +  | +  | +  |
sochra and Scottopsyllus, the latter three confirming the general dominance of Paramesochridae in this area. The four mentioned taxa face a number of 23 remaining genera not reaching 20% of relative abundance.

Composition and diversity of harpacticoid species

Due to the high abundance, further analysis at species level was done on the representatives (= 1,916 adult specimens) of 6 selected taxa (Ancorabolidae Sars, 1909, Argestidae Por, 1986, Cletodidae sensu Por, 1986, Diosaccinae Sars, 1906, Paramesochridae Lang, 1944, Paranannopinae Por, 1986) (Table 2). They can be assigned to 122 different species, 103 of which (= 84.4%) must be considered as new to science (see Table 4 for species list). Recently, a few new species have been described (George, 1998; 2001; 2002; George and Schminke, 1998; 2003) (Fig. 4).

Specific composition indicates both similarities and differences between the geographic areas. A total number of six species (Cletodes sp. 2, Stylicle-todes longicaudatus (Brady and Robertson, 1880), Amphiascus sp. 1, Haloschizopera exigua (Sars, 1906), Stenhelia (D.) sp. 2, Typhlamphiascus sp.) was recorded in the whole investigation area, again meaning a decrease of common taxa compared with the results at family and genus level. In addition,
each geographical area shares some species with one of the remaining areas (Fig. 5). SM and BC show a relatively high number of species in common, whereas adjacent BC and PCS share only few species, falling even below the value shown by distant SM/PCS.

Apart from similarities between the geographical areas due to common species, all of them can be characterised by several exclusive species (Fig. 5), thus confirming the distinction between the areas already indicated at family and genus level. To underline the results obtained, quantitative similarity and diversity analyses were done.

**Similarity analysis**

The ordination plot (Fig. 6A) (cf. Fig. 6B for Shepard diagram) indicates a general mixing of the stations, independent of their geographical location. Most of the SM, BC, and PCS stations form a big group on the right side of the plot. Only two small distinct groups are discernible, one formed by 2 stations of the SM and one enclosing 3 BC stations (dotted circles in Fig. 6). Both groups match the geographic locality of the corresponding stations. The SM group is located in the northern Paso Ancho and encloses stations 954 and 956. Both stations are unique in presenting the species Diosaccinae sp. 2 (Table 4). Moreover, they differ from all remaining SM stations in the presence of Paramesochra sp. 1, a species collected also from station 40/110 (PCS).

The BC group is located in the eastern BC, comprising stations 1144, 1181, and 1234. They share Bulbamphiascus sp. 2 (although single specimens were also collected at two SM stations) (Table 4) and Paradanielssenia sp. 1 (although in common

**Additional Notes**

- **Fig. 5.** Numbers of harpacticoid species in common between the respective geographic areas (arrows with corresponding species (spp.) numbers). The graphic illustration shows the numbers of exclusive harpacticoid species reported from the respective geographical areas: WSA = Whole Study Area, SM = Straits of Magellan, BC = Beagle Channel, PCS = Patagonian Continental Slope.

- **Fig. 6.** A, Ordination plot resulting from the similarity matrix using Cosine Similarity. Ordination is two-dimensional (monotonic, non-parametric regression, Stress 0.12). White rhomboid dots: SM stations, white circles: BC stations, black squares: PCS stations. B, Shepard diagram of the nMDS.

- **Fig. 7.** Illustration of the compared species numbers ($S$), species richness ($H'$), and evenness ($E$) values at the three investigated geographic areas Straits of Magellan (SM), Beagle Channel (BC), and Patagonian Continental Slope (PCS).
Table 4. – List of harpacticoid species collected in the Magellan region (individual numbers at corresponding stations).

| No. | species/station | SM | BC | PCS |
|-----|-----------------|----|----|-----|
| 1   | Arthropyllus australis | 1  | 1  | 1   |
| 2   | Dendropsyllus magellanicus | 1  | 8  | 9   |
| 3   | Laophontodes sp.1 | 1  | 1  | 1   |
| 4   | Laophontodes typicus | 29 | 29 | 29  |
| 5   | Laophontodes whitsoni | 1  | 1  | 1   |
| 6   | Argestidae sp.1 | 1  | 1  | 1   |
| 7   | Argestidae sp.2 | 1  | 2  | 6   |
| 8   | Argestidae sp.3 | 2  | 7  | 1   |
| 9   | Argestidae sp.4 | 5  | 5  | 5   |
| 10  | Argestidae sp.5 | 3  | 3  | 3   |
| 11  | Argestidae sp.6 | 1  | 1  | 1   |
| 12  | Argestidae sp.7 | 2  | 2  | 2   |
| 13  | Argestidae sp.8 | 1  | 1  | 1   |
| 14  | Euryctelodes (O.) abyssi | 4  | 4  | 4   |
| 15  | Euryctelodes (O.) monardi | 2  | 2  | 2   |
| 16  | Euryctelodes (O.) oblongus | 1  | 1  | 1   |
| 17  | Euryctelodes (O.) sp.1 | 1  | 1  | 1   |
| 18  | Euryctelodes (O.) sp.2 | 1  | 1  | 1   |
| 19  | Euryctelodes (O.) sp.3 | 2  | 3  | 1   |
| 20  | Fultonia bougisi | 1  | 2  | 2   |
| 21  | Fultonia sarsi | 1  | 1  | 1   |
| 22  | Fultonia sp.1 | 1  | 1  | 1   |
| 23  | Fultonia sp.2 | 2  | 2  | 2   |
| 24  | Fultonia sp.3 | 2  | 4  | 2   |
| 25  | Fultonia sp.4 | 2  | 3  | 3   |
| 26  | Fultonia sp.5 | 2  | 2  | 2   |
| 27  | Mesocletodes abyssicola | 1  | 1  | 1   |
| 28  | Mesocletodes soyeri | 1  | 1  | 1   |
| 29  | Mesocletodes sp.1 | 10 | 10 | 10  |
| 30  | Mesocletodes sp.2 | 1  | 1  | 1   |
| 31  | AcenhydrOsoma sp.1 | 3  | 1  | 1   |
| 32  | Cletodes lairostris | 2  | 10 | 1   |
| 33  | Cletodes sp.1 | 5  | 2  | 8   |
| 34  | Cletodes sp.2 | 5  | 1  | 3   |
| 35  | Cletodes sp.3 | 1  | 1  | 1   |
| 36  | Cletodes sp.4 | 1  | 3  | 6   |
| 37  | Cletodes sp.5 | 4  | 4  | 4   |
| 38  | Cletodes sp.6 | 2  | 2  | 2   |
| 39  | Cletodes sp.7 | 1  | 1  | 1   |
| 40  | Enhydrosoma hopkinsi | 4  | 2  | 6   |
| 41  | Enhydrosoma litorale | 1  | 1  | 1   |
| 42  | Enhydrosoma sp.1 | 1  | 1  | 1   |
| 43  | Enhydrosoma sp.2 | 3  | 3  | 3   |
| 44  | Enhydrosoma sp.3 | 1  | 2  | 2   |
| 45  | Enhydrosoma sp.4 | 1  | 1  | 1   |
| 46  | Enhydrosoma sp.5 | 3  | 1  | 1   |
| 47  | Enhydrosoma sp.6 | 5  | 59 | 84  |
| 48  | Enhydrosoma sp.7 | 1  | 3  | 4   |
| 49  | Stylicletodes longicaudatus | 3  | 1  | 1   |
| 50  | Stylicletodes oligochoaeta | 1  | 1  | 1   |
| 51  | Diosaccinae sp.1 | 1  | 1  | 1   |
| 52  | Diosaccinae sp.2 | 9  | 17 | 26  |
| 53  | Diosaccinae sp.3 | 4  | 3  | 3   |
| 54  | Diosaccinae sp.4 | 1  | 1  | 1   |
| 55  | Diosaccinae sp.5 | 1  | 1  | 1   |
| 56  | Diosaccinae sp.6 | 4  | 4  | 4   |
| 57  | Diosaccinae sp.7 | 1  | 1  | 1   |
| 58  | Diosaccinae sp.8 | 1  | 1  | 1   |
| 59  | Amphiascoides subdebilis | 1  | 1  | 1   |
| 60  | Amphiascoides sp.1 | 1  | 1  | 1   |
| 61  | Amphiascus minutus | 1  | 1  | 1   |
| 62  | Amphiascus sp.1 | 1  | 1  | 1   |
| 63  | Bulbamphiascus sp.1 | 1  | 1  | 1   |
| 64  | Bulbamphiascus sp.2 | 1  | 1  | 1   |
| 65  | Haloschizopera abyssi | 7  | 27 | 20  |
| 66  | Haloschizopera exigua | 18 | 1  | 33 |
| 67  | Haloschizopera sp.1 | 6  | 6  | 6   |
| 68  | Paramphiascella sp.1 | 5  | 1  | 5   |
| 69  | Paramphiascella sp.2 | 3  | 3  | 3   |
| 70  | Robertgunneya sp.1 | 3  | 4  | 4   |
| 71  | Robertgunneya sp.2 | 3  | 3  | 3   |
with stations 977 and 1123), but in particular they are absolutely dominated by *Enhydrosoma* sp. 6. This species was collected in remarkably high individual numbers only from these three stations, reaching 84 specimens at station 1234 (Table 4).

### Diversity analysis

SM and BC, both characterised by $S = 70$, may show the same species number, which is nearly twice the PCS value ($S = 38$). This trend is generally confirmed by Shannon’s $H'$ and Pielou’s evenness $E$, which are considerably higher at SM and BC than at PCS (Fig. 7). The highest species richness was at SM, with higher $H'$ and $E$ values than at BC. To verify these results, a second diversity analysis was done, applying rarefaction to the three different areas. Comparison of the geographic areas revealed similar results to using diversity indices (Fig. 8A). SM and BC show a considerably higher species richness than PCS. However, in contrast with the results obtained from calculating the diversity

| No. | species/station | SM | BC | PCS |
|-----|----------------|----|----|-----|
| 72  | Schizopera sp.1 |    |    |     |
| 73  | *Stenhelia* (D.) sp.1 | 2 | 3 | 3 |
| 74  | *Stenhelia* (D.) sp.2 | 7 | 14 | 3 |
| 75  | *Stenhelia* (D.) sp.3 | 1 | 2 | 2 |
| 76  | *Stenhelia* (D.) sp.4 | 2 | 1 | 2 |
| 77  | *Stenhelia* (D.) sp.5 | 1 | 1 | 1 |
| 78  | *Stenhelia* (D.) sp.6 | 5 | 3 | 3 |
| 79  | *Stenhelia* (D.) sp.7 | 2 | 1 | 1 |
| 80  | *Stenhelia* (D.) sp.8 | 5 | 1 | 1 |
| 81  | *Stenhelia* (D.) sp.9 | 1 | 1 | 1 |
| 82  | *Stenhelia* (D.) sp.10 | 1 | 1 | 1 |
| 83  | *Stenhelia* (D.) sp.11 | 4 | 4 | 4 |
| 84  | *Stenhelia* (D.) sp.12 | 2 | 2 | 2 |
| 85  | *Stenhelia* (S.) sp.1 | 1 | 1 | 1 |
| 86  | *Typhlamphiascus* sp. | 3 | 5 | 107 |
| 87  | Paramesochridae sp.1 | 15 | 15 | 15 |
| 88  | Paramesochridae sp.2 | 1 | 1 | 1 |
| 89  | Diarthrodella sp. | 2 | 2 | 2 |
| 90  | Kliopsyllus sp.1 | 1 | 1 | 1 |
| 91  | Kliopsyllus sp.2 | 1 | 1 | 1 |
| 92  | Kliopsyllus sp.3 | 1 | 1 | 1 |
| 93  | Kliopsyllus sp.4 | 1 | 1 | 1 |
| 94  | Kliopsyllus sp.5 | 1 | 1 | 1 |
| 95  | Kliopsyllus sp.6 | 1 | 1 | 1 |
| 96  | Kliopsyllus sp.7 | 1 | 1 | 1 |
| 97  | Leptopsyllus sp.1 | 7 | 7 | 7 |
| 98  | Leptopsyllus sp.2 | 9 | 9 | 9 |
| 99  | Paramesochra sp.1 | 8 | 10 | 28 |
| 100 | Paramesochra sp.2 | 75 | 75 | 75 |
| 101 | Rossopsyllus sp. | 3 | 3 | 3 |
| 102 | Scutosyllis sp.1 | 73 | 73 | 73 |
| 103 | Scutosyllis sp.2 | 1 | 1 | 1 |
| 104 | Paranannopidae sp.1 | 1 | 1 | 1 |
| 105 | Paranannopidae sp.2 | 1 | 1 | 1 |
| 106 | Paranannopidae sp.3 | 1 | 1 | 1 |
| 107 | Carolincola sp.1 | 1 | 1 | 1 |
| 108 | Carolincola sp.2 | 3 | 3 | 3 |
| 109 | Jonesiella sp. | 1 | 1 | 1 |
| 110 | Paranannopsenina sp.1 | 1 | 1 | 1 |
| 111 | Paranannopsenina sp.2 | 1 | 1 | 1 |
| 112 | Paranannopus sp.1 | 6 | 5 | 11 |
| 113 | Paranannopus sp.2 | 1 | 1 | 1 |
| 114 | Paranannopus sp.3 | 1 | 1 | 1 |
| 115 | Paranannopus sp.4 | 1 | 1 | 1 |
| 116 | Psammis sp.1 | 1 | 1 | 1 |
| 117 | Psammis sp.2 | 1 | 1 | 1 |
| 118 | Pseudomesochra longifurcata | 2 | 2 | 2 |
| 119 | Pseudomesochra sp.1 | 3 | 1 | 3 |
| 120 | Pseudomesochra sp.2 | 1 | 1 | 1 |
| 121 | Pseudomesochra sp.3 | 1 | 1 | 1 |
| 122 | Pseudomesochra sp.4 | 4 | 4 | 4 |

Sum | 28 | 52 | 49 | 127 | 145 | 107 | 26 | 72 | 18 | 35 | 80 | 30 | 76 | 87 | 123 | 155 | 582 | 18 | 79 | 1916
indices, rarefaction indicates a tendency of slightly higher species richness at BC than in SM. Due to this deviation, a second analysis was done, comparing all single stations. This analysis reveals a remarkable small-scale variability even between stations within the same geographic area (Fig. 8B), which may conceal probable large-scale influences.

DISCUSSION

The Magellan region is generally characterised by a high variability in topographic, sedimentological, hydrographical, oceanographic and climatological conditions (e.g. Brattstrom and Johansen, 1983; Artegiani et al., 1991, Brambati et al., 1991, Antezana et al., 1996, Klöser, 1996). Therefore, the question arose whether the three geographically, topographically, and hydrographically distinct areas SM, BC and PCS might show differences also with respect to their inhabiting sublittoral and bathyal harpacticoid fauna. This question becomes particularly important for future comparisons with corresponding harpacticoid assemblages of Antarctica. Against the background of a supposed high affinity between the Antarctic and the South American (i.e. Magellan) fauna, it is of importance to know whether the Magellan region is characterised by geographically separated, clearly distinct faunas which may prohibit the consideration of the region as a whole for interregional faunistic comparisons, as has been done for macrofauna. The results obtained in this study indicate a remarkable variety of the Magellan region with respect to species composition and species diversity. Instead of being clearly distinct, the three studied areas show a considerable overlap of taxa composition and diversity, as shown by MDS and rarefaction. However, this overlap is due not to homogeneous but to heterogeneous distribution of taxa. This leads to the conclusion that for future comparisons with Antarctic harpacticoid associations, the MR should be considered as a whole.

The results presented here reveal an impressive harpacticoid diversity within the Magellan region. Wells (1986) presumed that at family level, Harpacticoida would show a world-wide distribution. For the Magellan region, his assumption was already confirmed by George and Schminke (1999), who presented a list of 19 families. However, it must be pointed out that the authors included Cerviniidae (George and Schminke, 1999, p. 135, Table 2), a taxon that was ignored in this contribution because it was represented exclusively by juveniles, which were not taken into account in the analyses.

The record of several specimens of Supernatiremidae Huys, 1996 was somewhat surprising. They are considered as being restricted to anchialine caves and showing an amphi-Atlantic/Mediterranean distribution (Huys, 1996). The specimens collected at station 40/110 (PCS) extend both the distribution and habitat preference considerably. All specimens belong to the same new species (George and Martínez Arbizu, in press).

In the past, several investigations concluded that for faunistic investigations it was sufficient to deal with taxa at higher taxonomic levels such as genera or even families (e.g. Hartmann, 1982, 1986; Heip et al., 1988; Ray, 1992; Lambshead, 1993). The results of the qualitative comparison of the geographic areas SM, BC and PCS contradict this assumption. For example, families and genera show

![Rarefaction curves](image)
a much wider distribution than the species they enclose, clearly demonstrating the fact that families and even genera are united groups of different species with quite different ecological claims. Whereas a family (e.g. Ancorabolidae) may be distributed within the whole Magellan region, the corresponding species (e.g. Breviconia, Dendropsyllus) may be restricted to small areas. Therefore, although community analyses at higher taxonomic level may allow more taxa to be considered (here: all Harpacticoidea), they undoubtedly generalise and bias real distribution patterns or community structure instead of describing almost real patterns. At family level, the geographical areas SM, BC and PCS show a relatively high degree of similarity (~40%), which decreases at generic level (~17%) and reaches at most ~5% at species level. Therefore, it is advisable to select the species level for community analyses, even if this involves a restriction of the taxa dealt with.

The remarkably high number of 122 species reported from the six investigated harpacticoid families confirms the conclusion of Wells (1986) that the apparent poverty in species of the southern hemisphere reflects a lack of investigations rather than real species numbers. The report of 103 scientifically new species from the Magellan region means an increase of nearly 30% for the whole Southern Hemisphere compared with Wells’ (1986) data. This points to the urgent need for further investigations in this region.

The qualitative comparisons allow three areas to be distinguished, each of which is characterised by exclusively collected species. It is surprising that BC and PCS show such little similarity in both species composition and species diversity. One would expect these areas especially to be more similar, due to a supposed continuous organism input into PCS from BC caused by predominating eastward currents. However, apart from some taxa showing a distribution in the whole study area, BC and PCS have no taxa in common, even at generic level. Still, as shown by quantitative analysis, a characterisation based only on presence and absence of species would be too superficial. Firstly, it is obvious that the non-registration of a species in an area may be an artefact of sampling; it does not necessarily reflect the distribution of the species. Secondly, the species composition of each area is quite complex, leading to similarities and differences between them. This complexity may already be indicated by the qualitative analysis, which apart from differences also revealed certain similarities between areas, due to species in common. The MDS approaches the actual conditions best. Just two small areas, one in the northern SM and one in the eastern BC, seem to be characterised by specific harpacticoid assemblages. The remaining study area shows a remarkable variety, with neither clear differences nor great similarities between the geographical areas SM, BC and PCS. On the other hand, stations of different areas often show greater similarity than stations of the same area. The same applies to the results of the diversity analysis. The results of rarefaction are favoured here because of its better “response” to smaller samples, paired with several general disadvantages of diversity indices (Hurlbert 1971, Achtziger et al. 1992). However, both methods applied to the geographical areas show that SM and BC have nearly the same species richness. The difference between the results of calculating $H'$ and $E$, which estimated SM to be richer than BC, and rarefaction, which shows the opposite, may be neglected because of the relatively small database on which they are based. However, the results presented in Fig. 8B show clearly that, as in the similarity analysis, the study area also shows a considerable variety with respect to species richness, thus making it impossible to distinguish the three geographical areas SM, BC and PCS. In summary, it is concluded that both similarity and diversity analysis point towards a considerable influence of small-scale biotic and abiotic variables, leading to a high local variability in harpacticoid communities of the Magellan region.

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