

# Polychaete assemblages on the Magellan and Weddell Sea shelves: comparative ecological evaluation

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**ABSTRACT:** Similarities between the soft-bottom polychaete assemblages on either side of the Drake Passage and spatial patterns of these assemblages were analysed based on data from 273 corer samples collected in the Magellan region (42 to 55° S, 254 m mean water depth) and on the Weddell Sea shelf (70 to 71° S, 263 m mean water depth). Paraonidae, Ampharetidae and Maldanidae were the most abundant families in the Magellan region, while in the Weddell Sea, Syllidae, Terebellidae and Spionidae were most abundant. The total species number found in the Magellan region (199) was higher than in the Weddell Sea (163), and significantly higher values of heterogeneity diversity, species richness and density were found in the Weddell Sea. At most of the Weddell Sea stations, all 3 trophic guilds (suspension feeders, detritus feeders and predators) were present, whereas suspension feeders were almost absent in the Magellan samples. The species abundance distribution showed a high number of species represented by only 1 specimen in both regions. This causes low dominance and similar high values of evenness in both regions. We suggest that the polychaete assemblage structures in both regions are influenced by environmental stress through ice and the physical complexity of the areas, which results in many different habitats.

**KEY WORDS:** Polychaetes · Species composition · Diversity · Geographic distribution · Trophic guilds · Magellan region · Weddell Sea

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## INTRODUCTION

Soft bottoms are the most common habitats in the world's ocean (Wilson 1991, Snelgrove 1998). Traditionally, the understanding of community patterns in this kind of habitat has been an important task of marine ecology (Gray 2002). Many studies over the last 30 yr have compared community attributes along depth (Sanders 1968, Rex et al. 1993, Gray 1994, Cosson-Sarradin et al. 1998) or latitudinal gradients (Ellingsen 2001, Clarke & Johnston 2003, Valdovinos et al. 2003). Recently, scientific interest has also concentrated on zoogeography and diversity patterns (Gaston 1996, Foggo et al. 2003, Barnes & Brockington 2003) along these gradients.

In the northern hemisphere, Petersen (1913) and Thorson (1957), pioneers in marine benthic ecology, compared patterns in shelf communities and showed that assemblages in different areas are seldom similar even when bottom type conditions are identical (Rosenberg 2001). In the southern hemisphere, Arntz & Ríos (1999) summarised studies of different authors comparing the Magellan versus the Weddell Sea shelves, with special focus on ecological and evolutionary relations by describing distinct differences in species composition and community structure between these ecosystems. For example, a quantitative study in shallow waters performed in the northernmost part of the Magellan region yielded 38 species belonging to 24 families, with Nereidae and Orbiniidae being the

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most speciose families (Cañete et al. 1999). Gambi & Mariani (1999) archived 119 polychaete species belonging to 34 families from the Straits of Magellan, and identified Syllidae and Ampharetidae as the most speciose families. In both studies, more than 50% of the species were common to the Magellan and Antarctic areas. The latter report suggests that no major differences between polychaete assemblages on either side of the Drake Passage exist. However, the reliability of species identification for polychaete assemblages and their quantitative attributes requires improvement.

The aims of the present study are (1) to provide a detailed description of shelf polychaete assemblages in the Magellan region and the high Antarctic Weddell Sea based on quantitative samples, and (2) to use biodiversity and density values to elucidate potential faunistic and zoogeographical links of the polychaete assemblages between the Magellan and the Antarctic Weddell Sea shelves.

## MATERIALS AND METHODS

**Study areas.** The biogeographic Magellan region sensu Camus (2001) extends from about 42 to 55° S on the western coastal shelf of South America (Strub et al. 1998). The shelf has a mean width of 6.54 km (Gallardo 1984), whereas the Atlantic shelf extends to a width of about 850 km at 51° S (Piccolo 1998). Successive glaciation periods have structured the west coast with more than 200 fjords and channels (Syvitski et al. 1987), with water depths frequently less than 150 m, and maximum depths of around 1050 m. Sediments are mostly characterised by silt and clay, but coarser sediments such as pebbles and biogenic deposits from molluscs and barnacles are also present (Brambati et al. 1991). Three permanent ice fields exist: Campo de Hielo Norte (46 to 47° S), Campo de Hielo Sur (48 to 52° S) and the Darwin mountain range (54 to 55° S, Naruse & Aniya 1992). The hydrographic regime is characterised by strong freshwater input due to high precipitation and concomitant runoff, producing a strong and shallow pycnocline (Dávila et al. 2002).

A mosaic of diverse soft-bottom habitats exists in the Magellan region (Arntz 1999). Taxa such as ascidians, brittle stars, decapods and brachiopods dominate the megafauna (Gutt et al. 1999), whereas polychaetes, amphipods and bivalves contribute considerably to the macrofauna (Gerdes & Montiel 1999, Montiel et al. 2001).

The Weddell Sea stations are located on the SE shelf (71° S, 10° W; 71° S, 12° W). Due to the continent's ice cover, the shelf's depth is down to 800 m (Teixidó et al. 2002). The Weddell Sea shelf has a width range of

between 10 and 40 km, although a maximum of 90 km can be observed (Camarck & Foster 1975). Near-bottom water temperatures are rather constant with values between -1.7 and -1.9°C, apart from common but unpredictable 'Warm Deep Water' intrusions, which may occasionally increase temperatures to 0.5°C (Gerdes et al. 1992). The sediment is dominated by sand, gravel and biogenic substrates (sponge and bryozoan debris), with numerous drop stones in between being transported by the continental ice sheet.

During winter, the sea ice covers a maximum of almost  $20 \times 10^6$  km<sup>2</sup> of the Antarctic Ocean. In austral summer, the coverage is reduced to less than  $4 \times 10^6$  km<sup>2</sup> (Eicken 1992). Along the SE Weddell Sea shelf, icebergs originating from the shelf ice often run aground and affect benthos communities down to about 300 m water depth. Due to this disturbance, the community structure of the Weddell Sea shelf benthos is the result of a combination of a rather constant temperature regime and considerable disturbance mainly by icebergs, all with implications for the function and structure of benthic communities (Piepenburg et al. 2002, Teixidó et al. 2002, Gerdes et al. 2003, Knust et al. 2003).

**Sampling.** Samples in the Magellan region (MR) were collected during 3 expeditions: (1) the Joint Chilean-German-Italian Magellan Campaign with RV 'Victor Hensen' in 1994 provided samples from stations in the Strait of Magellan and the Beagle Channel, (2) the Cimar-Fiordo II Expedition with RV 'Vidal Gormaz' in 1996 provided additional samples from the South Patagonian Icefield (47 to 53° S) and (3) during the expedition ANT XIII/4 with RV 'Polarstern' in 1996, more samples were collected on the continental shelf and slope of the eastern entrance of the Beagle Channel (55° S). The high Weddell Sea shelf samples (WS) were collected during expeditions ANT XV/3 and ANT XVII/3 with RV 'Polarstern' in 1998 and 2000, respectively (Fig. 1).

A total of 257 cores from 59 stations were collected with a multibox corer (Gerdes 1990) and a Reineck box corer (Reineck 1958). In MR, 41 stations (171 cores) were sampled and 18 stations (86 cores) in WS. The total area sampled was 4.3 m<sup>2</sup> in MR and 2.1 m<sup>2</sup> in WS. The mean depths at the MR and WS stations were 254 and 263 m, respectively (Table 1). The macrofauna was sieved through 0.5 mm mesh, sorted and fixed in 4% buffered formaldehyde seawater solution prior to counting and identification of all polychaetes to species level.

**Data processing.** For comparison of the polychaete assemblages, we used the following attributes: (1) density (ind. m<sup>-2</sup>) per station, (2) dominance of species (%), (3) trophic guild, (4) species composition, (5) diversity (exp  $H'$ ) and (6) evenness ( $J$ ). Additionally, point spe-

cies richness and sample species richness ( $SR_p$  and  $SR_s$ , respectively) were calculated following the recommendations of Gray (2001a);  $SR_p$  is the species richness of a single sampling unit (core) and  $SR_s$  is the species richness of a number of sampling units from the same sampling location. According to Gray (2000), the heterogeneity of the species diversity ( $HD_1$ ) was measured by the exponential form of the Shannon-Wiener index, based on  $\log_2$  density data.

For the analysis of the trophic guild distribution patterns, each species was classified into a feeding category following the classification of Fauchald & Jumars (1979) and Gaston (1983), modified according to Crame (1992); predators include carnivorous and omnivorous species, detritus feeders include all (sub-)surface deposit feeders and burrowing motile and sessile species, and suspension feeders were considered as a single group. According to this classification, the percentage of each trophic category per station was calculated and plotted in a triangular chart.

To elucidate any potential zoogeographic links between both sides of the Drake Passage, we compared data provided by the literature for the distribution and depth ranges of those polychaete species found in both areas under investigation. Species accumulation curves were calculated in order to compare the polychaete inventory among the different sample sizes from each region (Gray 1981, Lawrence & Walters 1979) and to consider the high number of rare species in the samples (Cosson-Sarradin et al. 1998).

We established species-accumulation curves in the 2 regions according to the following procedure. The accumulation of the number of species  $S$  with increasing number of individuals  $N$  was computed using the *EstimateS* program (R. Colwell [2001] Online user's guide *EstimateS* at <http://viceroy.eeb.uconn.edu/estimates>). *EstimateS* generates  $n$  data pairs of average  $S$  and  $N$  (averages refer to 100 randomised runs with replacement), where  $n$  is the number of samples considered ( $n = 171$  for MR;  $n = 86$  for WS). Subsequently, a simple exponential model was fitted to these  $n$  data pairs of average  $S$  and  $N$ .

Completeness of sampling of the species inventory was checked by computing the number of new species  $S_N$  to be expected if a further 1000 individuals had been collected:

$$S_N = a \times N^b \Leftrightarrow \ln(S_N) = \ln(a) + (b \times N)$$

where  $a$  and  $b$  are regression parameter and coefficient, respectively. The smaller  $S_N$  is, the more comprehensively the inventory has been

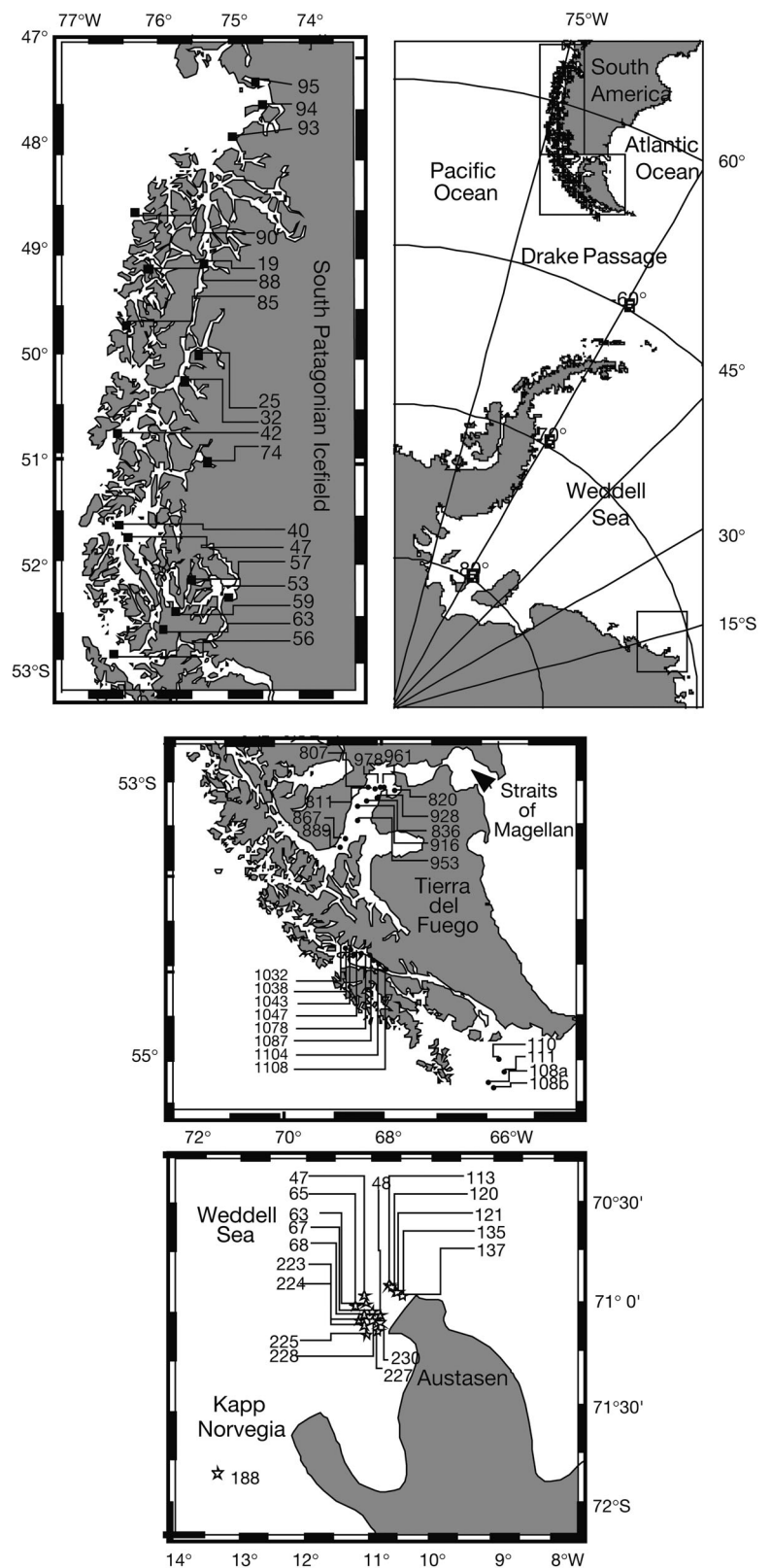


Fig. 1. Study area in the Magellan region (South America) and the Weddell Sea (Antarctica), with sampling locations indicated

Table 1. Station data of sampling locations. BC: Reineck box corer; MG: multibox corer; VG: 'Vidal Gormaz'; VH: 'Victor Hensen'; PS: 'Polarstern'

Code	Cruise	Leg	Stn	Gear	No. of cores	Date (d.mo.yr)	Location	Lat.	Long.	Depth (m)
<b>Magellan region</b>										
1	VG	Leg b	95	BC	2	07.11.1996	B. San Quintín	46° 48.85	74° 26.9	20
2	VG	Leg b	94	BC	2	07.11.1996	Golfo de Penas	46° 57.50	74° 15.0	92
3	VG	Leg b	93	BC	2	07.11.1996	Golfo de Penas	47° 22.20	74° 38.7	130
4	VG	Leg b	90	BC	2	06.11.1996	C. Fallos	48° 23.40	75° 06.5	550
5	VG	Leg a	19	BC	2	20.10.1996	C. Messier	48° 39.10	74° 27.2	410
6	VG	Leg b	88	BC	2	05.11.1996	C. Ladrilleros	48° 56.60	75° 02.0	630
7	VG	Leg b	85	BC	2	04.11.1996	C. Picton	49° 28.90	75° 25.2	98
8	VG	Leg a	25	BC	2	21.10.1996	C. Ice	49° 33.60	74° 12.4	538
9	VG	Leg a	32	BC	2	24.10.1996	Seno Penguín	49° 54.29	74° 18.6	711
10	VG	Leg a	42	BC	2	25.10.1996	C. Concepción	50° 35.70	75° 04.5	532
11	VG	Leg b	74	BC	2	02.11.1996	Estero Calvo	50° 37.90	73° 37.4	385
12	VG	Leg a	40	BC	2	24.10.1996	C. Concepción	50° 9.55	74° 42.1	323
13	VG	Leg a	47	BC	2	26.10.1996	Estrecho Nelson	51° 35.00	74° 31.0	615
14	VG	Leg b	57	BC	2	31.10.1996	E. las Montañas	51° 49.00	73° 19.4	136
15	VG	Leg a	53	BC	2	27.10.1996	S.Ult.Esperanza	51° 54.30	72° 33.7	32
16	VG	Leg b	59	BC	3	27.10.1996	C. Kirke	52° 10.30	73° 21.7	238
17	VG	Leg b	63	BC	2	31.10.1996	C. Smith	52° 26.40	73° 29.5	175
18	VG	Leg b	56	BC	2	30.10.1996	C. Kirke	52° 5.66	73° 07.5	136
19	VH	Leg 1	928	MG	6	28.10.1994	Magellan Straits	52° 57.8	70° 25.6	44
20	VH	Leg 1	961	MG	6	31.10.1994	Magellan Straits	52° 57.9	70° 43.5	38
21	VH	Leg 1	807	MG	6	18.10.1994	Magellan Straits	52° 57.9	70° 47.2	14
22	VH	Leg 1	811	MG	6	18.10.1994	Magellan Straits	52° 58.4	70° 42.2	119
23	VH	Leg 1	953	MG	8	31.10.1994	Magellan Straits	52° 59.8	70° 33.0	80
24	VH	Leg 1	820	MG	8	18.10.1994	Magellan Straits	53° 02.5	70° 17.1	8
25	VH	Leg 1	836	MG	8	23.10.1994	Magellan Straits	53° 08.4	70° 38.4	120
26	VH	Leg 1	916	MG	8	28.10.1994	Magellan Straits	53° 10.2	70° 52.3	26
27	VH	Leg 1	978	MG	8	01.11.1994	Magellan Straits	53° 32.7	70° 39.3	459
28	VH	Leg 1	867	MG	8	25.10.1994	Magellan Straits	53° 40.7	70° 54.6	445
29	VH	Leg 1	889	MG	5	26.10.1994	Magellan Straits	53° 42.7	70° 57.3	114
30	VH	Leg 2	1047	MG	4	04.11.1994	Beagle C	54° 50.1	69° 56.6	101
31	VH	Leg 2	1038	MG	6	04.11.1994	Beagle C	54° 50.9	69° 55.7	38
32	VH	Leg 2	1043	MG	4	04.11.1994	Beagle C	54° 51.9	69° 55.2	216
33	VH	Leg 2	1032	MG	8	04.11.1994	Beagle C	54° 52.7	69° 54.5	330
34	VH	Leg 2	1104	MG	7	06.11.1994	Beagle C	54° 53.1	69° 30.3	91
35	VH	Leg 2	1078	MG	8	05.11.1994	Beagle C	54° 53.5	69° 31.0	348
36	VH	Leg 2	1108	MG	6	06.11.1994	Beagle C	54° 55.0	69° 19.5	100
37	VH	Leg 2	1087	MG	8	05.11.1994	Beagle C	54° 55.3	69° 19.7	169
38	PS	XIII/4	110	MG	7	17.05.1996	Continental shelf	55° 26.1	66° 15.5	102
39	PS	XIII/4	111	MG	6	17.05.1996	Continental slope	55° 28.8	66° 04.4	1162
40	PS	XIII/4	108	MG	4	16.05.1996	Continental shelf	55° 44.1	66° 16.7	202
41	PS	XIII/4	108	MG	3	16.05.1996	Continental shelf	55° 44.1	66° 16.7	204
<b>Weddell Sea shelf</b>										
42	PS	XV/3	227	MG	6	20.02.1998	Kapp Norvegia	70° 49.5	10° 38.5	360
43	PS	XV/3	224	MG	7	19.02.1998	Kapp Norvegia	70° 49.8	10° 34.4	279
44	PS	XV/3	228	MG	6	20.02.1998	Kapp Norvegia	70° 49.8	10° 37.9	284
45	PS	XV/3	67	MG	7	01.02.1998	Kapp Norvegia	70° 49.9	10° 36.7	293
46	PS	XVII/3	113	MG	4	06.04.2000	Austasen	70° 49.9	10° 36.8	275
47	PS	XV/3	225	MG	6	19.02.1998	Kapp Norvegia	70° 50.1	10° 35.2	276
48	PS	XV/3	223	MG	3	19.02.1998	Kapp Norvegia	70° 50.2	10° 34.9	273
49	PS	XV/3	68	MG	3	01.02.1998	Kapp Norvegia	70° 50.3	10° 38.1	269
50	PS	XV/3	230	MG	7	20.02.1998	Kapp Norvegia	70° 50.8	10° 32.2	229
51	PS	XVII/3	135	MG	2	10.04.2000	Austasen	70° 50.2	10° 34.5	256
52	PS	XVII/3	137	MG	3	10.04.2000	Austasen	70° 50.2	10° 34.7	272
53	PS	XVII/3	120	MG	4	08.04.2000	Austasen	70° 50.3	10° 35.0	271
54	PS	XV/3	63	MG	4	31.01.1998	Kapp Norvegia	70° 51.8	10° 34.4	234
55	PS	XV/3	65	MG	2	30.01.1998	Kapp Norvegia	70° 51.9	10° 34.2	227
56	PS	XV/3	47	MG	7	30.01.1998	Kapp Norvegia	70° 52.2	10° 29.3	243
57	PS	XV/3	48	MG	5	30.01.1998	Kapp Norvegia	70° 52.2	10° 29.3	245
58	PS	XVII/3	121	MG	5	08.10.2000	Austasen	70° 53.6	10° 34.2	249
59	PS	XV/3	188	MG	5	15.02.1998	Kapp Norvegia	71° 31.5	13° 30.6	225

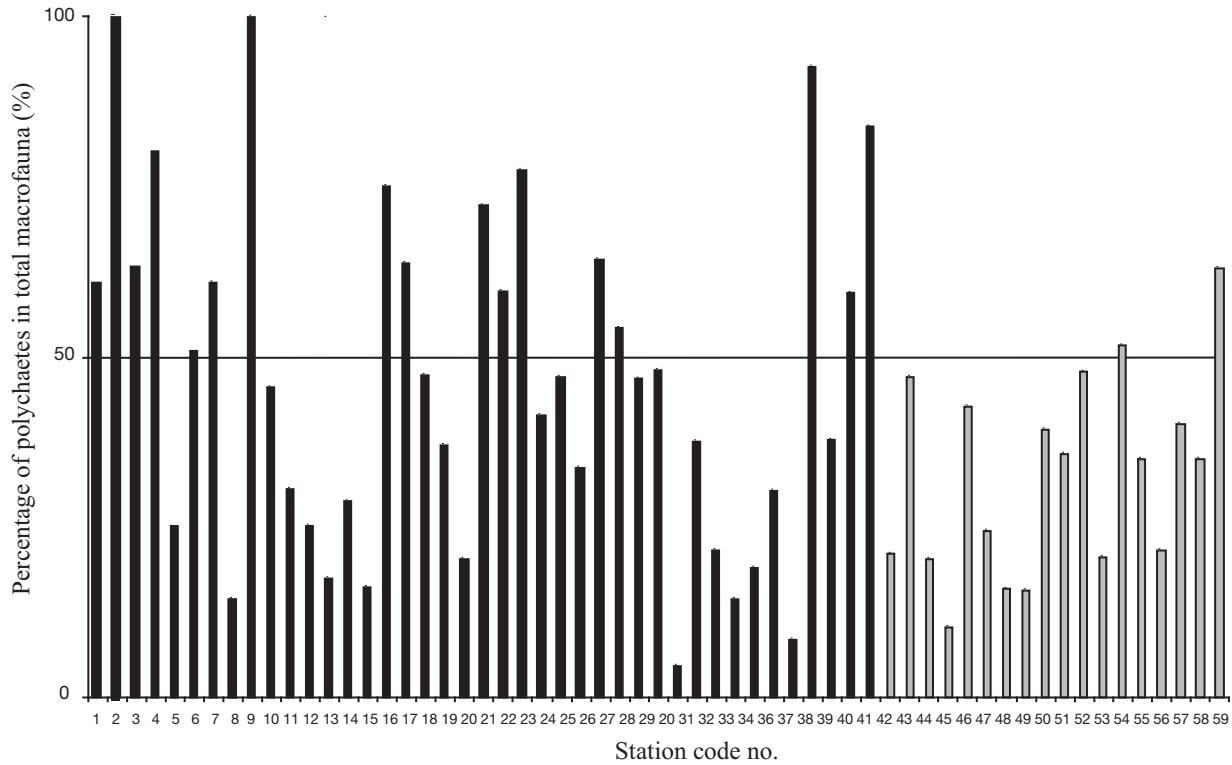


Fig. 2. Comparison of the percentage of polychaete individuals in the total macrofauna obtained at each station (in the Magellan region,  $n = 5508$  ind.; in Weddell Sea,  $n = 4225$  ind.). All stations plotted are arranged in a N-S direction; for code number see Table 1. Magellan region: black bars; Weddell Sea: grey bars

performed; i.e., in this case, more specimens  $N$  are included.

An objective and comparable measure of species richness was derived by determining the points of equal slope in both species-individual curves, i.e. the number of individuals  $N$  at which the addition of a further  $X$  individuals would result in exactly 1 additional species,  $P_{X,1}$ :

$$S_{N+X} - S_N \leq 1$$

This equation had to be solved iteratively by minimising:

$$\text{abs}[N - (N + X)^b - 1/a]^{1/b}$$

$N$  and the corresponding  $S$  which are computed from the exponential model defining the point of equal slope:

$$P_{X,1} \approx \{N; S\}$$

Confidence limits for the true mean of  $S_N$  were computed according to standard linear regression procedures (Draper & Smith 1981).

Multidimensional scaling ordination (MDS), based on 4th root-transformed density values (Bray-Curtis similarity coefficients) was performed to identify differences between MR and WS. The multivariate statis-

tical methods of classification and ordination used the software package PRIMER Version 5.2.1 (Clark & Warwick 1994). The differences between the remaining community parameters were tested with a Mann-Whitney  $U$ -test (Zar 1999).

## RESULTS

### Family composition

A total of 2974 polychaete individuals were collected; 1668 in MR and 1306 in WS. The percentage of polychaetes in the total macrofauna per station varied between 4.5 and 100% in MR, and between 30 and 60% in WS (Fig. 2).

Of the 334 species belonging to 179 genera, 199 species were found in MR and 163 in WS; 28 species and 58 genera occurred in both regions. Of the 44 families, 37 were found in MR and 36 in WS. Thirty-two families were common in both regions while Onuphidae, Cossuridae, Oeonidae, Eunicidae, Goniadidae, Sigalionidae, Magellonidae and Sternaspidae were restricted to MR, and Lacydoniidae, Chrysopetalidae, Polygordiidae and Spintheridae were only recorded in WS.

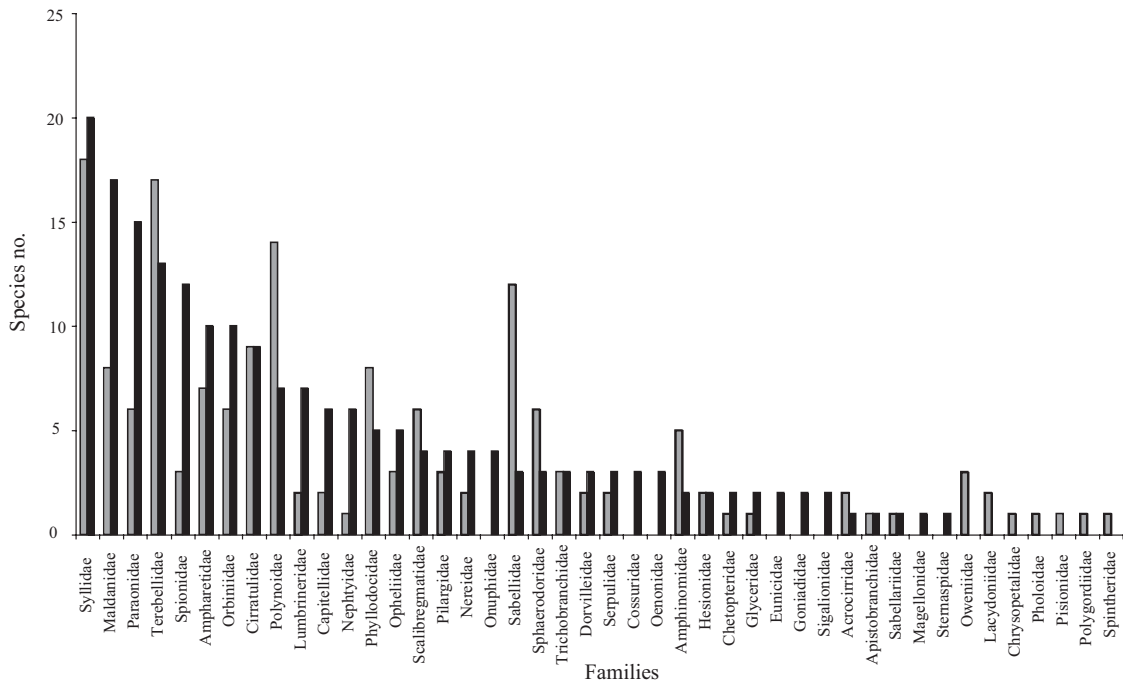


Fig. 3. Comparison of the total species number per polychaete family obtained from the study areas. Magellan region: black bars; Weddell Sea: grey bars

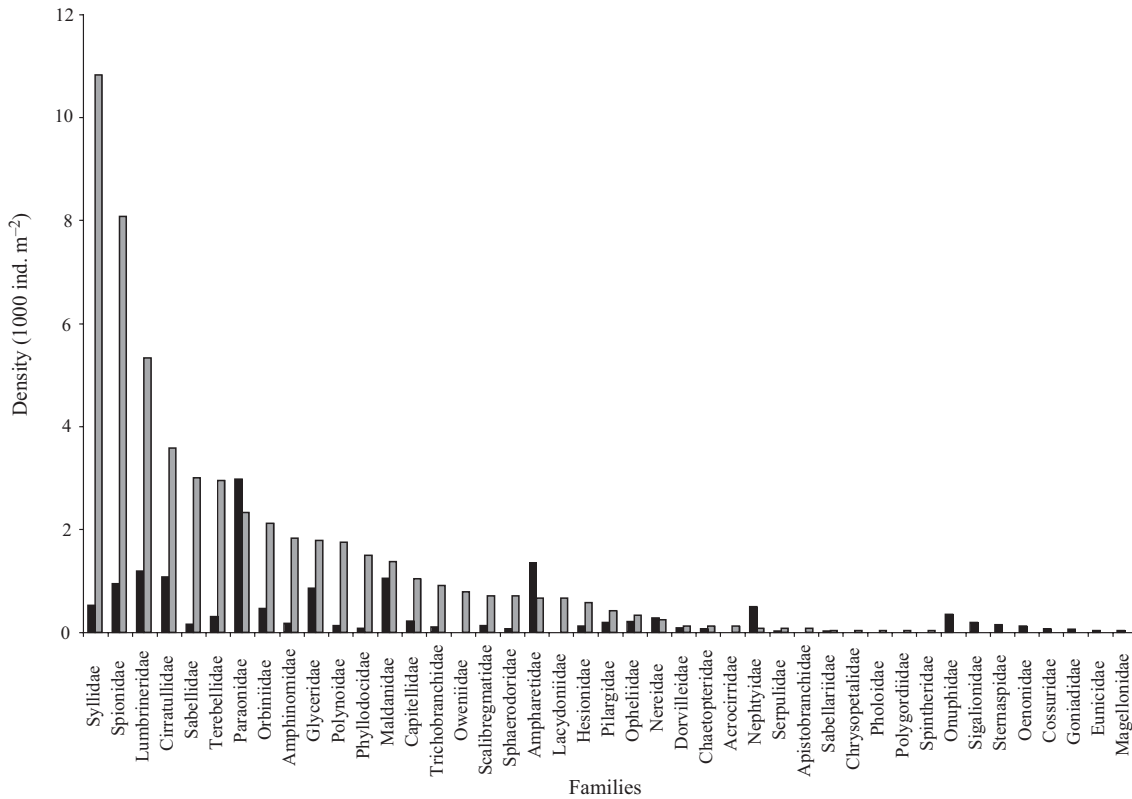


Fig. 4. Comparison of total density values (ind. m<sup>-2</sup>) per family obtained in the study areas. Magellan region: black bars; Weddell Sea: grey bars

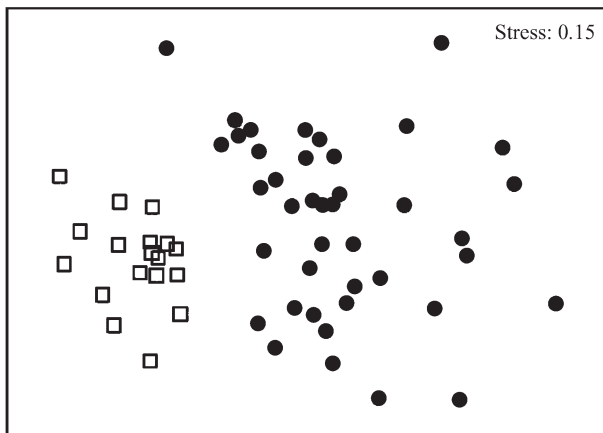


Fig. 5. MDS plot for  $\sqrt{\sqrt{\quad}}$  transformation of the mean density data using group average linkage on Bray-Curtis similarities for differences between study areas. Magellan region: ●; Weddell Sea: □

The most speciose families were Syllidae (10% of all polychaete species), Maldanidae (9%) and Paraonidae (7%) in MR, and Terebellidae (12%), Syllidae (11%) and Polynoidae (9%) in WS (Fig. 3). The most abundant families were Paraonidae (21% of all individuals), Ampharetidae (9%) and Lumbrineridae (8%) in MR, and Syllidae (20%), Spionidae (15%) and Lumbrineridae (10%) in WS (Fig. 4).

### Structure of the polychaete species assemblage

The result of the MDS (stress of 0.15) clearly discriminates between MR and WS (Fig. 5). A Mann-Whitney *U*-test was carried out separately and confirmed this result, showing that the mean densities per station (see Fig. 6a) were significantly higher ( $n = 257$ , *U*-test = 5873,  $p = 0.0085$ ) in WS (mean =  $582 \pm 448$ ) than in MR (mean =  $352 \pm 319$ ; Table 2).

The species abundance distribution in both regions showed a high number of species represented by only 1 specimen (Fig. 7a,b). This led to high values of evenness (Table 2) and low dominance values on either side of the Drake Passage. In MR, the maximum dominance value at the species level was 9% of the total density for *Aricidea strelzovi*, and 50% cumulative dominance was achieved with 14 species in MR (Table 3). The remaining 185 species only contributed between 0.1 and 2% per species. In WS, *Spiophanes tcherniai* accounted for the maximum dominance value (10%) at the species level, and 14 species made up 54% of the cumulative dominance (Table 3). The remaining 149 species only reached percentages between 0.1 and 2% per species.

Detritus feeders (57% of all individuals) constituted the dominant trophic guild in both regions, followed by

predators (38%) and suspension feeders (5%). Suspension feeders accounted for only 17% of species at the MR stations, whereas detritus feeders and predators prevailed at all stations. In contrast, at most of the WS stations, all 3 trophic guilds were present (Fig. 8). Among the detritus feeders in MR, the highest numbers of individuals were those of *Aricidea strelzovi*, *A. pisanoi* and *Prionospio oreansanzi*; the predator guild was represented by *Glycera capitata* and *Aglaophamus peruana*; and the suspension feeders consisted mainly of *Hypsicomus phaeotaenia*.

In WS, *Spiophanes tcherniai* contributed the highest individual number of detritus feeders; the predator guild was mainly represented by *Syllis spongiphila* and *Glycera kerguelensis*; and among the suspension feeders, *Jasmineira crumenifera*, *Euchone pallida* and *Galathowenia wilsoni* were dominant.

Mean point species richness ( $SR_s$ ; Fig. 6b) and heterogeneity diversity ( $HD_1$ ; Fig. 9) showed significantly lower values at the MR than at the WS stations (*U*-test = 5336.0 and 5207.0, respectively;  $p < 0.05$ ; Table 2). Evenness values of cores containing more than 1 individual per species were not significantly different (*U*-test = 5471.0;  $p > 0.05$ ) between the MR and WS stations (Table 2).

The randomised cumulative species plots (Fig. 10) for both regions showed significant differences. The shape of the curves did not reach an asymptote in either region, because the individual numbers were low and both species' inventories were not considered completely.

Twenty-eight species were common to both regions (Table 4). Four species were cosmopolitans; *Artacama proboscidea* had a bipolar distribution. Ten species showed a circumpolar distribution around the (sub-) Antarctic; e.g. *Augeneria tentaculata*. The remaining species occurred from low to high latitudes; e.g. *Aricidea strelzovi* and *Sphaerodoropsis parva* along the Chilean coast through the Drake Passage into the high Weddell Sea. Concerning the depth distribution of these species, 57% showed a eurybathic distribution or a wide depth range, whereas the remaining species showed stenobathic distribution patterns.

## DISCUSSION

This study improves and updates the precision of the distribution limits of polychaete species on either side of the Drake Passage, and presents empirical ecological data from 2 research areas in the Southern Ocean, where taxonomic information is still scarce and, as Clarke & Johnston (2003) concluded, a revision of polychaetes is urgently needed.

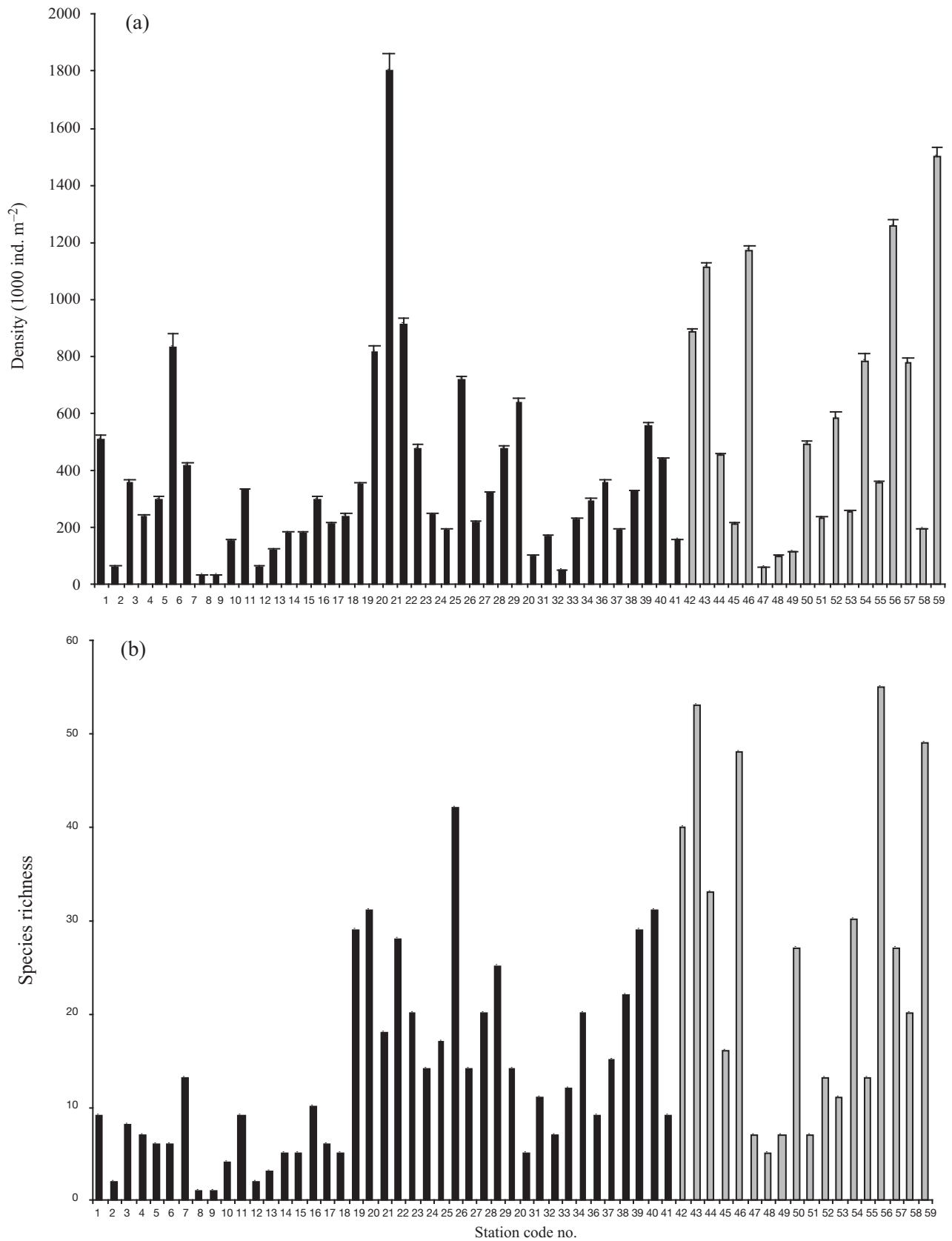


Fig. 6. Plot showing (a) mean density and (b) species richness ( $SR_s$ ) per station in the study areas. Magellan region: black bars; Weddell Sea: grey bars. Error bars are SD



Table 2. Mann-Whitney *U*-test for differences in density, species richness, diversity and evenness values (means  $\pm$  SD) between the Magellan region (MR) and Weddell Sea (WS) areas at  $\alpha = 0.05$ . Significant p-values are shown in bold. The sample numbers for evenness values were 145 for MR and 77 for WS

	MR (n = 171)	WS (n = 86)	Mann-Whitney <i>U</i> -test	p-values
Mean density (ind. m <sup>-2</sup> )	352 $\pm$ 319	582 $\pm$ 448	5873.0	<b>0.0085</b>
Mean point species richness (SR <sub>p</sub> )	5.0 $\pm$ 3.9	8.9 $\pm$ 7.0	5336.0	<b>0.0003</b>
Heterogeneity diversity (HD <sub>1</sub> )	4.7 $\pm$ 3.0	7.5 $\pm$ 5.4	5207.0	<b>0.0001</b>
Evenness ( <i>J'</i> )	0.7 $\pm$ 0.3	0.9 $\pm$ 0.04	5471.0	0.8056

Inventories of polychaete assemblages at the species level in WS and MR waters have been little studied in the last 30 yr. The lack of descriptions of assemblages up to now complicates the establishment and comparison of polychaete assemblage patterns in both areas. This study provides the most comprehensive

description of polychaete assemblages at the species level on either side of the Drake Passage based on the same sampling methods, enabling us to compare data from these ecosystems which remained closely together for a considerable period of time and became separated rather late during the break-up of Gondwana some 20 to 30 million yr ago.

Our data suggest that today both areas differ significantly in terms of polychaete density, diversity, species

richness and affiliation to different trophic guilds. In both regions, the assemblages are characterised by high variability in these attributes; this might be explained by the heterogeneity of local environmental properties, which are often shaped by ice. On the WS shelf, benthic communities are disturbed directly by grounding ice bergs, while in MR, effects are due to melting glaciers, which might change the hydrographic regime and sedimentation processes, thus indirectly affecting benthic assemblages.

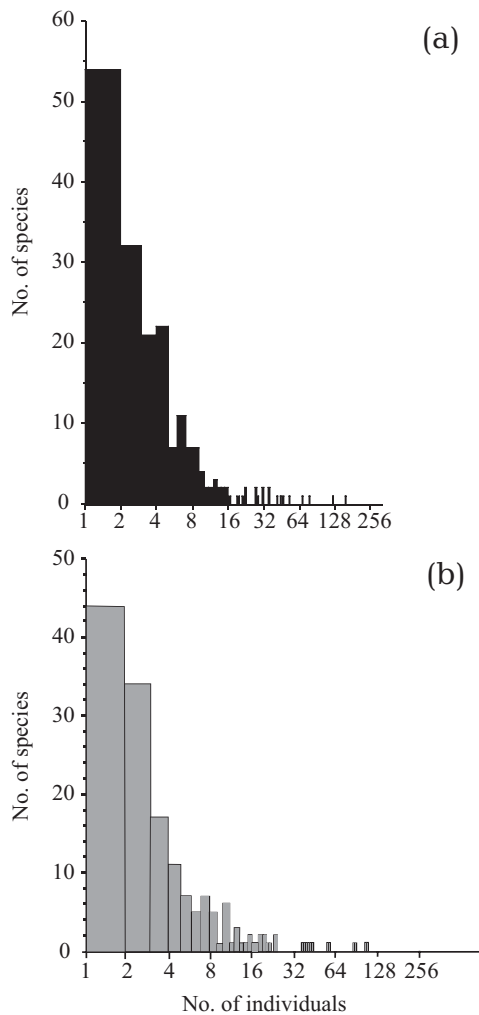


Fig. 7. Species abundance distribution in the (a) Magellan region and (b) Weddell Sea (expressed on a log<sub>2</sub> scale)

Table 3. Polychaete dominance patterns in the Magellan region and Weddell Sea

Species MR	Density (ind. m <sup>-2</sup> )	Dominance (%)	Cumulative dominance
<b>Magellan region</b>			
<i>Aricidea strelzovi</i>	6613	9	9
<i>Glycera capitata</i>	5119	7	16
<i>Aricidea pisanoi</i>	3209	4	21
<i>Prionospio orensanzi</i>	3125	4	25
<i>Levinsenia gracilis</i>	2845	4	29
<i>Monticellina</i> sp.	2184	3	32
<i>Chaetozone</i> sp. 2	1917	3	35
<i>Lumbrineris magelhaensis</i>	1833	3	37
<i>Leitoscoloplos</i> sp.	1708	2	39
<i>Ampharete kerguelensis</i>	1617	2	42
<i>Melinna cristata</i>	1565	2	44
<i>Aglaophamus peruana</i>	1494	2	46
<i>Abyssoninoe abyssorum</i>	1327	2	48
<i>Ninoe falklandica</i>	1308	2	50
<b>Weddell Sea</b>			
<i>Spiophanes tcherniai</i>	5459	10	10
<i>Syllis spongiphila</i>	4500	8	18
<i>Lumbrineris</i> cf. <i>kerguelensis</i>	3750	7	25
<i>Laonice weddellia</i>	2542	5	30
<i>Cirrophorus brevicirratu</i> s	1833	3	33
<i>Glycera kerguelensis</i>	1792	3	37
<i>Chaetozone</i> sp. 3	1708	3	40
<i>Sphaerosyllis antarctica</i>	1667	3	43
<i>Augeneria tentaculata</i>	1583	3	46
<i>Notomastus latericeus</i>	958	2	47
<i>Scoloplos marginatus</i>	958	2	49
<i>Jasmineira crumenifera</i>	875	2	51
<i>Harmothoe spinosa</i>	833	2	52
<i>Typosyllis armillaris</i>	792	1	54

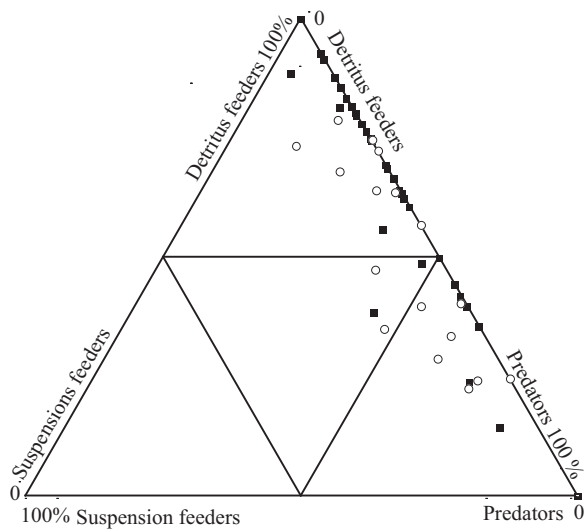


Fig. 8. Triangular chart showing polychaete feeding modes in the study areas. Values refer to percent per station in the Magellan region (■) and Weddell Sea (○) areas

The actual patterns derived from this study are based on 163 species and 36 families in WS, and 199 species and 37 families in MR. The latter figures represent the highest numbers of species/families reported up to now for the little studied MR. Maurer & Williams (1988) reported 76 polychaete species belonging to 33 families for the Straits of Magellan, while Cañete et al. (1999) distinguished 38 species from 24 families in 39 corer samples from the northern border of MR. Bremec et al. (2000) found 119 polychaete species from 34 families in the Straits of Magellan and 36 species from 20 families on the eastern Patagonian shelf in their qualitative and quantitative samples.

Comparable quantitative information from the high Antarctic WS is also very scarce. Somewhat better is

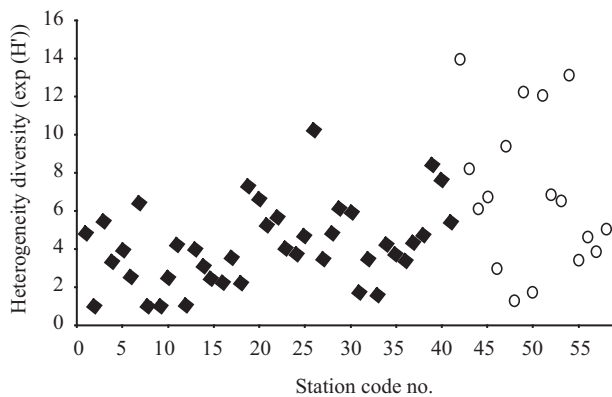


Fig. 9. Plot of  $HD_1$  per station through the studied areas, where  $HD_1 = \exp(H')$ . Magellan region: ◆; Weddell Sea: ○

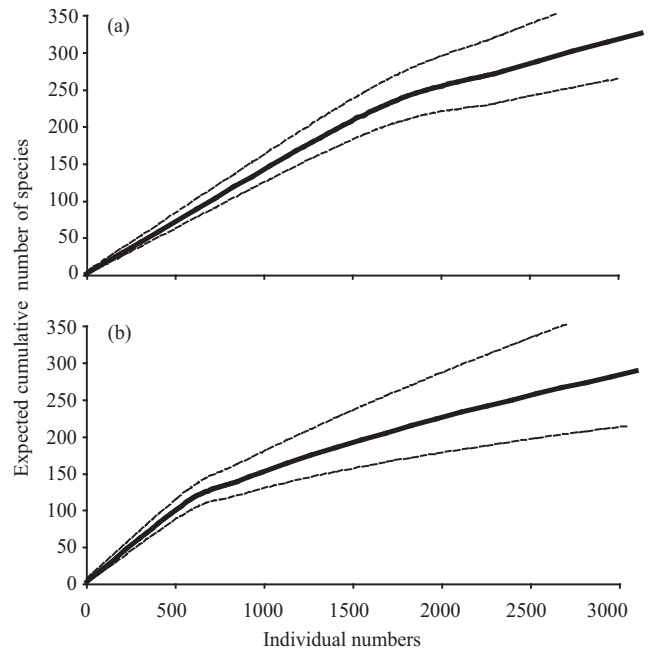


Fig. 10. Estimated cumulative species richness in the (a) Magellan region and (b) Weddell Sea using the *EstimateS* program (R. Colwell [2001] at <http://viceroy.eeb.uconn.edu/estimates>), with 50 randomisations and no replacement. --- = SD

the available information from the Subantarctic Islands and the Antarctic Peninsula. From the high Antarctic Weddell Sea, Hartman (1978) described 37 polychaete species with Cirratulidae and Maldanidae being the most speciose families from just 2 van Veen grab samples. Stiller (1996) reported 20 polynoid and 2 aphroditid species from the WS and Lazarev Sea shelves. Additional information from WS, reported by Hartman (1964, 1966), was obtained from qualitative sampling with towed gear.

Gallardo et al. (1988) reported 206 polychaete species from 26 families from the Subantarctic Greenwich Island. Terebellidae, Spionidae and Phyllodocidae were the most speciose families on sublittoral soft-bottoms at this location. Recently, San Martín et al. (2000) recorded 29 families with 89 species off Livingston Island, Deception Island and the South Shetland Islands; the most speciose families in their samples were Terebellidae, Syllidae and Maldanidae.

The species composition per family on the WS shelf resembles that reported by Clarke & Johnston (2003) for waters south of the Polar Front. The most speciose families Syllidae and Terebellidae are represented most dominantly by *Syllis spongiphila* and *Pista corrientis*, respectively, whereas in MR, the most speciose families Syllidae, Maldanidae and Paranoidae were represented particularly by *Typosyllis hyalina*, *Maldane sarsi* and *Aricidea strelzovi*, respectively.

Table 4. List of polychaete species occurring in both regions (Magellan region [MR] and Weddell Sea [WS] and their respective densities and bathymetric distribution patterns [D]). LaD: latitudinal distribution; CiP: circum (sub-)Antarctic; BiD: bipolar distribution; CoD: cosmopolitan distribution

Species	Density (ind. m <sup>-2</sup> )		Depth (m) min-max	D
	MR	WS		
<i>Amphicteis gunneri</i> (Sars, 1835)	83	208	5–7686 <sup>a</sup>	CoD
<i>Anobothrella antarctica</i> (Monro, 1939)	292	167	40–4099 <sup>a</sup>	LaD
<i>Sphaerodoropsis parva</i> (Ehlers, 1913)	167	42	128–3980 <sup>b</sup>	LaD
<i>Harmothoe spinosa</i> Kinberg, 1855	83	42	55–3400 <sup>c</sup>	CiP
<i>Notoproctus oculatus antarcticus</i> Arwidsson, 1811	296	208	218–3397 <sup>d</sup>	CiP
<i>Artacama proboscidea</i> Malmgren, 1865	125	42	20–3380 <sup>a</sup>	BiD
<i>Paramphionome australis</i> Monro, 1930	702	333	128–3197 <sup>e</sup>	LaD
<i>Ampharete kerguelensis</i> MacIntosh, 1885	1617	83	64–2700 <sup>f</sup>	CiP
<i>Augeneria tentaculata</i> Monro, 1930	226	1583	80–2350 <sup>g</sup>	CiP
<i>Travisia kerguelensis</i> MacIntosh, 1885	208	42	40–1784 <sup>j</sup>	LaD
<i>Aricidea simplex</i> (Day, 1963)	83	83	35–1615 <sup>b</sup>	CoD
<i>Aricidea strelzovi</i> Hartmann-Schröder & Rosenfeldt, 1990	6613	83	300–1600 <sup>j</sup>	LaD
<i>Maldane sarsi antarctica</i> Arwidsson, 1811	184	333	75–1116 <sup>j</sup>	CiP
<i>Aricidea antarctica</i> Hartmann-Schröder & Rosenfeldt, 1988	42	125	20–1100 <sup>k</sup>	LaD
<i>Amage sculpta</i> Ehlers, 1908	42	42	244–1080 <sup>b</sup>	LaD
<i>Aphelocheata cincinnata</i> (Ehlers, 1908)	570	458	61–1079 <sup>a</sup>	LaD
<i>Harmothoe magellanica</i> MacIntosh, 1885	83	208	0–900 <sup>l</sup>	CiP
<i>Leodamas marginatus</i> (Ehlers, 1897)	167	958	20–640 <sup>d</sup>	LaD
<i>Euphrosine antarctica</i> Kudenov, 1993	101	500	60–494 <sup>e</sup>	LaD
<i>Phyllochaetopterus monroi</i> Hartman, 1967	42	125	270–485 <sup>o</sup>	LaD
<i>Nereis eugeniae</i> Kinberg, 1866	167	125	40–455 <sup>m</sup>	LaD
<i>Gyptis incompta</i> Ehlers, 1897	202	500	300–445 <sup>m</sup>	?
<i>Axiothella antarctica</i> Monro, 1930	119	42	207–344 <sup>d</sup>	CiP
<i>Lysilla loveni macintoshi</i> Gravier, 1907	42	42	25–335 <sup>b</sup>	CiP
<i>Leitoscoloplos kerguelensis</i> (MacIntosh, 1885)	375	292	3–276 <sup>i</sup>	LaD
<i>Scalibregma inflatum</i> Rathke, 1843	500	42	110–247 <sup>d</sup>	CoD
<i>Autolytus charcoti</i> Gravier, 1906	83	250	0–165 <sup>b</sup>	CiP
<i>Typosyllis armillaris</i> Müller, 1776	167	792	0–100 <sup>n</sup>	CoD

<sup>a</sup>Hartmann-Schröder & Rosenfeldt (1989), <sup>b</sup>Rozbaczylo (1985), <sup>c</sup>Hartmann-Schröder & Rosenfeldt (1988), <sup>d</sup>Hartman (1966), <sup>e</sup>Kudenov (1992), <sup>f</sup>Knox & Cameron (1998), <sup>g</sup>Orensanz (1990), <sup>h</sup>Strelzov (1973), <sup>i</sup>Palma et al. (2005), <sup>j</sup>Hartman (1967), <sup>k</sup>Montiel et al. (2002), <sup>l</sup>Orensanz (1974), <sup>m</sup>This study, <sup>n</sup>Licher (2002), <sup>o</sup>Parapar & San Martin (1997)

Polynoidae only occurred in our samples in low species numbers and especially low individual numbers, possibly because the quantitative corers used in our study are known to more efficiently capture sessile organisms or those with low motility.

Significant differences between MR and WS polychaete assemblages also became evident by comparing the proportions of species representing different trophic guilds. The analysis of trophic guilds is an appropriate method for describing benthic communities, because they evidence the relationships of animals with their environment and/or interactions with other species (Muniz & Pires 1999, Paiva 1993).

In our study, the trophic structures in the MR and WS assemblages were dominated by detritus feeders and predators, whereas a higher percentage of suspension feeders (which were of minor importance in both areas) in WS made up the main difference in such structures between the 2 regions. These results resemble data commonly reported for benthic communities

in WS, where suspension feeders from different taxa dominate high Antarctic shelf communities. The hydrographic regime with strong currents provides sufficient food via vertical flux and advection, thus allowing the existence of dense populations of suspension feeders (Teixidó et al. 2002).

Most of the MR stations were located in fjords and channels, which typically form the MR and which are widely described in the literature (e.g. Syvitski et al. 1987). The prevailing environmental conditions with low water currents and exchange (Pinochet & Salinas 1995), and frequently high sedimentation rates (Pickard & Stantor 1980, Heiskanen & Tallberg 1999) favour the existence of motile detritus feeders and predators, not only in case of polychaetes but also for other taxa, while suspension feeders are almost absent. This composition found in MR seems to be a typical feature for fjord and channel communities and is also reported for other regions worldwide (Rosenberg 2001).

No significant differences became obvious in the evenness values between both areas. Due to relatively high species numbers and low numbers of specimens per species, evenness in both assemblages was high. In the polychaete-related literature, typically 1 or 2 species contribute considerably to the overall abundance with dominance values of 27% (Gambi et al. 1997) or even 36% (Gallardo et al. 1988). In contrast to our study, the maximum dominance values were lower and more species contributed to the 50% cumulative dominance value as compared to the literature data mentioned above. Hughes (1984) made similar observations in benthic invertebrate communities. Hughes' model, based on his observations, predicted a stable stage with a high dominance of a common species and few rare species, whereas high numbers of rare species with low abundance characterising early stages of colonization.

In the present study, the resulting pattern could also reflect disturbance in the 2 assemblages under study; the impact of ice scouring in WS and the impact of a permanent ice field with salinity gradients and high rates of sedimentation in MR, could maintain the assemblages in both areas in a stage of permanent early recolonisation (Gray 2001b, Gerdes et al. 2003). There clearly is some evidence to suggest a relationship between polychaete assemblage parameters and ice influence, but more quantitative documentation will be required to confirm this hypothesis.

In view of the common history of the Magellan region and the Antarctic, and considering the fact that they are neighbouring ecosystems, separated only by the Drake Passage and the Antarctic Convergence (which, however, acts like a filter for the dispersal of many aquatic organisms), the number of common species in both areas should be quite high. Surprisingly, we only found an 8% overlap of polychaete species and a 32% overlap at the genus level north and south of the Drake Passage. We have to keep in mind, however, that our 2974 polychaete specimens from 59 stations do not sufficiently represent the whole species inventories. Neither MR nor WS has been adequately sampled for this purpose, although our data set is the biggest considered so far. In a recent paper, Montiel (2005) reported a considerably higher overlap (>30%) of polychaete species based, however, on quantitative and qualitative samples as well as literature data. Our present results revealed further important insights into polychaete distribution patterns, but more comparable studies are urgently needed to answer the questions addressed with greater accuracy.

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