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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
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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 batial 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 harpacticoideos para verificar si estas diferentes áreas geográficas también se distinguen con respecto a la fauna harpacticoidea. A nivel supra-específico, se determinaron 25 familias diferentes, más varias especies desconocidas que no pudieron ser asignadas a ningún taxon harpacticoideo. Debido al gran número de harpacticoideos 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, focussing 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-

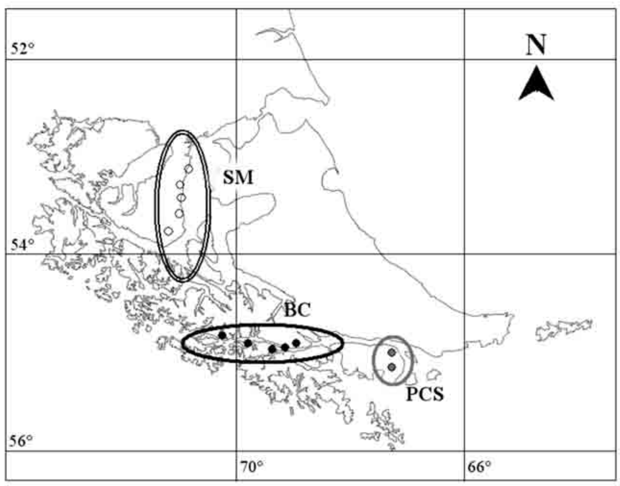

FIG. 1. – Map of Tierra del Fuego, showing the three geographic areas Straits of Magellan (SM), Beagle Channel (BC) and Patagonian Continental Slope (PCS), as well as the respective sampling localities. For station numbers and their geographical position, see Table 1.

TABLE 1. – Station list including sedimentological data: Granulometric data after Chen *et al.* (1999). “Median” describing median grain size (μm).

Geogr. area	Station	Locality	Depth (m)	Sand (%)	Silt (%)	Clay (%)	Median
	840	53°08.8’S/70°38.4’W	123	22.3	59.43	18.27	28.52
	847	53°21.2’S/70°42.7’W	200	50.99	39.85	9.16	65.4
	864	53°42.6’S/70°48.7’W	550	20.15	57.86	21.99	17.19
	866	53°51.8’S/70°54.6’W	440	11.87	65.17	22.96	12.97
SM	872	53°43.4’S/70°56.0’W	351	23.87	52.55	23.58	17.3
	877	53°41.5’S/70°56.5’W	227	-	-	-	-
	954	53°59.7’S/70°33.0’W	79	4.98	37.3	57.72	2.742
	956	53°59.9’S/70°32.9’W	80	0	33.88	66.12	2.082
	977	53°33.0’S/70°39.2’W	459	2.02	67.78	30.2	8.649
	1033	54°52.7’S/69°55.2’W	309	1.04	72.29	26.67	8.001
	1076	54°53.6’S/69°30.3’W	346	7.2	75.04	17.76	15.12
	1123	54°58.7’S/68°49.9’W	219	8.02	67.65	24.33	11.18
BC	1135	54°58.1’S/68°49.9’W	257	0	67.53	32.47	7.02
	1138	54°54.5’S/68°38.7’W	320	6.56	71.83	21.61	11.01
	1144	55°08.4’S/66°54.5’W	110	0	66.23	33.77	7.535
	1181	55°07.0’S/66°55.4’W	110	0	58.89	41.11	5.295
	1234	55°00.4’S/66°53.6’W	100	0	70.16	29.84	8.891
	40/110	55°26.4’S/66°14.0’W	101	-	-	-	-
PCS	40/111	55°29.0’S/66°04.4’W	1168	-	-	-	-
	40/116	55°27.8’S/66°09.1’W	336	-	-	-	-

ples 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 Harpacticoida, 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, Paramesochridae 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):

$$\cos(ob_x, ob_y) = \frac{\sum_{k=1}^{N} x_k y_k}{\sqrt{\sum_{k=1}^{N} x_k^2}\sqrt{\sum_{k=1}^{N} y_k^2}} = \cos(\vec{x}, \vec{y})$$

where ob_x and ob_y are considered as n-dimensional vectors $\vec{x} = [x_1,...x_k,...x_N]^T$ as well as $\vec{y} = [y_1,...y_k,...y_N]^T$. Consequently, the Cosine Similarity then corresponds to *cos* α between vectors $\vec{x}$ and $\vec{y}$ 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 Harpacticoida at family level

With 91.9%, Harpacticoida 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

TABLE 2. – List of Harpacticoida collected in the Magellan region, sorted per station and supraspecific taxon. Family names written in capitals indicate selected families for investigations at species level.

	MS									BC								PCS				Presence/abcense		
Station	840	847	864	866	872	877	954	956	977	1033	1076	1123	1135	1138	1144	1181	1234	40110	40111	40116	Sum	MS	BC	PCS
Ameiridae	11	17	6	6	26	17	19	12	21	1	21	4	4	20	38	57	159	511	29	21	1000	+	+	+
ANCORABOLIDAE		2				8											1	30			41	+	+	+
ARGESTIDAE	4	2	1	6	8	3			28	3	19	15	4	36	1	8	5	2		2	147	+	+	+
"Canthocamptidae"		2		5	6	10						1		2	53	43	3	28	5	2	160	+	+	+
CLETODIDAE	14	4	12	22	19	22					1	34	13	9	66	83	102		2		403	+	+	+
DIOSACCINAE	9	33	24	74	109	59	10	17	31	4	15	25	11	28	12	14	17	212	15	48	767	+	+	+
Ectinosomatidae	14	41	43	78	84	121	8	8	65	16	6	63	24	87	169	157	365	207	56	26	1638	+	+	+
PARANANNOPINAE	1	10	12	23	9	15			12	11		6	2	3	8	18	30	1	1		162	+	+	+
Thalestridae		1	4			17	1		15	2		2	2	1	13	7		48	5		118	+	+	+
Tisbidae	1			9	27	4			15	12	25	12	5	7	4	10	4	14		6	155	+	+	+
(remaining specimens	8									12		14	15		12	12	23	24	3	2	125)			
Cerviniidae		3		4	6	2			6		11			43							75	+	+	
Normanellidae				5	11	12						2	5								35	+	+	
Huntemanniidae		1								3											4	+	+	
Cristacoxidae							1											1			2	+		+
Leptastacidae							47	20										19			86	+		+
PARAMESOCHRIDAE		1		2			16	10	1									337		29	396	+		+
Laophontidae												1					1	59	1		62		+	+
Tetragonicipitidae															5	2	24	1			32		+	+
Harpacticidae							1														1	+		
Adenopleurellidae	1			2		5			1												9	+		
Leptopontiinae																		36			36			+
Neobradyidae																			1		1			+
Peltidiidae																		1	1	1	3			+
Superornatiremidae																		29	1		30			+
Tegastidae																		5			5			+
Sum	63	117	102	236	305	295	103	67	195	64	98	179	85	236	381	411	734	1565	120	137	5493			

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 Paramesochridae. 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%. BC shows different dominance patterns. Although this area is also clearly dominated by Ectinosomatidae (42.2%), Diosaccinae (6.0%) play a secondary role only, while Cletodidae (14.7%) and Ameiridae (14.5%) show a higher relative abundance. Moreover, 11 additional families were recorded from this area, reaching 23% of relative abundance. PCS differs from both geographic areas in having Ameiridae (31.4%) as the dominating taxon, followed by a more interstitial group, the Paramesochridae (20.4%). Ectinosomatidae play only a minor role, not reaching 17%.

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

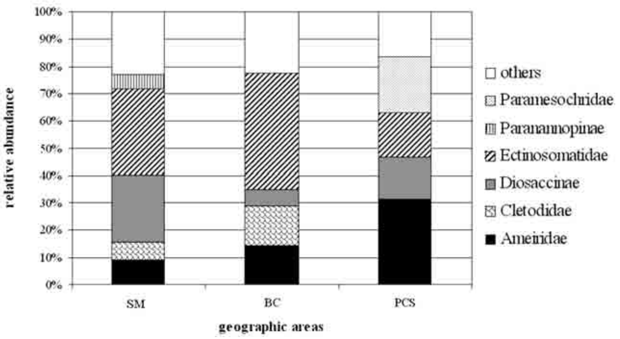

FIG. 2. – Harpacticoid composition of SM, BC and PCS. The relative abundance (%) of the dominating taxa Ameiridae, Cletodidae, Diosaccinae, Ectinosomatidae, Paranannopinae, and Paramesochridae is presented. The remaining families collected at SM (13), BC (11) and PCS (19) are summarised as "others".

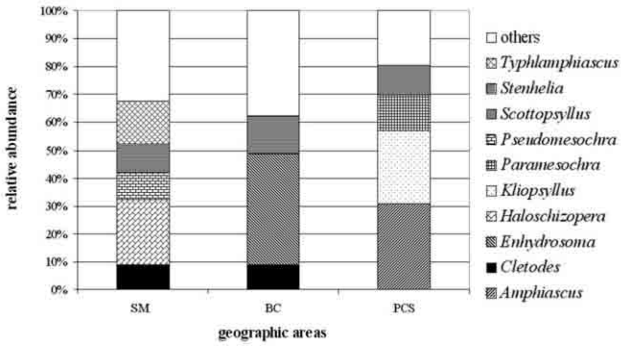

FIG. 3. – Harpacticoid composition of the SM, BC and PCS. The relative abundance (%) of the dominating taxa *Amphiascus*, *Cletodes*, *Enhydrosoma*, *Haloschizopera*, *Kliopsyllus*, *Paramesochra*, *Pseudomesochra*, *Scottopsyllus*, *Stenhelia,* and *Typhlamphiascus* is presented. The remaining genera collected at SM (31), BC (28) and PCS (23) are summarised as "others".

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*, *Parame-*

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

No.	Genus/area	SM	BC	PCS	No.	Genus/area	SM	BC	PCS
1	*Fultonia*	+	+	+	**25**	*Laophontodes*	+		+
2	*Cletodes*	+	+	+	**26**	Diosaccinae sp. 1	+		+
3	*Amphiascus*	+	+	+	**27**	*Paramphiascella*	+		+
4	*Bulbamphiascus*	+	+	+	**28**	*Kliopsyllus*	+		+
5	*Haloschizopera*	+	+	+	**29**	*Leptopsyllus*	+		+
6	*Robertgurneya*	+	+	+	**30**	*Paramesochra*	+		+
7	*Stenhelia*	+	+	+	**31**	*Scottopsyllus*	+		+
8	*Typhlamphiascus*	+	+	+	**32**	*Dendropsyllus*	+		
9	*Paradanielssenia*	+	+	+	**33**	Argestidae sp. 8	+		
10	Argestidae sp. 1	+	+		**34**	Diosaccinae sp. 2	+		
11	Argestidae sp. 2	+	+		**35**	Diosaccinae sp. 6	+		
12	Argestidae sp. 3	+	+		**36**	Paranannopinae sp. 1	+		
13	*Eurycletodes (O.)*	+	+		**37**	*Arthropsyllus*		+	
14	*Mesocletodes*	+	+		**38**	Argestidae sp. 4		+	
15	*Acrenhydrosoma*	+	+		**39**	Argestidae sp. 5		+	
16	*Enhydrosoma*	+	+		**40**	Argestidae sp. 6		+	
17	*Stylicletodes*	+	+		**41**	Diosaccinae sp. 4		+	
18	*Amphiascoides*	+	+		**42**	Diosaccinae sp. 5		+	
19	Diosaccinae sp. 3	+	+		**43**	Paranannopinae sp. 2		+	
20	*Carolinicola*	+	+		**44**	Argestidae sp. 7			+
21	*Jonesiella*	+	+		**45**	Diosaccinae sp. 7			+
22	*Paranannopus*	+	+		**46**	Diosaccinae sp. 8			+
23	*Psammis*	+	+		**47**	*Schizopera*			+
24	*Pseudomesochra*	+	+		**48**	Paramesochridae sp. 1			+
					49	Paramesochridae sp. 2			+
					50	Paranannopinae sp. 3			+
					51	*Diarthrodella*			+
					52	*Rossopsyllus*			+

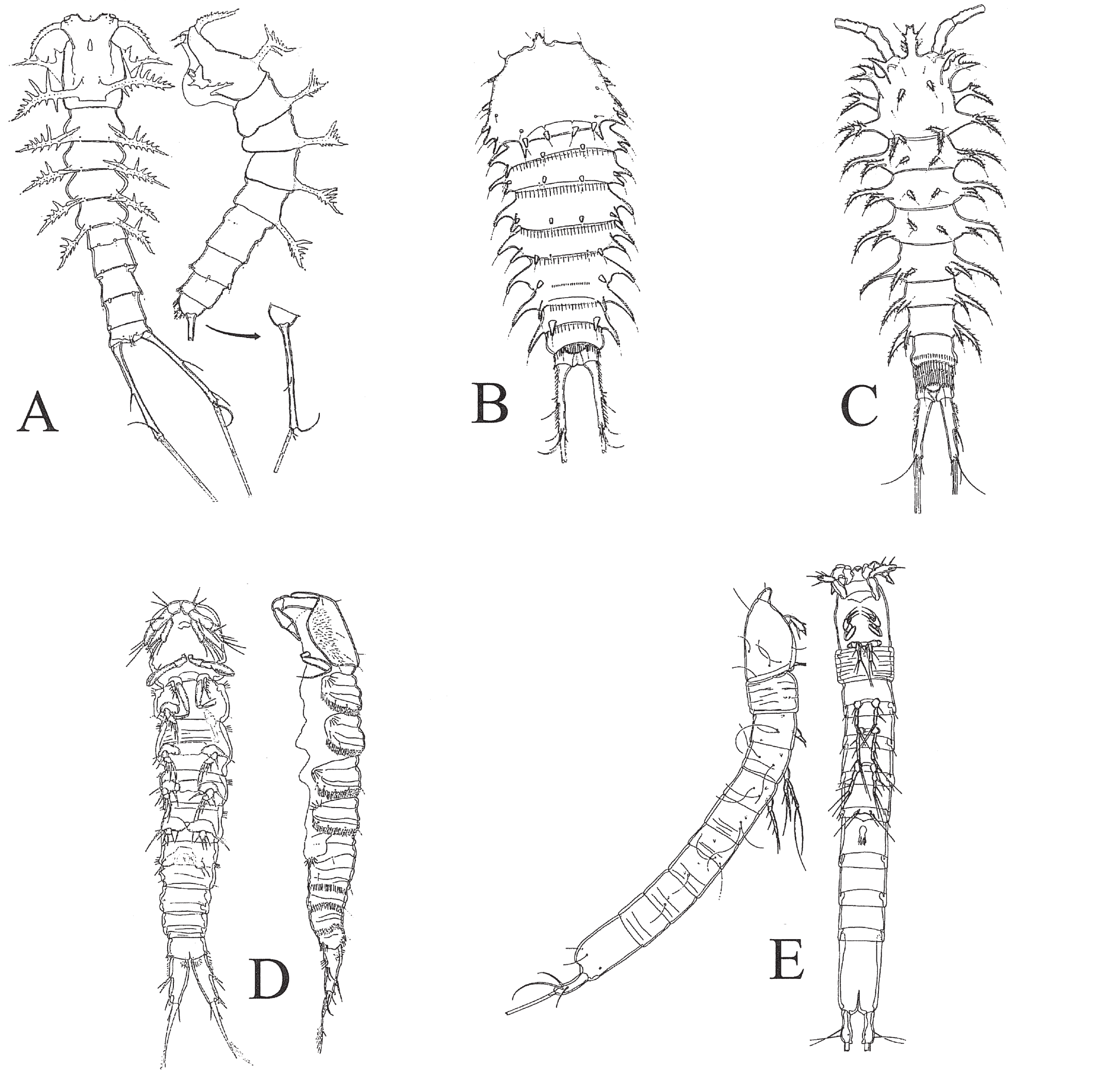

FIG. 4. – Some Harpacticoida of the Magellan region, A. *Dendropsyllus magellanicus* (Ancorabolidae Sars, 1909), B. *Breviconia australis* (Ancorabolidae), C. *Ancorabolus ilvae* (Ancorabolidae), D. *Laophontisochra maryamae* (Cristacoxidae Huys, 1990), E. *Isthmiocaris longitelson* (Canthocamptidae Sars, 1906). A after George and Schminke 1998, B after George 1998, C after George 2001, D after George 2002, E after George and Schminke 2003.

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, *Stylicletodes longicautdatus* (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,

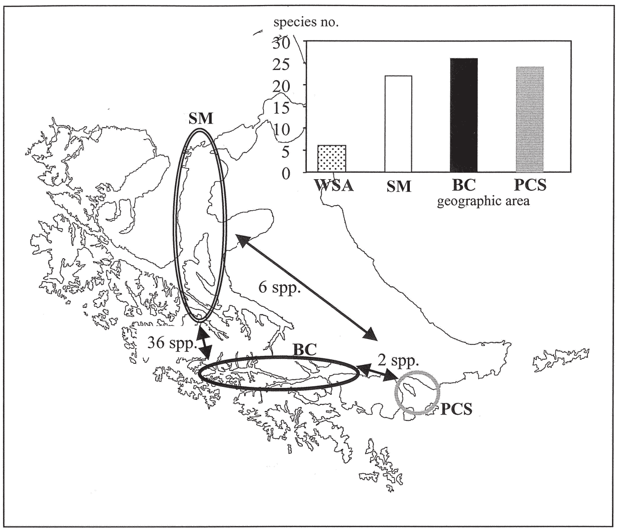

FIG. 5. – Numbers of harpacticoid species in common between the respective geographic areas (arrows with corresponding species (spp.) numbers). The graphic illustration shows the numbers of exclusive harpacticoid species reported from the respective geographical areas: WSA = Whole Study Area, SM = Straits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

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).

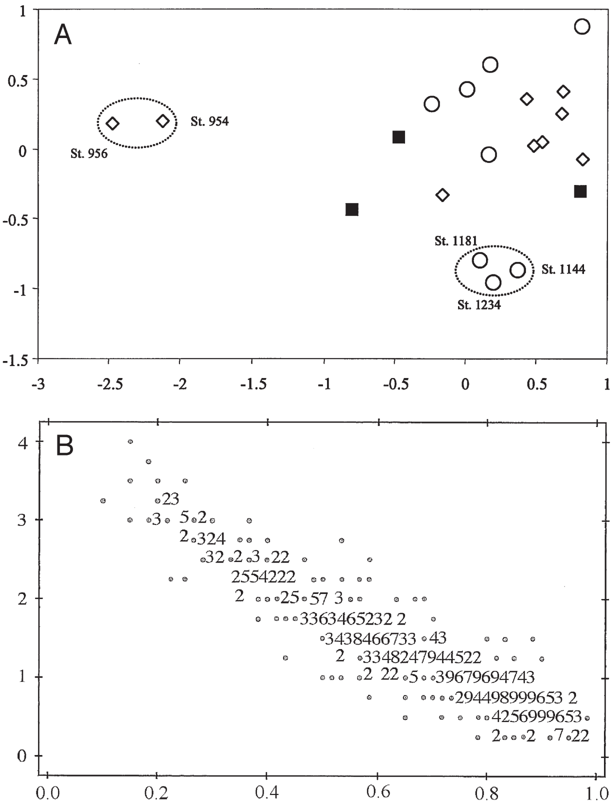

FIG. 6. – A, Ordination plot resulting from the similarity matrix using Cosine Similarity. Ordination is two-dimensional (monotonous, non-parametric regression, Stress 0,12). White rhomboid dots: SM stations, white circles: BC stations, black squares: PCS stations. B, Shepard diagram of the nMDS.

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

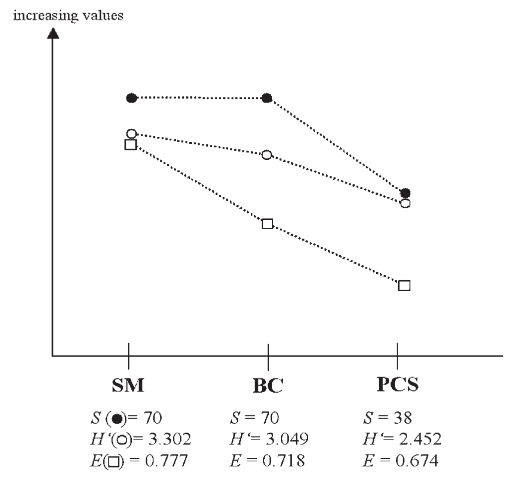

FIG. 7. – Illustration of the compared species numbers (S), species richness (H'), and evenness (E) values at the three investigated geographic areas Straits of Magellan (SM), Beagle Channel (BC), and Patagonian Continental Slope (PCS).

TABLE 4. – List of harpacticoid species collected in the Magellan region (individual numbers at corresponding stations).

					SM							BC						PCS		
No.	species\station	840	847	864	866	872	877	954	956	977	1033	1076	1123	1135	1138	1144	1181	1234	40110	40111	40116	Sum
1	*Arthropsyllus australis*																	1				1
2	*Dendropsyllus magellanicus*		1																			1
3	*Laophontodes* sp.1		1				8															9
4	*Laophontodes typicus*																		29			29
5	*Laophontodes whitsoni*																		1			1
6	Argestidae sp.1	1	1		1										1							4
7	Argestidae sp.2				1	1				2					6		5					15
8	Argestidae sp.3					2				7					1							10
9	Argestidae sp.4											5										5
10	Argestidae sp.5														3							3
11	Argestidae sp.6											1			1							2
12	Argestidae sp.7																				2	2
13	Argestidae sp.8			1																		1
14	*Eurycletodes (O.) abyssi*																	5				5
15	*Eurycletodes (O.) monardi*												4									4
16	*Eurycletodes (O.) oblongus*		1				2						4									7
17	*Eurycletodes (O.)* sp.1	1			1	1				9					3	1	3					18
18	*Eurycletodes (O.)* sp.2												1									1
19	*Eurycletodes (O.)* sp.3					2							3	1								6
20	*Fultonia bougisi*												1						2			3
21	*Fultonia sarsi*						1						1									2
22	*Fultonia* sp.1	1																				1
23	*Fultonia* sp.2	1													2							3
24	*Fultonia* sp.3				2					4					9							15
25	*Fultonia* sp.4										3											3
26	*Fultonia* sp.5											2										2
27	*Mesocletodes abyssicola*				1	1				4												6
28	*Mesocletodes soyeri*												1	1								2
29	*Mesocletodes* sp.1											10		1	3							14
30	*Mesocletodes* sp.2					1				2		1		1	7							12
31	*Acrenhydrosoma* sp.1			3	1									1	1			2				8
32	*Cletodes latirostris*				2	10	1															13
33	*Cletodes* sp.1	5	1	2	8		6						2									24
34	*Cletodes* sp.2	5		1	3	3	8					1	10	1			21	4		1		58
35	*Cletodes* sp.3						1															1
36	*Cletodes* sp.4						1							3	6							10
37	*Cletodes* sp.5												4									4
38	*Cletodes* sp.6												2									2
39	*Cletodes* sp.7													1								1
40	*Enhydrosoma hopkinsi*				4													2				6
41	*Enhydrosoma littorale*																	1				1
42	*Enhydrosoma* sp.1	1	1										1	5								8
43	*Enhydrosoma* sp.2			3		3	1															7
44	*Enhydrosoma* sp.3												2					2				4
45	*Enhydrosoma* sp.4					1							5	1		1						8
46	*Enhydrosoma* sp.5			3	3									1	1		2	4				14
47	*Enhydrosoma* sp.6															65	59	84				208
48	*Enhydrosoma* sp.7																1	3				4
49	*Stylicletodes longicaudatus*	3	1			1	3						7		1					1		17
50	*Stylicletodes oligochaeta*		1		1	1	1						1									5
51	Diosaccinae sp.1		1																1			2
52	Diosaccinae sp.2							9	17													26
53	Diosaccinae sp.3	4					3						1									8
54	Diosaccinae sp.4												1									1
55	Diosaccinae sp.5												1									1
56	Diosaccinae sp.6				4																	4
57	Diosaccinae sp.7																		1			1
58	Diosaccinae sp.8																		1			1
59	*Amphiascoides subdebilis*	1																		1		2
60	*Amphiascoides* sp.1														1							1
61	*Amphiascus minutus*																		4		1	5
62	*Amphiascus* sp.1	1										1	1			1			192		13	209
63	*Bulbamphiascus* sp.1							1												4		5
64	*Bulbamphiascus* sp.2			1		1										1	13	2				18
65	*Haloschizopera abyssi*			7	27	20																54
66	*Haloschizopera exigua*		18	1	33	20	21			1			6		1	4		2			22	129
67	*Haloschizopera* sp.1																				10	10
68	*Paramphiascella* sp.1					5	1												5			11
69	*Paramphiascella* sp.2					3																3
70	*Robertgurneya* sp.1	3																1				4
71	*Robertgurneya* sp.2																		3			3

TABLE 4 (Cont.). – List of harpacticoid species collected in the Magellan region (individual numbers at corresponding stations).

No.	species\station	SM 840	SM 847	SM 864	SM 866	SM 872	SM 877	SM 954	SM 956	SM 977	BC 1033	BC 1076	BC 1123	BC 1135	BC 1138	BC 1144	BC 1181	BC 1234	PCS 40110	PCS 40111	PCS 40116	Sum
72	*Schizopera* sp.1																		5	1		6
73	*Stenhelia (D.)* sp.1		2													1						3
74	*Stenhelia (D.)* sp.2		7	3	1	3	2			2		14	13		6	3				2		56
75	*Stenhelia (D.)* sp.3			1	4	8	3			4					2							22
76	*Stenhelia (D.)* sp.4						2							1	2							5
77	*Stenhelia (D.)* sp.5						1															1
78	*Stenhelia (D.)* sp.6			5		6				2				4	14							31
79	*Stenhelia (D.)* sp.7													3	2							5
80	*Stenhelia (D.)* sp.8			2			1															3
81	*Stenhelia (D.)* sp.9				5									1			1	12				19
82	*Stenhelia (D.)* sp.10																			1		1
83	*Stenhelia (D.)* sp.11																			4		4
84	*Stenhelia (D.)* sp.12																			2		2
85	*Stenhelia (St.)* sp.1															1						1
86	*Typhlamphiascus* sp.		3	4		43	25			22	4		2	2							2	107
87	Paramesochridae sp.1																		15			15
88	Paramesochridae sp.2																		1			1
89	*Diarthrodella* sp.																		2			2
90	*Kliopsyllus* sp.1		1																15		1	17
91	*Kliopsyllus* sp.2							1														1
92	*Kliopsyllus* sp.3																		37		13	50
93	*Kliopsyllus* sp.4																		95			95
94	*Kliopsyllus* sp.5				2																	2
95	*Kliopsyllus* sp.6																				6	6
96	*Kliopsyllus* sp.7																		2		9	11
97	*Leptopsyllus* sp.1							7														7
98	*Leptopsyllus* sp.2																		9			9
99	*Paramesochra* sp.1							8	10										10			28
100	*Paramesochra* sp.2																		75			75
101	*Rossopsyllus* sp.																		3			3
102	*Scottopsyllus* sp.1																		73			73
103	*Scottopsyllus* sp.2									1												1
104	Paranannopidae sp.1				1																	1
105	Paranannopidae sp.2														1							1
106	Paranannopidae sp.3																		1			1
107	*Carolinicola* sp.1						1				2											3
108	*Carolinicola* sp.2										3											3
109	*Jonesiella* sp.	1					3			1					1		5	19				30
110	*Paradanielssenia* sp.1									1			1			4	7	9				22
111	*Paradanielssenia* sp.2										1									1		2
112	*Paranannopus* sp.1		6								5											11
113	*Paranannopus* sp.2		1																			1
114	*Paranannopus* sp.3		1											1								2
115	*Paranannopus* sp.4		1			1	2						1									5
116	*Psammis* sp.1				1									1		3		2				7
117	*Psammis* sp.2				1										1	2	6					10
118	*Pseudomesochra longifurcata*												2									2
119	*Pseudomesochra* sp.1		3		1		3						1									8
120	*Pseudomesochra* sp.2					3				1			1									5
121	*Pseudomesochra* sp.3			12	19	5	2			9												47
122	*Pseudomesochra* sp.4						4															4
	Sum	28	52	49	127	145	107	26	27	72	18	35	80	30	76	87	123	155	582	18	79	1916

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

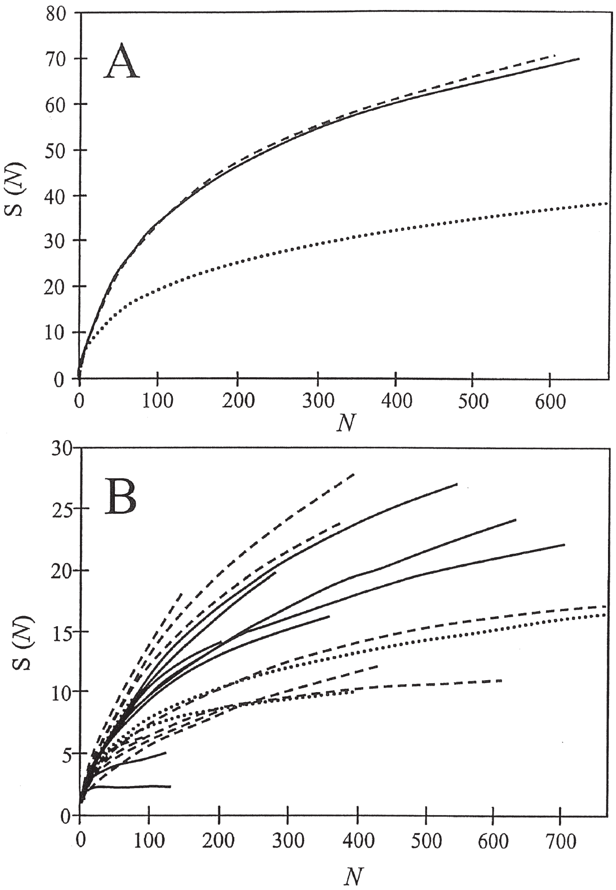

FIG. 8. – Rarefaction curves A. of the three geographic areas Straits of Magellan (SM; black line), Beagle Channel (BC; dark grey line), and Patagonian Continental Slope (PCS; light grey line). *S(N)* = number of estimated species, with *N* = individual numbers, B. of all single stations of the investigated region (SM=black lines, BC=dark grey lines, PCS=light grey lines). *S(N)* = number of estimated species, with *N* = individual numbers.

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. Brattstrøm and Johanssen, 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 Superornatiremidae 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 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 Harpacticoida), 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 inolves 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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