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Julian Gutt · Andreas Starmans

Structure and biodiversity of megabenthos in the Weddell and Lazarev Seas (Antarctica): ecological role of physical parameters and biological interactions

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Abstract A community analysis of the mega-zoo-epibenthos at water depths between 99 and 1243 m was carried out for the Weddell and Lazarev Seas (47°W 77°S–12°E 70°S). A total of 144,531 specimens were counted and 313 taxa were identified from 3,768 photographs at 55 stations, which represented approximately 3,304 m^2 of seafloor. The stations were classified into six groups according to their inventory of taxa although they represented rather a gradient from a rich and diverse suspension feeder assemblage to a poorer assemblage. In the latter, the proportion of deposit feeders was higher than in the former. A statistical comparison between biological and physical data showed that the faunistic pattern could best be explained by a combination of water depth and a geographical gradient. A positive correlation between the abundance of large sponges and the number of all other taxa was found.

Introduction

At large scale, the rich and diverse benthos of the Antarctic shelves (Dearborn 1968; Hedgpeth 1969; Dayton et al. 1994; Arntz et al. 1997) is regarded zoogeographically to have a circumpolar distribution (Arnaud 1977; White 1984). This is thought to be primarily related to the relatively stable and homogeneous physical setting (Hedgpeth 1977; Picken 1985). The shelves, covering an area of 2.2×10^6 km^2, are located along a 35,000-km-long coastline, 45% of which is shelf ice, and are up to 800 m in depth.

Ecological analyses, on a spatial scale from one metre to a few hundred kilometres, showed a patchy distribution of species assemblages (e.g. Voß 1988; Gutt 1991a; Gutt and Piepenburg 1991; Barthel and Gutt 1992). However, not much is known about long-term processes that shape such benthic communities; ecological demands have only been investigated for very few species (Arntz and Gallardo 1994).

The shelves of the southeastern Weddell and Lazarev Seas in the Atlantic sector of the Southern Ocean belong to the permanent pack-ice zone (Hempel 1985a). As most of the 2,250-km-long coastline is defined by shelf ice, no water depths shallower than 99 m could be sampled. Faunistically, the Lazarev Sea belongs to the East Antarctic, whose characteristics are poorly known. For the Weddell Sea, however, parts of the benthos and fish fauna are well known (Gutt 1991a,b; Barthel and Gutt 1992; Gutt et al. 1994; Gutt and Ekau 1996) and the environmental characteristics are more diverse. They include, among others, a narrow or wide shelf, innershelf depressions, varying sediments, a coastal current, diverging water masses, and varying predictability of ice cover during the summer. Underwater photography was chosen to provide reliable quantitative data on the epifauna in this region.

The objectives of this benthic survey were to: (1) identify assemblages of taxa and key species, (2) describe their composition and biodiversity, and (3) determine environmental factors and biological interactions that may influence faunal composition.

Materials and methods

Fieldwork

Data were collected during the expeditions ANT III/3, ANT VI/3, ANT VII/4, and ANT IX/3 with R/V "Polarstern" during the austral summers from 1985 to 1991 (Hempel 1985b; Fütterer 1989; Arntz et al. 1990; Bathmann et al. 1992). A 70-mm underwater camera was used at 55 stations with a depth range between 99 and 1,243 m. Most stations were located on the continental shelf (depth < 500 m; Fig. 1a). A total of 3,768 seafloor photographs (Kodak

J. Gutt (✉) · A. Starmans
Alfred Wegener Institute for Polar and Marine Research,
Columbusstrasse,
D-27568 Bremerhaven, Germany
e-mail: jgutt@awi-bremerhaven.de, Fax: +49 (0) 471 4831 149

Table 1 Station data for the area under investigation

	Minimum	25% percentile	Median	75% percentile	Maximum
No. of photos per stn	26	65	72	76	82
m^2 photographed per stn	28.4	42.6	63.6	69.9	100.8
Total abundance per stn ($n/100\ m^2$)	67.1	1,297.9	2,784.6	6,770.3	33,048.8
No. of taxa per stn	4	49	76	95	125

Ektachrome 64) were taken, which represent an area of 3,304 m^2. The optical resolution was approximately 0.3 mm. Camera and strobe (Hasselblad 500EL/M with two Metz Mecablitz 40 CT4) were triggered at a constant distance above the seafloor. Each station was represented by a transect consisting of 26–82 photographs, taken at approximately evenly spaced time intervals, which covered an area from 28.8 to 100.8 m^2 (median 63.6 m^2; Table 1). The size of the vertically photographed area ranged from 0.56 to 1.20 m^2 (+/−3%) per frame; it was calculated using stations at which the trigger weight was photographed and served as a spatial scale.

Identification and counting

Megabenthic organisms visible in photographs were identified to lowest possible taxonomic level by referring to the literature (Thomson and Murray 1880–1889; Discovery Committee Colonial Office 1929–1980; Kott 1969; Sieg and Wägele 1990). The most important support was provided by experts (see Acknowledgements). The term "Synascidians" does not describe a systematic group but a life form. Data for fish and decapod crustaceans were taken from Gutt et al. (1994); some unidentified sponges (e.g. "TWWSS" or "Yellow Branches") were named according to Barthel and Gutt (1992) who gave short descriptions. With few exceptions all photographed organisms >0.5 cm were counted, but encrusting forms were not considered. Colonial taxa were counted as single individuals when possible; if this was not possible, the cover of the seafloor in percent was multiplied by 2 to obtain a value roughly equivalent to the abundances of other taxa. Infaunal species were considered when part of their body was visible. Abundances were standardized to numbers per 100 m^2.

Community analysis and key taxa

Taxa photographed at only one or two stations were excluded to avoid bias by random co-occurrences. Organisms identified at coarse taxonomic levels were also omitted (Table 2). Abundances were 4th-root transformed, and faunistic similarities were computed between each possible station pair using the Bray-Curtis index (Bray and Curtis 1957). At this combination the similarity coefficient is invariant to a scale change (Field et al. 1982). A classification (complete linkage) of the similarity matrix was calculated for all stations and taxa. The Multidimensional Scaling (MDS) as the method of ordination (Field et al. 1982) shows the similarities of all stations to each other in two dimensions.

Key taxa that serve as good discriminators between each station cluster and all other stations were determined by a modified Bray-Curtis index (Clarke 1993). Good key taxa contribute greatly to the average dissimilarity between the clusters and the rest of the stations d_i and have a high quotient between d_i and its standard deviation.

Diversity

Calculations only involved organisms identified at genus or species level. The Shannon diversity index (H′, Shannon and Weaver 1964) and the Pielou evenness index (J, Pielou 1977) were determined for each station. Mean values of station clusters were compared by a Kruskal-Wallis test (2-tailed, $P < 0.05$).

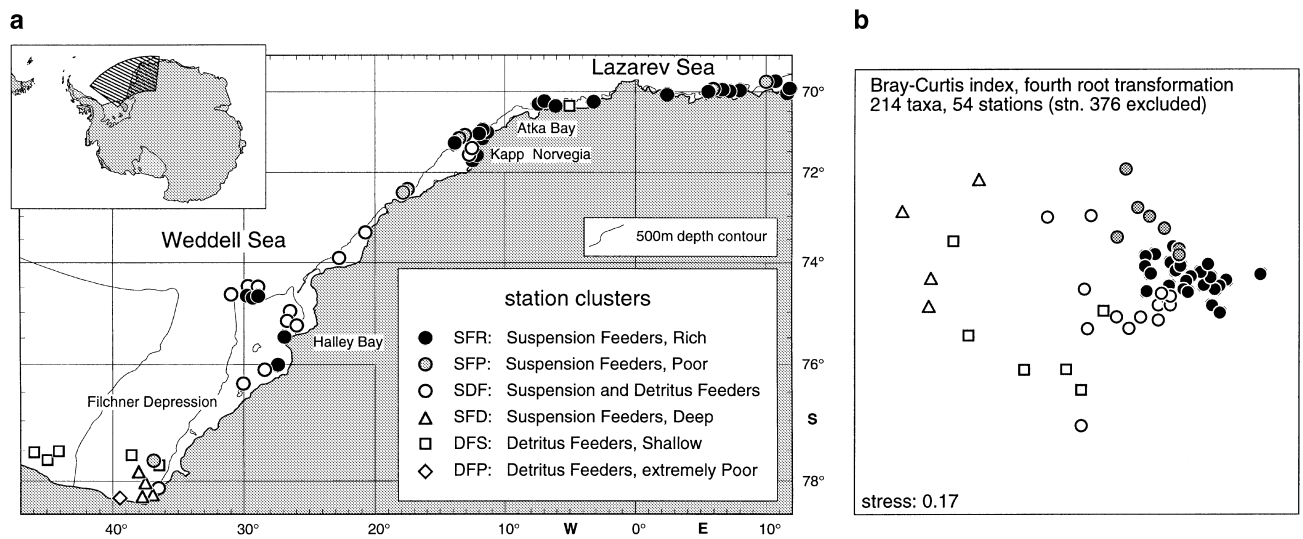

Fig. 1 a Station map **b** Plot of the Multidimensional Scaling, MDS, visualizing the faunistic similarities between megabenthic stations; 214 taxa (Table 2) considered. Stations are indicated by different *symbols* according to their affiliation to faunistic station groups delineated by cluster analysis

Table 2 Taxa by station cluster matrix. One asterisk indicates intermediate sized, two asterisks large sponges used for the correlation between abundance of sponges and number of species (*ACT* Actiniaria, *ALC* Alcyonaria, *AMP* Amphipoda, *ANT* Anthozoa, *ASC* Ascidiacea, *AST* Asteroidea, *BIV* Bivalvia, *BRA* Brachiopoda, *BRY* Bryozoa, *CEP* Cephalopoda, *CER* Ceriantharia, *CRI* Crinoidea, *CRU* Crustacea, *CTE* Ctenophora, *DEC* Decapoda, *DEM* Demospongiae, Porifera, *ECN* Echinoidea, *ECU* Echiurida, *GAS* Gastropoda, *GOR* Gorgonaria, *HEM* Hemicordata, *HEX* Hexactinellida, Porifera, *HIR* Hirudinea, *HOL* Holothuroidea, *HYD* Hydrozoa, *ISO* Isopoda, *NEM* Nemertini, *OPH* Ophiuroidea, *PEN* Pennatularia, *PIS* Pisces, *POC* Polychaeta, *POP* Polyplacophora, *POR* other porifera, *PYC* Pycnogonida, *SCL* Scleractinia, *SCY Scyphozoa*, *SIP* Siphonophora, *ZOA* Zoantharia)

Taxa used for the community analysis and all other calculations

Taxa clusters				Total abundance (n/100 m^2)	Presence (%)	Mean abundance per station cluster (n/100 m^2)					
	Station clusters					SFR	SFP	SDF	SFD	DFS	DFP
	Area photographed (m^2)					1413.0	324.9	780.7	307.0	417.1	61.1
	Depth, 25% percentile (m)					183	594	323	977	253	
	Depth, median (m)					223	761	458	1124	438	1243
	Depth, 75% percentile (m)					484	1055	573	1162	839	
	"Yellow Lobate"*	n	DEM	0.2	10.9	0.5		0.1			
	Hydrozoa sp. 5	n	HYD	1.2	12.7	2.9					
	Nuttallochiton mirandus	n	POP	0.9	23.6	1.8	1.2	0.1			
	Austrodoris kerguelensis	n	GAS	0.5	16.4	1.1					
	Limopsis marionensis	n	BIV	1.3	18.2	2.7	1.2				
	Synascidians sp. 12	n	ASC	120.5	29.1	277.4	11.4			6.0	
	Terebellidae sp. 1	n	POC	32.5	18.2	75.9		0.1			
	Pterobranchia sp. 1	n	HEM	7.4	18.2	16.3		1.8			
	Synascidians sp. 13	n	ASC	6.7	18.2	14.3	5.5	0.3			
	Styolocordyla borealis (spheric)*	n	DEM	1.1	27.3	2.0	0.6	0.8			
	Edwardsia spp.	n	ACT	3.8	29.1	6.7	0.6	3.6			
	Isodictya sp. 2*	n	DEM	5.8	20.0	13.4		0.3			
	Chorismus antarcticus	n	DEC	0.9	21.8	1.8		0.3		0.5	
	Isodictya sp. 1*	n	DEM	1.9	14.5	4.5					
	Acodontaster conspicuus	n	AST	0.6	21.8	1.1	1.5				
	Solaster sp. 1	n	AST	0.7	21.8	1.6					
	Asteroidea sp. 14	n	AST	0.4	20.0	0.8	0.3	0.1			
	Synascidians sp. 20	n	ASC	0.9	16.4	2.1		0.1			
	Nudibranchia sp. 3	n	GAS	0.6	21.8	1.4					
	Parmaphorella mawsoni	n	GAS	2.1	29.1	4.8	0.3				
	Henricia spp.	n	AST	1.9	49.1	3.5	2.5	0.6			
	Ascidiacea sp. 4	n	ASC	1.2	30.9	2.3	1.5	0.1			
	Alloeoflustra angusta	%	BRY	11.9	27.3	27.4	0.3	0.8			
	Chondriovelum adeliensis	%	BRY	27.1	30.9	60.2		4.8		1.8	
	Cellarinella sp. 2	%	BRY	12.8	27.3	20.9	0.2	16.3			
I	*Rossella antarctica group***	n	HEX	45.9	40.0	90.0		31.5			
	Hydrozoa sp. 2	n	HYD	26.4	50.9	55.5	1.2	10.8			
	Cellarinella spp.	%	BRY	38.4	54.5	76.0	20.9	15.2		2.2	
	Synoicium spp.	n	ASC	140.0	49.1	235.5	1.2	165.6			
	"Yellow Branches"*	n	DEM	22.5	29.1	50.2	0.9	4.1			
	*Monosyringa longispina**	n	DEM	14.9	27.3	34.7	0.3				
	Stylocordyla borealis (oblong)*	n	DEM	8.7	29.1	19.7	1.5	0.8			
	Sycozoa sigillinoides	n	ASC	6.2	34.5	12.4	8.9	0.1			
	Synascidians sp. 25	n	ASC	112.1	23.6	262.1					
	Sabellidae sp. 4	n	POC	4.6	30.9	10.8	0.3				
	Sabellidae sp. 5	n	POC	14.3	38.2	29.9	12.9	1.2			
	Apodida sp. 1	n	HOL	1.6	23.6	3.5		0.6			
	Hydrozoa sp. 4	n	HYD	7.6	38.2	17.3	1.2	0.3	0.3		

Table 2 (continued)

Taxa clusters	Station clusters			Total abundance (n/100 m^2)	Presence (%)	Mean abundance per station cluster (n/100 m^2)					
						SFR	SFP	SDF	SFD	DFS	DFP
	Trematomus lepidorhinus	n	PIS	3.2	43.6	6.2	0.9	1.9		0.2	
	*Cinachyra antarctica**	n	DEM	10.0	30.9	22.8	0.9	0.9			
	*C. barbata/T. leptoderma group***	n	DEM	8.8	38.2	19.0	0.9	2.6		0.2	
	Pterobranchia sp. 2	n	HEM	8.3	21.8	13.0	1.0	11.3			
	*Polymastia isidis**	n	DEM	1.8	25.5	4.0	0.3	0.1			
	Sabellidae sp. 1	n	POC	16.4	27.3	37.7		0.4		1.4	
	Pyura setosa	n	ASC	4.3	29.1	7.9		3.8			
	Alcyonidium sp.	n	BRY	14.5	49.1	23.6	2.5	11.0		12.2	
	Bryozoa sp. 5	%	BRY	8.6	49.1	12.2	4.1	11.2	0.2	0.2	2.7
	Fasciculipora ramosa	%	BRY	6.3	45.5	7.9	0.3	11.3		1.7	
	Rhodalia miranda	n	SIP	1.8	32.7	2.0		3.3		1.4	
	Trematomus scottii	n	PIS	1.3	30.9	0.8		4.1		0.2	
	Ascidiacea sp. 15	n	ASC	0.1	5.5	0.2					
	Trematomus spp.	n	PIS	0.2	12.7	0.4		0.1		0.2	
	Tedania vanhoeffeni	n	DEM	8.3	38.2	6.6	37.6	6.4		2.2	
	Thouarella spp.	n	GOR	55.1	74.5	109.0	31.1	22.5		0.5	
	Pista spp.	n	POC	53.1	72.7	22.2	321.6	50.5		0.5	
	Sedentaria sp. 2	n	POC	12.5	50.9	5.7	55.4	18.4		1.0	
	Dendrochirotida sp. 1	n	HOL	14.9	29.1	22.7	5.2	17.0		4.8	
	Cellaria spp.	%	BRY	52.0	32.7	80.0	150.8	12.7			
	Cellarinella sp. 1	%	BRY	148.2	67.3	266.1	124.7	80.3		24.9	
	Melicerita obliqua	n	BRY	595.6	50.9	1350.3	69.9	39.1		16.3	
	Austroflustra vulgaris	%	BRY	27.9	47.3	18.3	197.1	2.8			
	*Tendania tantula**	n	DEM	56.1	40.0	126.8	12.6	2.6			
	Camptoplites tricornis	%	BRY	49.4	52.7	93.0	66.8	12.7		0.7	
	Sabellidae sp. 7	n	POC	56.9	40.0	131.6	3.1	1.2			
	Psolus dubiosus	n	HOL	7.8	54.5	11.7	16.9	4.7	0.3	0.2	
	Iophon radiatus	n	DEM	19.1	45.5	42.9	3.4	1.4			
	Lageneschara lyrulata	%	BRY	102.7	60.0	226.6	16.9	15.7		3.9	
	*Rossella racovitzae***	n	HEX	31.3	61.8	69.8	3.1	4.7		0.2	
	Reteporella spp.	%	BRY	41.2	72.7	88.5	23.4	4.4		0.5	
	Carbasea curva	%	BRY	15.1	49.1	32.5	5.5	2.7			
	Taeniogyrus contortus	n	HOL	9.6	43.6	21.7	1.8	0.6			
	Homocidaris or Ctenocidaris spp.	n	ECN	0.8	14.5	0.9		1.5			
	Rossella/Scolymastra group**	n	HEX	5.7	45.5	11.9	0.9	2.0			
	Notocidaris spp.	n	ECN	24.7	60.0	56.2	2.8	1.4	0.7		
	Synascidians sp. 5	n	ASC	4.1	34.5	7.5	3.7	1.7		1.0	
	Magellania fragilis	n	BRA	67.3	54.5	150.4	1.5	10.5	2.6	0.7	
II	*Sterechinus* spp.	n	ECN	80.6	76.4	170.8	2.5	4.5	3.3	47.2	
	Pterobranchia sp. 3	n	HEM	7.9	50.9	9.6	2.2	12.4		5.5	
	Synascidians sp. 1	n	ASC	5.2	50.9	8.6	2.2	5.4		0.2	
	Pyurva bouvetensis	n	ASC	2.8	50.9	2.1	0.6	6.5		1.9	
	Pyurva discoveryi	n	ASC	13.9	54.5	19.6	6.2	20.5		0.2	
	Latrunculia apicalis	n	DEM	7.7	27.3	14.7	1.5	1.8	9.4		
	Corymorpha microrhiza	n	HYD	4.7	38.2	5.6	1.2	9.4			
	Isodictya sp. 3*	n	DEM	0.5	12.7	0.6	1.2	0.3			
	Alcyonaria sp. 3	n	ALC	1.3	23.6	2.6	1.5	0.3			
	Ceriantharia sp. 4	n	CER	1.8	25.5	3.5	1.2	0.9			

	Pterasteridae sp. 1	n	AST	1.0	27.3	1.8	1.2	0.3			
	Phorbas areolata	n	DEM	1.5	21.8	3.3	1.2				
	Bathyplotes rubipunctatus	n	HOL	1.7	27.3	2.1	8.3	0.1			
	Echiuroidea sp. 2	n	ECU	1.6	25.5	3.1	0.3	1.2			
	Eunoe hartmanae	n	POC	0.7	21.8	1.1	0.3			1.7	
	Cnemidocarpa verrucosa	n	ASC	1.4	21.8	2.8	0.9	0.3			
	*Polymastia invaginata**	n	DEM	2.2	38.2	2.8	7.4	1.2		0.2	
	Pontiothauma ergata	n	GAS	3.1	38.2	4.5	8.3	1.0	0.7	0.5	
	Primnoella spp.	n	GOR	9.1	61.8	11.4	7.7	4.7		18.5	
	Cyclostomata sp. 1	%	BRY	16.1	45.5	30.9	18.1	3.4		2.4	
	Alcyonaria sp. 1	n	ALC	3.1	32.7	5.7	4.6	0.3		1.0	
	Colossendeis spp.	n	PYC	1.3	29.1	2.1	0.9	1.0			4.9
	Synascidians sp. 9	n	ASC	2.9	25.5	3.1	0.6	6.5			
	Pyura tunica	n	ASC	1.3	18.2	2.3	1.5	0.8			
	Neobuccinum eatoni	n	GAS	0.6	21.8	0.8	1.8	0.4			
	Laetmonice producta	n	POC	0.6	23.6	0.2	2.2	1.3			
	Bathyplotes fuscivinculum	n	HOL	0.3	16.4	0.1	0.9	0.6		0.2	
	Synascidians sp. 7	n	ASC	1.3	27.3	2.4	0.3	1.2			
	Isosicyonis alba	n	ACT	1.3	34.5	0.9	1.2	3.2			
	Harpovoluta charcoti	n	GAS	1.4	41.8	1.3	1.2	3.2			
	Sedentaria sp. 1	n	POC	2.1	38.2	0.8	0.6	6.7	0.3	1.0	
	Chiridota weddellensis	n	HOL	4.7	45.5	2.6	13.9	9.5			
III	Gorgonaria sp. 6	n	GOR	17.5	36.4	28.5	17.9	14.7		0.5	
	Ascidiacea sp. 10	n	ASC	2.1	32.7	3.3	2.2	2.2			
	Actiniaria sp. 15	n	ACT	0.2	9.1	0.1		0.6			
	Ceriantharia sp. 5	n	CER	0.6	12.7	0.2		2.0			
	Gorgonaria sp. 8	n	GOR	0.8	18.2	0.6		1.8		0.5	
	Aforia magnifica	n	GAS	0.4	14.5		0.3	1.3	0.3	0.2	
	Sabellidae sp. 10	n	POC	1.3	10.9	0.1		5.3			
	Sabellidae sp. 9	n	POC	0.5	14.5	0.4		1.2			
	Terebellidae sp. 4	n	POC	0.5	18.2	0.6		1.2			
	Gerlachea australis	n	PIS	0.2	9.1	0.1		0.4	0.3		
	Gorgonaria sp. 7	n	GOR	0.2	10.9	0.3	0.3	0.1			
	Nematoflustra flagellata	%	BRY	1.9	14.5	4.4	0.1				
	Marginella ealesae	n	GAS	0.3	10.9	0.4		0.5			
	Laternula elliptica	n	BIV	7.7	23.6	15.6		4.1			
	Sabellidae sp. 2	n	POC	26.5	9.1	61.9					
IV	Actiniaria sp. 12	n	ACT	1.3	27.3	2.5		1.0			
	Urticinopsis antarcticus	n	ACT	0.4	16.4	1.0					
	Ascidacea sp. 1	n	ASC	3.1	10.9	7.1		0.1			
	Sabellidae sp. 11n	n	POC	0.5	12.7	1.0		0.3			
	Synascidians sp. 8	n	ASC	0.5	21.8	1.1	0.3	0.3			
	Lepidonotothen nudifrons	n	PIS	0.2	7.3	0.5					
	Trematomus penellii	n	PIS	0.2	7.3	0.4					
	*Clathria pauper**	n	DEM	0.2	9.1	0.3	0.3	0.4			
	*Phorbas glaberrima**	n	DEM	2.6	12.7	6.0		0.3			
	Gorgonaria sp. 5	n	GOR	1.5	18.2	3.1		0.6			
	Gorgonaria sp. 9	n	GOR	1.2	16.4	2.5	0.3	0.1		0.2	
	Demospongia so. 3	n	DEM	0.1	7.3	0.2	0.3				
V	Alcyonaria sp. 2	n	ALC	0.4	14.5	0.6	0.6	0.3		0.2	
	Latrunculia sp. 1	n	DEM	0.4	10.9	0.7	0.3	0.1		0.5	
	*Tedania oxeata**	n	DEM	0.1	7.3	0.3					

Table 2 (continued)

Taxa clusters	Station clusters			Total abundance (n/100 m^2)	Presence (%)	Mean abundance per station cluster (n/100 m^2)					
						SFR	SFP	SDF	SFD	DFS	DFP
	Falsimargarita gemma	n	GAS	0.3	10.9	0.7					
	Serolis bouvieri	n	ISO	0.4	7.3	0.6	1.5				
	Labidiaster annulatus	n	AST	0.4	7.3	0.5	1.5				
	Amauropsis grisea	n	GAS	0.1	5.5		0.6	0.1			
	Tentorium semisuberites	n	DEM	10.8	12.7		109.3	0.3	0.3		
	Nematocarcinus lanceopes	n	DEC	1.3	16.4		8.6	1.7		0.5	
	*Isodictya toxophilla**	n	DEM	1.5	20.0	2.3	5.2				
VI	*Hornera* sp. 1	n	BRY	1.8	16.4	1.7	9.2	0.5			
	Hornera sp. 2	n	BRY	2.2	18.2	1.4	16.0	0.1			
	Cyclostomata sp. 2	n	BRY	0.9	12.7	1.6	2.5	0.1			
	Asteroidea sp. 18	n	AST	0.8	21.8	1.5	1.5			0.2	
	Ascidiacea sp. 13	n	ASC	85.0	7.3	104.5	409.7				
	Demospongia sp. 8	n	DEM	0.3	5.5	0.6		0.1			
	Haliclonidae sp. 2	n	DEM	0.4	5.5	0.8		0.3			
	"TWWSS"	n	DEM	2.2	14.5		6.8	6.4			
VII	Ampeliscidae sp. 1	n	AMP	9.3	18.2	0.2	1.8	38.2			
	Cyclostomata sp. 3	n	BRY	3.5	18.2	1.9	25.2	0.9			
	Enteropneusta sp.	n	HEM	1.2	20.0	1.8	1.8	0.9			
	Asteroidea sp. 17	n	AST	1.4	41.8	2.1		1.9	0.3	0.2	
	Pseudostichopus villosus	n	HOL	0.9	21.8	1.3	0.3	1.0		0.5	
	Ceriantharia sp. 1	n	CER	3.4	18.2	0.4		1.7	0.3	22.1	
	Ceriantharia sp. 3	n	CER	29.8	40.0	1.3		5.4	2.3	219.6	
	Gorgonaria sp. 4	n	GOR	3.3	20.0			13.3		1.2	
VIII	*Notocrangon antarcticus*	n	DEC	8.3	36.4	1.9	0.3	23.4	1.0	14.6	
	Gorgonaria sp. 3	n	GOR	0.9	14.5	0.6		2.4		0.5	
	Umbellula sp. 1	n	PEN	0.5	14.5	0.1	0.3	1.9		0.2	
	Prionodraco evansii	n	PIS	0.9	14.5	0.5		2.3		1.2	
	Demospongia sp. 5*	n	DEM	0.2	5.5	0.3	0.3				
	Probuccinum tenuistriatum	n	GAS	0.2	5.5	0.2	0.6				
IX	*Ekmocucumis turqueti*	n	HOL	0.3	5.5	0.6					
	*Isodictya cavicornuta**	n	DEM	0.2	5.5	0.3	0.3				
	Glyptonotus antarcticus	n	ISO	0.2	9.1	0.5					
	Artedidraco orianae	n	PIS	0.2	5.5	0.4					
	Achlyonice violaecuspidata	n	HOL	15.1	18.2	0.6	2.5	32.0	0.3	55.6	
	*Mycale acerata**	n	DEM	1.8	12.7	1.1	1.2	5.4			
X	*Ceriantharia* sp. 2	n	CER	0.4	10.9	0.1		0.5	1.6	0.5	
	Tentorium papillatum	n	DEM	0.6	9.1		4.0	0.9			
	Bathydraco spp.	n	PIS	0.1	5.5		0.3	0.4			
	Newnesia antarctica	n	GAS	0.1	5.5	0.1				0.2	
	Asteroidea sp. 16	n	AST	0.1	5.5	0.2					
XI	Synascidians sp. 6	n	ASC	12.7	29.1	28.1	1.8	2.2			
	Synascidians sp. 17	n	ASC	8.9	20.0	17.0		6.8			
	Gorgonaria sp. 2	n	GOR	0.5	18.2	1.0		0.5			
	Cygnodraco mawsoni	n	PIS	0.2	9.1	0.3		0.1			
	Serolidae sp. 1	n	ISO	0.5	5.5			0.3		3.8	
	Lunulariidae sp. 1	n	BRY	0.9	5.5					7.4	

XII	Synascidians sp. 19	n	ASC	1.0	9.1			0.1		7.9	
	Echiuroinea sp. 1	n	ECU	0.5	16.4	0.4		0.1		2.2	
	Pseudostichopus mollis	n	HOL	0.4	10.9			0.5	0.3	1.7	
	Pogonophryne spp.	n	PIS	0.2	9.1	0.3		0.1		0.5	
	Asteroidea sp. 8	n	AST	0.2	10.9	0.4	0.3				
	Asteroidea sp. 24	n	AST	0.2	9.1	0.4					
XIII	*Diplasterias brucei*	n	AST	0.6	20.0	1.5					
	Lucernaria spp.	n	SYC	0.2	10.9	0.3		0.5			
	Astrotoma agassizii	n	OPH	1.0	12.7	1.8		1.0			
	Actiniaria sp. 13	n	ACT	0.5	12.7	0.8		0.6			
	Psolidae sp. 1	n	HOL	0.6	9.1	1.3	0.3	0.1			
XIV	*Isodictya* spp.*	n	DEM	0.4	9.1	0.7		0.3			
	Macroptyaster sp.	n	AST	0.1	5.5	0.2	0.3				
	Ascidia challengeri	n	ASC	0.2	5.5	0.1			1.6		
	Hydrozoa sp. 3	n	HYD	0.6	9.1	0.2		2.3			
	Synascidians sp. 4	n	ASC	0.4	9.1	0.4		0.9			
XV	Synascidians sp. 16	n	ASC	0.8	14.5	1.1		1.2		0.5	
	Haliclonidae sp. 3*	n	DEM	0.2	9.1	0.1		0.4		0.5	
	Ascidiacea sp. 14	n	ASC	0.2	5.5	0.2		0.1		0.2	
	Actiniaria sp. 4	n	ACT	0.4	14.5	0.5		0.4	0.3	0.2	
	Bryozoa sp. 19	n	BRY	0.2	5.5			0.9			
XVI	*Dolliodraco longedorsalis*	n	PIS	0.3	7.3			1.2			
	Lyrocteis flavopallidus	n	CTE	0.5	21.8	0.4	0.6	0.8		1.0	
	Trematomus leonnbergii	n	PIS	0.4	14.5	0.4		0.5	0.3	0.5	
	Demospongia sp. 9	n	DEM	0.9	12.7		3.7		4.9	0.5	
XVII	Actiniaria sp. 5	n	ACT	0.6	18.2	0.4			2.6	1.2	
	Hymenaster sp. 1	n	AST	0.8	9.1		3.1		2.3	1.9	
	Alcyonaria sp. 4	n	ALC	0.1	5.5	0.2					
XVIII	Serolidae spp.	n	ISO	0.2	5.5	0.1		0.4			
	Chionodraco myersi	n	PIS	0.2	7.3	0.2	0.3	0.4			
Taxa not used for the cluster analysis but for all other calculations e.g. diversity											
	"BYNTB"	n	DEM	0.1	3.6	0.1	0.6				
	*Bathydorus spinosus**	n	HEX	0.2	3.6				0.3		6.5
	Ectydoryx anacantha	n	DEM	0.1	3.6	0.2					
	Ectydoryx ramilobosa	n	DEM	0.1	1.8	0.2					
	Haliclonidae sp. 1*	n	DEM	0.1	3.6	0.3					
	Haliclonidae sp. 9*	n	DEM	0.1	3.6	0.1	0.6				
	*Larunculia brevis**	n	DEM	0.1	3.6	0.1					
	Petrosiada spp.	n	DEM	< 0.1	1.8			0.1			
	Plakina sp. 1	n	DEM	0.2	1.8			0.9			
	Poecilosderidia sp.**	n	DEM	0.1	1.8	0.2					
	Porifera sp. 2**	n	DEM	0.2	3.6	0.2				1.0	
	Porifera sp. 22	n	DEM	1.1	1.8	2.5					
	Porifera sp. 26**	n	DEM	0.1	3.6			0.3			
	Porifera sp. 27**	n	DEM	0.2	3.6		2.2				
	Porifera sp. 34**	n	DEM	< 0.1	1.8	0.1					
	Porifera sp. 40**	n	DEM	0.2	1.8	0.4					
	Ceriantharia sp. 7	n	CER	0.3	3.6	0.6		0.1			
	Zoantharia sp. 1	n	ZOA	0.5	3.6	1.3					
	Alcyonaria spp.	n	ALC	< 0.1	1.8	0.1					

Table 2 (continued)

Taxa clusters	Station clusters			Total abundance (n/100 m^2)	Presence (%)	Mean abundance per station cluster (n/100 m^2)					
						SFR	SFP	SDF	SFD	DFS	DFP
	Alcyonaria sp. 5	n	ALC	0.1	3.6			0.1		0.2	
	Bryozoa/Porifera sp. 1	%		0.3	1.8		2.8				
	Adamussium colbecki	n	BIV	0.1	3.6				1.0		
	Amauropsis rossiana	n	GAS	0.1	3.6	0.1	0.3				
	Marseniopsis mollis	n	GAS	0.3	1.8	0.8					
	Marseniopsis sp. 1	n	GAS	< 0.1	1.8	0.1					
	Notaeolidia subgigas	n	GAS	< 0.1	1.8	0.1					
	Echiuroinea spp.	n	ECU	< 0.1	1.8			0.1			
	Hirudinea sp.	n	HIR	< 0.1	1.8		0.3				
	Polynoidae sp. 1	n	POC	0.1	3.6	0.1	0.3				
	Polynoidae sp. 2	n	POC	< 0.1	1.8					0.2	
	Polynoidae sp. 3	n	POC	< 0.1	1.8	0.1					
	Sedendtaria sp. 4	n	POC	24.2	3.6				67.4	141.9	
	Serolidae sp. 2	n	ISO	0.1	3.6				0.3	0.2	
	Asteroidea sp. 7	n	AST	< 0.1	1.8			0.1			
	Asteroidea sp. 15	n	AST	0.1	3.6	0.1					
	Porania antarctica	n	AST	0.1	3.6	0.1					
	Solaster sp. 2	n	AST	< 0.1	1.8	0.1					
	Elpidia glacialis	n	HOL	28.9	3.6			0.1		228.5	
	Laetmogone wyvillethompsoni	n	HOL	< 0.1	1.8			0.1			
	Scotoplanes globosa	n	HOL	0.1	3.6			0.1		0.2	
	Ascidiacea sp. 16	n	ASC	< 0.1	1.8	0.1					
	Synascidians sp. 29	n	ASC	0.1	3.6	0.1	0.3				
	Akrotaxis nudiceps	n	PIS	< 0.1	1.8					0.2	
	Artedidraco sp.	n	PIS	0.1	3.6		0.6			0.5	
	Dissostichus mawsoni	n	PIS	< 0.1	1.8	0.1					
	Gymnodraco acuticeps	n	PIS	0.1	3.6	0.1		0.1			
	Histodraco velifer	n	PIS	0.1	3.6	0.1					
	Notolepis coatsi	n	PIS	< 0.1	1.8	0.1					
	Notothenia spp.	n	PIS	0.1	3.6	0.1	0.3				
	Pagetopsis bernacchii	n	PIS	0.1	3.6	0.1					
	Pagetopsis macropterus	n	PIS	< 0.1	1.8					0.2	
	Pagetopsis maculatus	n	PIS	< 0.1	1.8			0.1			
	Pleuragramma antarcticum	n	PIS	0.1	3.6	0.2					
	Taxa of coarse identification level only considered for the calculation of abundances										
	Porifera spp.	n	POR	27.9	72.7	21.9	32.9	25.6	4.9	70.0	
	Demospongia spp.*	n	DEM	32.1	72.7	69.1	11.1	3.3	4.6	1.9	
	Hexactinellida spp.**	n	HEX	8.6	47.3	17.8	4.9	1.8	0.7		
	Gorgonaria spp.	n	GOR	6.2	54.5	9.7	2.8	7.7			
	Hydrozoa/Bryozoa spp.	%		336.0	83.6	571.5	545.3	122.8	1.0	70.4	
	Hydrozoa spp.	%	HYD	1.8	12.7	4.0	0.3	0.1		0.2	
	Actiniaria spp.	n	ACT	5.4	70.9	7.4	4.3	4.5	2.3	4.8	
	Anthozoa spp.	n	ANT	19.2	87.3	29.0	8.9	13.1	19.5	5.3	18.0
	Bryozoa spp.	%	BRY	1.2	14.5	1.9		1.5	0.2		
	Cyclostomata spp.	n	BRY	1.2	23.6	1.3	4.9	0.5			

Flustridae spp.	%	BRY	18.9	25.5	8.9	149.6	1.8			
Nemertini spp.	n	NEM	1.6	47.3	2.5	1.2	1.5	0.3	0.2	
Mollusca spp.	n	GAS	< 0.1	1.8	0.1					
Gastropoda spp.	n	GAS	0.3	10.9		2.2	0.3			
Nudibranchia spp.	n	GAS	1.5	32.7	2.7	1.5	0.6			
Octopoda spp.	n	CEP	1.1	38.2	2.0	0.3	0.6		0.2	
Polychaeta spp.	n	POC	1.9	34.5	1.2	3.1	3.2		2.6	
Flabelligeridae spp.	n	POC	1.2	21.8	2.3		0.5		1.0	
Polynoidae spp.	n	POC	0.6	18.2	1.3	0.9				
Sabellidae spp.	n	POC	40.0	76.4	76.4	20.6	22.3		0.5	
Sedentaria spp.	n	POC	3.1	41.8	4.8	4.3	2.0	1.3	0.2	
Serpulidae spp.	n	POC	0.6	9.1	0.8		1.3			
Pycnogonida spp.	n	PYC	20.5	74.5	36.2	11.1	15.9	0.3	1.0	
Ammotheidae spp.	n	PYC	1.7	14.5	3.4		1.2			
Crustacea spp.	n	CRU	0.2	5.5	0.1	1.2		0.7		
Amphipoda spp.	n	AMP	7.1	70.9	11.3	0.3	7.2	1.3	3.4	
Isopoda spp.	n	ISO	< 0.1	1.8	0.1					
Arcturidae spp.	n	ISO	0.3	10.9	0.6				0.2	
Pterobranchia spp	n	HEM	0.1	3.6	0.1					
Crinoidea spp.	n	CRI	53.8	80.0	82.0	84.6	43.4	0.7	0.7	
Cidaridae spp.	n	ECN	0.3	10.9	0.5		0.3			
Irregularia spp.	n	ECN	4.4	52.7	7.1	1.5	5.4			
Asteroidea spp.	n	AST	36.5	92.7	68.5	39.1	11.9	1.3	3.1	
Ophiuroidea spp.	n	OPH	963.1	100.0	1657.7	635.6	705.6	42.0	161.1	37.6
Gorgonocephalidae spp.	n	OPH	2.3	20.0	5.0	0.3	0.6		0.2	
Aspidochirotida spp.	n	HOL	< 0.1	1.8		0.3				
Dendrochirotida spp.	n	HOL	150.2	80.0	328.0	38.5	25.2		1.2	
Elasipodida spp.	n	HOL	1.8	20.0	0.4	4.9	2.3		4.8	
Ascidiacea spp. (solitary)	n	ASC	10.0	78.2	14.0	15.1	9.2	0.7	2.2	
Synascidians spp.	n	ASC	60.7	80.0	126.3	15.7	20.1	1.0	2.4	
Pisces spp.	n	PIS	0.5	20.0	0.6	0.3	0.6		1.0	
Artedidraconidae spp.	n	PIS	< 0.1	1.8	0.1					
Bathydraconidae spp.	n	PIS	0.3	10.9	0.5	0.3	0.1			
Channichthyidae spp.	n	PIS	0.1	3.6			0.3			
Liparidae spp.	n	PIS	0.1	3.6	0.2					
Zoarcidae spp.	n	PIS	< 0.1	1.8	0.1					
$\Sigma(n/100\ m^2)$			4603.6		8402.3	3649.0	2019.3	188.6	1232.2	67.1
No. of taxa			313		273	173	216	46	110	4

Relationships between physical and biological data

Nine physical parameters were used: (1) water depth; (2) south-west-northeast gradient, represented by a line parallel to the coast on which the stations were aligned; distances between the south-westernmost end of this line and these quasi-positions of the stations were used for the analysis; (3) distance between the station and coast (shelf ice); (4) width of the continental shelf (only considered for stations on the shelf); (5) number of photographs with no small stones (0.5–10.0 cm long); (6) number of photographs with >20 small stones (0.5–10.0 cm long); (7) number of photographs with large stones (>10.0 cm long); (8) number of photographs with >1% cover of the sediment by biogenic debris; (9) cover of the sediment surface by phytodetritus (Gutt et al. in press). The explorative BIOENV procedure proposed by Clarke and Ainsworth (1993) was used to analyse to what degree these parameters were related to the faunistic distribution represented in the Bray-Curtis similarity matrix. None of the physical parameters were correlated when pairwise tested ($r < 0.75$). Harmonic Spearman rank correlation coefficients (s) were computed between faunistic and physical resemblances for each of the nine physical parameters alone ($k = 1$) and for all possible ($k = 2, 3, \ldots, 9$) combinations. It is then possible to identify the sub-set of physical parameters that correlates best with the megabenthic distribution. Station VI 376 was excluded because of the extremely low number of taxa.

Results

Numbers of taxa/abundances/presences

A total of 144,531 megabenthic specimens belonging to 313 taxa were counted on 3,768 underwater photographs taken at 55 stations (Table 2). The grand average megafaunal density was 46.0 n/m^2; the median was 27.8 n/m^2. These values included the percent seafloor cover by colonial taxa. The Porifera, Ascidiacea and Bryozoa accounted for the highest number of taxa (53, 29, 24). Mean abundances per station cluster, as well as mean abundances and frequencies of occurrence (presences) for the total study area, are listed for each taxon in Table 2. In Table 2, 214 taxa are ordered according to the cluster analysis result. Table 2 also lists 54 taxa included in the diversity calculations, but not in the cluster analysis or MDS; the table contains another 46 taxa identified at a coarse level. All undetermined species mentioned in the text and in Tables 3 and 4 are briefly described in the Appendix. To enable comparisons with other publications, a few undetermined species are not consecutively numbered. General results for abundances and presences are presented in Table 3. Overall, ophiuroids were most abundant, followed by the bryozoan *Melicerita obliqua*. Only 2.5% of all taxa had a total average abundance of >100.0/100 m^2 and 51% had a low abundance of <1.0/100 m^2. Of the 268 taxa that were identified to species or genus level, 37% were rare with presences at <10% of the stations. Only 7.5% occurred at more than 50% of the stations with the sea urchin *Sterechinus* spp. being the most common taxon (Table 3). For the entire area, 52% of the taxa and 68% of the specimens were sessile or sedentary suspension feeders.

Community analysis and key taxa

Stations were classified into six clusters (Table 2, Fig. 1a); a similar grouping was recognizable in the MDS-plot (Fig. 1b). For the taxa, 18 clusters were created at the 0% similarity level.

The "Suspension Feeders, Rich" (SFR) cluster consisted of stations in the northern part of the investigation area and of five more southern stations off Halley Bay (Figs. 1a, 2a,b). Its key taxa (Table 4) encompassed various suspension feeders, *Synoicium* spp. (ASC), *Lageneschara lyrulata* (BRY), *Rossella racovitzae* (HEX), and *Iophon radiatus* (DEM) and one detritus feeder, *Taeniogyrus contortus* (HOL) For abbreviations of higher taxa see legend of Table 2.

Most stations of the "Suspension Feeders, Poor" (SFP) cluster were scattered through the northern part of the study area, with only one station on the eastern slope of the Filchner Depression (Fig. 1a). This cluster had a similar faunistic composition, at a high taxonomic level, to SFR; however, abundances and numbers of taxa were

Table 3 Most abundant and common taxa in the entire area of investigation (for abbreviations of taxa see Table 2)

	Taxon	Grand average abundance (n/100 m^2)
Most abundant taxa	*Ophiuroidea* spp.	963.1
	Melicerita obliqua (BRY)	595.6
	Hydrozoa/Bryozoa spp.	249.9
Additional most abundant taxa (species/genus level)	*Synoicium* spp. (ASC)	140.0
	Synascidians sp. 12	120.5
		Presence across all stations (%)
Most common taxa	*Sterechinus* spp. (ECN)	76.4
	Thouarella spp. (GOR)	74.5
	Reteporella spp. (BRY)	72.7
	Pista spp. (POC)	72.7
	Cellarinella sp. 1 (BRY)	67.3
	Rossella racovitzae (HEX)	61.8
	Primnoella spp. (GOR)	61.8
	Lagenschara lyrulata (BRY)	60.0
	Notocidaris spp. (ECN)	60.0

Table 4 Key taxa that serve as discriminators between one cluster and the rest of the stations. Abundances in $n/100\ m^2$

Taxa	Cluster	Averaged abundance in the cluster	Averaged abundance outside the cluster	Average dissimilarity d_i	$d_i/SD(d_i)$
Rossella racovitzae (HEX)	SFR	41.08	1.60	1.13	1.41
Lagenschara lyrulata (BRY)	SFR	133.39	6.45	1.34	1.39
Taeniogyrus contortus (HOL)	SFR	12.75	0.37	0.84	1.34
Synoicium spp. (ASC)	SFR	138.67	42.23	1.38	1.31
lophon radiatus (DEM)	SFR	25.25	0.80	0.99	1.31
Pontiothauma ergata (GAS)	SFP	3.86	1.60	0.99	1.35
Austroflustra vulgaris (BRY)	SFP	91.49	5.99	1.86	1.25
Sedentaria sp. 2 (POC)	SFP	25.71	4.96	1.38	1.21
Fasciulipora ramosa (BRY)	SDF	6.76	2.90	0.84	1.23
Pyura discoveryi (ASC)	SDF	12.31	7.27	0.83	1.14
Notocrangon antarcticus (DEC)	SDF	14.08	2.24	1.25	1.12
Chiridota weddellensis (HOL)	SDF	5.69	2.00	0.92	1.12
Sedentaria sp. 1 (POC)	SDF	4.00	0.46	0.81	1.11
Actiniaria sp. 5 (ACT)	SFD	2.00	0.22	1.30	1.06
Latrunculia apicalis (DEM)	SFD	7.25	4.52	1.70	0.96
Ceriantharia sp. 3 (CER)	DFS	152.67	1.40	2.52	1.09
Primnoella spp. (GOR)	DFS	12.83	4.65	1.25	1.02
Ceriantharia sp. 1 (CER)	DFS	15.33	0.42	1.36	1.01

lower (Figs 3a,b, 4a). All key taxa, *Pontiothauma ergata* (GAS), *Austroflustra vulgaris* (BRY), and Sedentaria sp. 2 (POC), belonged to the taxon cluster II, which also dominated the SFR (Table 4).

The majority of stations belonging to the "Suspension and Detritus Feeders" (SDF) cluster were situated in the Halley Bay area. In addition, one station on the south-easternmost Weddell Sea shelf and two at Kapp Norvegia (Fig. 1a) belonged to this cluster. In contrast to SFR and SFP, the abundance proportion of ophiuroids was high and that of the bryozoans low (Fig. 4a). The abundances were lower than in SFP, while the numbers of taxa were similar (Fig. 3a,b). The key taxa (Table 4) were two detritus feeders, *Notocrangon antarcticus* (DEC) and the partly infaunal *Chiridota weddellensis* (HOL), two sessile suspension feeders, *Fasciulipora ramosa* (BRY) and *Pyura discoveryi* (ASC), and one polychaete, Sedentaria sp. 1.

The "Suspension Feeders, Deep" (SFD) cluster consisted of four stations with extremely low abundances and low numbers of taxa (Fig. 3a, b). These stations were concentrated at the eastern margin of the Filchner Depression (Fig. 1a). Ophiuroids, anthozoans and, at one station, polychaetes predominated (Fig. 4a). Consequently, Actiniaria sp. 5, was the only good key species found among the taxa identified at the genus or species level (Table 4).

Stations of the "Detritus Feeders, Shallow" (DFS) cluster were found in the southern Weddell Sea, in the Filchner Depression and once in the Lazarev Sea (Fig. 1a). This cluster was characterized by the dominance of detritus feeders (Fig. 2c) and a variety of higher taxa (Fig. 4a). The largest proportion of the dominant holothurians belonged to two deposit-feeding species, *Achlyonice violaecuspidata* and *Elpidia glacialis*, which occurred in dense patches. The half infaunal Ceriantharia were next in abundance, followed by polychaetes, ophiuroids, bryozoans, and echinoids. Key taxa were Ceriantharia sp. 3, Ceriantharia sp. 1, and the sessile suspension feeder, *Primnoella* spp. (Table 4).

The abundance of epibenthic taxa at station VI 376, cluster "Detritus Feeders, extremely Poor" (DFP), was so low (Fig. 3a) that no key species were calculated and general faunistic conclusions could not be drawn. This station was located in the southernmost Weddell Sea (Fig. 1a) at a water depth of 1,243 m.

Diversity

The numbers of taxa at single stations were highest in SFR, with a maximum of 124 (Fig. 3b). The clusters SFP and SDF had intermediate values and SFD and DFS contained less than half the taxa of the clusters mentioned above (Kruskal-Wallis test, 2-tailed, $P < 0.05$). The Shannon indices for diversity of SFR, SFP and SDF did not differ considerably. The medians between 2.0 and 2.5 of these station groups were higher than those of SFD, DFS and DFP (medians < 1.8; Kruskal-Wallis test, 2-tailed, $P < 0.05$). No significant differences between clusters with more than one station were found for evenness values with medians ranging from 0.45 to 0.80.

Biological interactions

The abundance of small (diameter < 5 cm) and intermediate-sized (diameter 5–10 cm) sponges and the number of all other species in the richest station cluster SFR showed no significant correlation (Spearman-Rank correlation; $P > 0.05$, 2-tailed). The correlation,

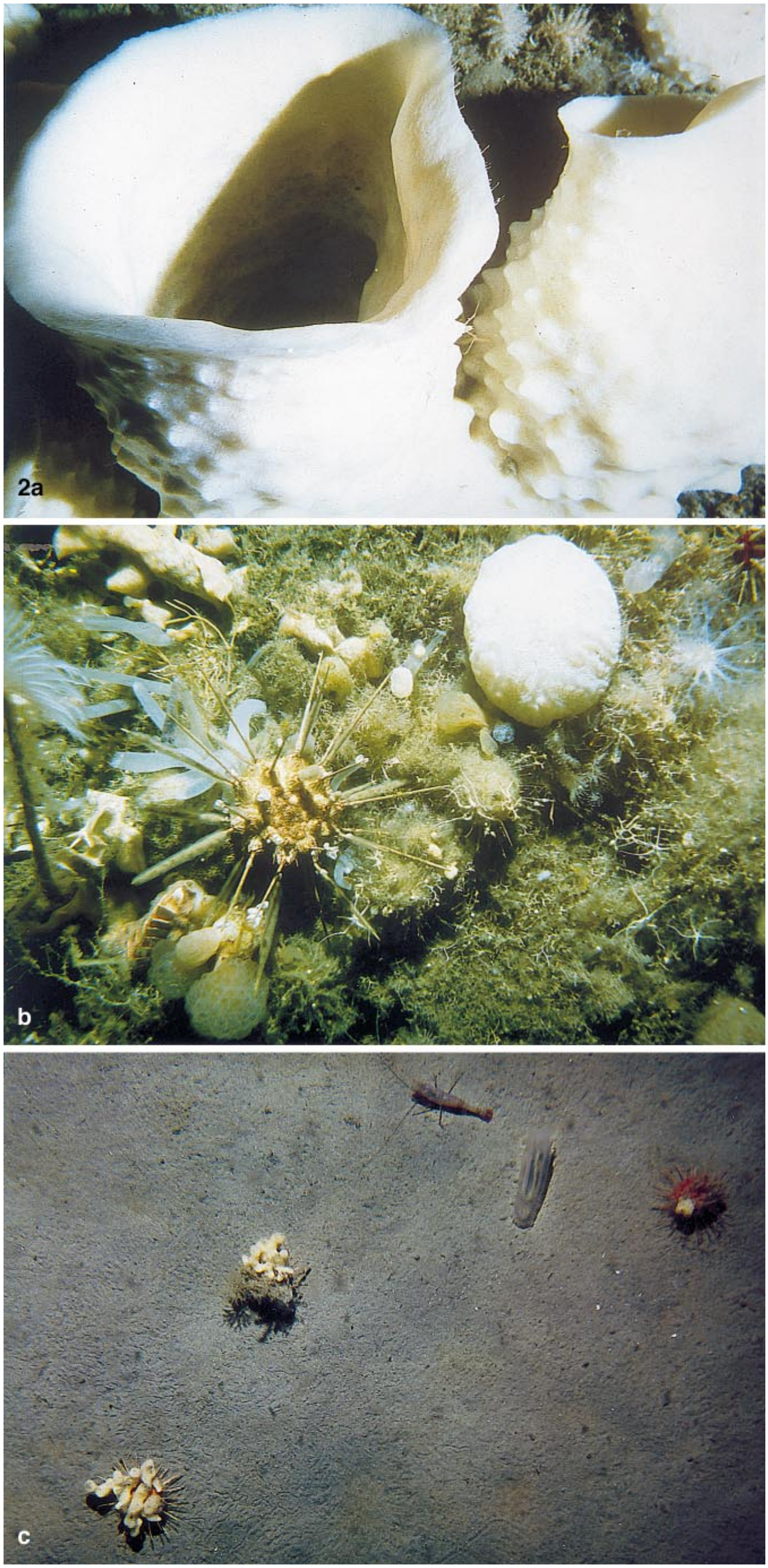

Fig. 2a–c Underwater photographs from the Weddell and Lazarev Seas (area photographed approximately 0.6 m^2). **a** "Suspension Feeder, Rich" station cluster, two glass sponges, *Rossella racovitzae*, 74°41′S 29°26′W, 580-m water depth. **b** "Suspension Feeder, Rich" station cluster, seafloor almost totally covered by epifauna: *upper left*: tubiform demosponges, *Monosyringa longispina* (translucent siphons of the infaunal demosponge); *lower left*: *Nutallochiton mirandus* (Polyplacophora) and compound ascidians *Synoicium* spp. *below centre*: pencil sea urchin *Homocidaris* or *Ctenocidaris* spp. with encrusting sponges and *Lissarca notorcadensis* (Bivalvia) as epizoites; small specimens of the glass sponges from the *Rossella antarctica* group *right* of it; *upper right*: pencil sea urchin *Notocidaris* spp., a dendrochirote holothurian, a large compound ascidian (Synascidians sp. 26) and with a few tiny, partly translucent, other compound ascidians *below* and *left* of it; *lower right*: small ophiuroids between bryozoan debris and sponge spicule mats. 71°07′S 11°41′W, 205-m water depth. **c** "Detritus Feeders, Shallow" station cluster, three sea urchins, *Sterechinus* spp. partly covered by sponges and other epizoites, one elasipode holothurian, one shrimp *Notocrangon antarcticus*. 70°23′S 05°02′E, 428-m water depth

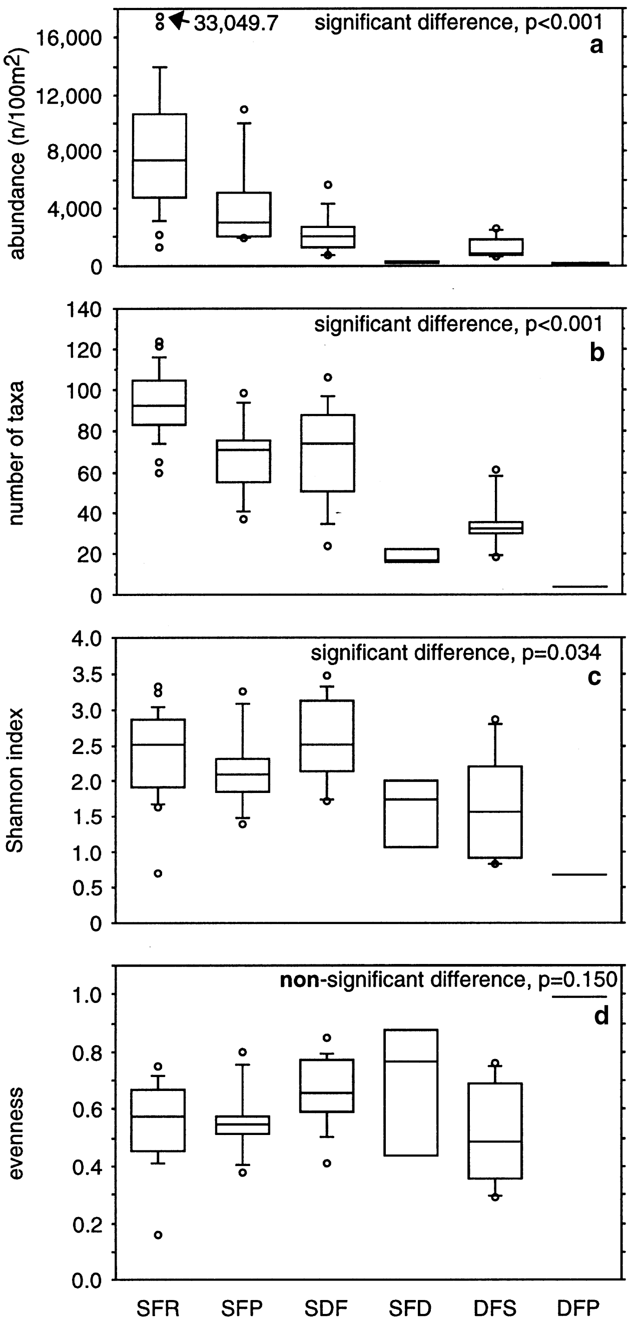

Fig. 3 Distribution of absolute abundances (**a**), numbers of taxa (**b**), diversity, H′ (**c**) and evenness values, J (**d**) within the six station clusters (for cluster abbreviations see Fig. 1). Total of 268 taxa considered. *Box plots* indicate median (*central line*), 25% and 75% percentiles (*lower* and *upper line* of the box), 10% and 90% percentiles (*lower* and *upper limit* of vertical line), and single values outside the 10% and 90% limits (*circles*)

however, was significant when only large sponges (diameter > 10 cm, Table 2) were considered (Fig. 5).

Relationship between physical and biological data

The highest correlation ($r = 0.55$) was found when the combination of no stones >10 cm, stones >10 cm, biogenic debris, water depth, SW-NE gradient, width of the shelf and phytodetritus was considered for the stations on the shelf (Table 5). The best single parameters ($r = 0.37$) were the SW-NE gradient and the width of the shelf ($r = 0.33$). If all stations were included, a combination of water depth and the SW-NE gradient had the best correlation with the biological data ($r = 0.52$).

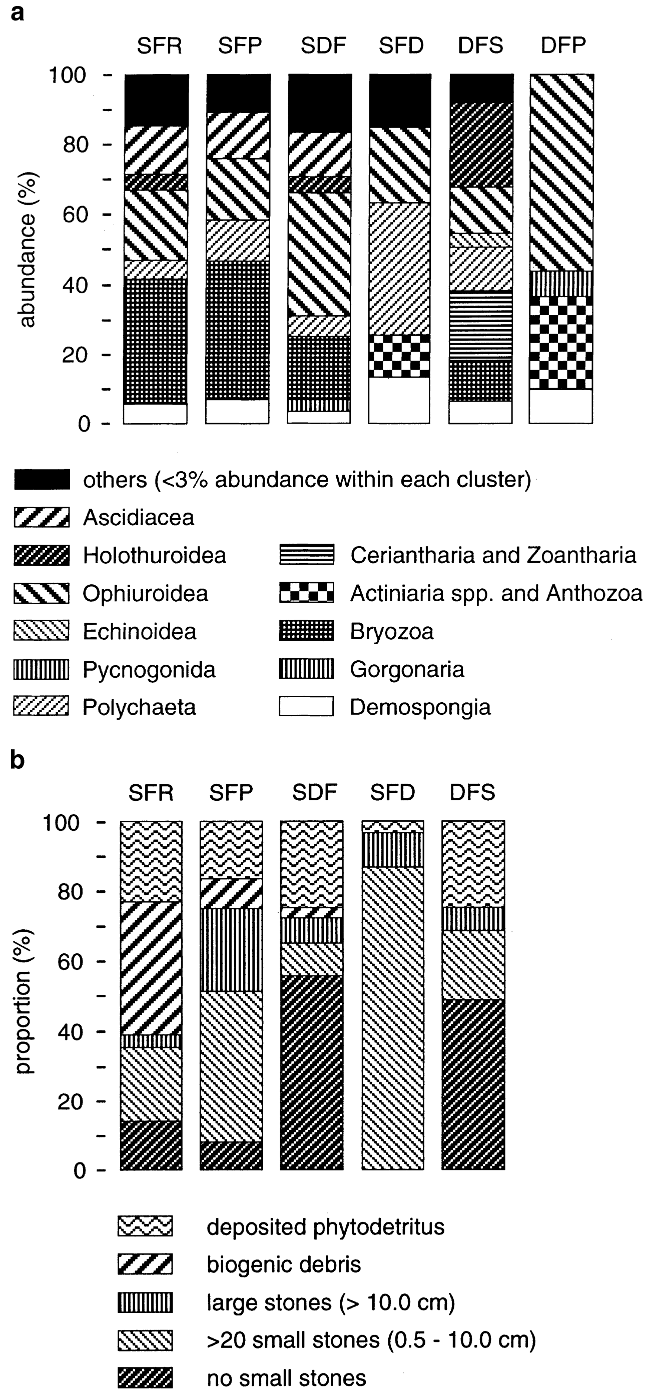

Fig. 4 **a** Relative abundance proportions on a coarse taxonomic level in the different station clusters (for abbreviations see Fig. 1). **b** Areal proportions of substrate surface types, analysed from underwater photographs in the different station clusters (not shown for the exceptional cluster DFP)

Discussion

Abundances (biomass)

A study using imaging methods on the Antarctic shelf at 70°E revealed abundances of more than 1 order of magnitude less than ours (Hamada et al. 1986), most likely because of a lower optical resolution. Photographs from the deeper shelf of the Ross Sea (Bullivant 1967) show benthic assemblages with abundances similar to our results. In Ellis Fjord (0–32 m, 68°E) Kirkwood and Burton (1988) found much higher abundances but only for one species each of the echinoids, polychaetes and gastropods.

Abundance values also obtained by underwater photography of Lemche et al. (1976) from the deep sea were lower by 1 or more orders of magnitude with very few exceptions (e.g. pennatularians). Comparable abundances for stations < 1,000 m (Ohta 1983) were higher than those of Lemche et al. (1976); however, they were lower than ours by at least 1 order of magnitude. A conversion of our abundance data can be used for a gross estimation of the wet biomass of the megabenthos. Average abundances of sponges with a mean wet weight

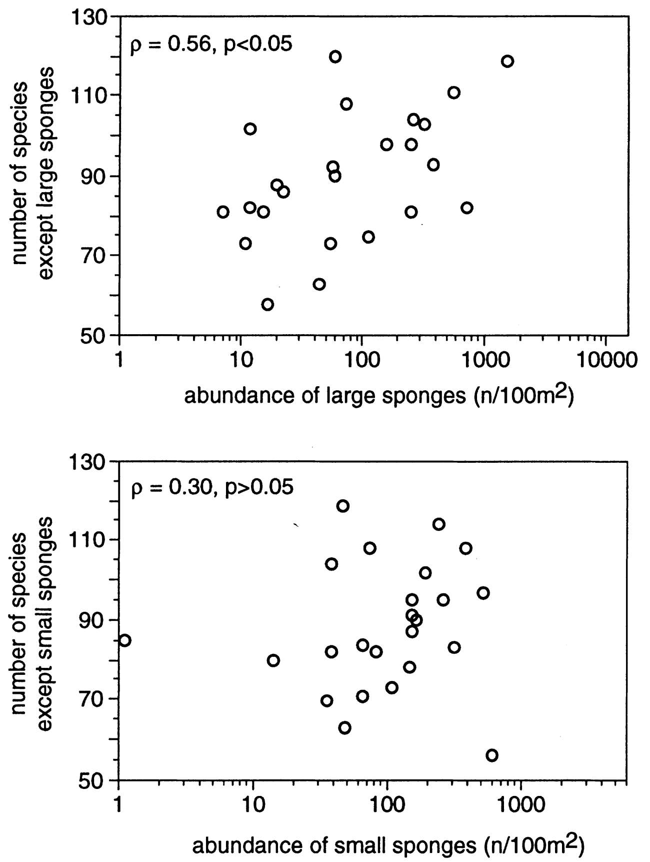

Fig. 5 Relationship between the abundance of large (diameter > 10 cm) and small-sized (diameter < 5 cm) sponges and the number of other species in the entire area of investigation. Sponge species considered are marked in Table 2 by asterisks

Table 5 Results of the BIOENV analysis. Highest rank-correlation coefficients (ρ) are listed for relationships between megabenthic distribution and single environmental factors and between megabenthic distribution and combinations of environmental factors, indicated by X

ρ	No stones < 10 cm	> 20 stones 5–10 cm	Stones > 10 cm	Biogenic debris	Depth (m)	SW-NE gradient	Width of shelf (km)	Distance from ice shelf	Phytodetritus (% cover)
Stations on the shelf									
0.369						X			
0.326							X		
0.551	X		X	X	X	X	X		X
0.547	X		X	X	X		X	X	
0.542	X		X	X			X	X	
Stations on the shelf and at the slope									
0.414					X				
0.252						X			
0.515					X	X			
0.490					X	X		X	

>1 kg (hexactinellid species, *Isodictya toxophila*, *Polymastia invaginata*, *Polymastia isidis*, *Cinachyra antarctica*, *Cinachyra barbata* group, *Monosyringa longispina*) were approximately 85/100 m^2, roughly corresponding to >0.8 kg/m^2. Assuming that all other organisms composed less than 30% of this sponge biomass, a total biomass of >1 kg/m^2 wet weight is reached. This corresponds with the highest biomass found by Belyaev and Ushakov (1957) in water depths ranging from 100 to 200 m between 90°E and 160°E, and by Propp (1970) at Haswell Island. Our estimate is higher than values reported for Signy Island (South Orkney Islands; Hardy 1972), where infauna composed a large proportion of the benthos, and from the Indian sector of the Antarctic shelf in water depths between 100 and 500 m (Belyaev 1964).

Numbers of taxa

It should be noted that the high proportion of taxa counted only once indicates that more species actually occurred in the area. Barthel and Gutt (1992) identified 34 sponge species in the Weddell Sea, using the same method. From the same locality, 150 species were found in 15 trawl catches (Barthel et al. 1990). The number of taxa recorded at the slope off Japan, 13–52 per station, (Ohta 1983) was lower than in our study area. Sessile fauna appears to be less abundant off Japan. From this we conclude that the number of all megabenthic species in the Weddell and Lazarev Seas can be assumed to be high.

Community analysis and diversity

The results show a gradient ranging from the suspension feeder cluster (SFR) through clusters with more detritus feeders (SFD, DFS) to one extremely poor station (no. 376, DFP). The majority of the stations belonged to SFR, SFP and SDF, which were relatively similar to each other. In SFP those taxa were mainly absent, which were rare in SFR. The differences between these three clusters were found at the species or genus level and did not concern life forms, feeding types or a higher taxonomic level. The sediment characteristics were also similar (Fig. 4b). Cluster SDF had a relatively low proportion of hard substrata. Motile deposit feeders were more abundant: *Notocrangon antarcticus* (DEC), Ampeliscidae sp. 1, and *Achlyonice violaecuspidata* (HOL), and on a higher taxonomic level ophiuroids also. The relatively similar values for diversity and evenness of SFR, SFP and SDF were not affected much by the variations in abundance and number of taxa within and between the clusters. The difference in water depth seems to cause a reduction of sessile suspension feeders in SFP. Cluster SFR was dominated by sessile suspension feeders, and some key species belonged to the systematic groups that were most abundant. One exceptional key species was the motile deposit feeder *Taeniogyrus contortus* (HOL), which prefers to live between branches of bryozoans or spines of sponges (Gutt 1991b). The sponge *Iophon radiatus* is also an exception because it encrusts itself on ophiuroids. The two vagile key species of SDF are known to prefer sediments not dominated by sessile species: *Notocrangon antarcticus* (DEC, see Gutt et al. 1991) and the semi-infaunal *Chiridota weddellensis* (HOL). Therefore these species mainly occur in areas with a low abundance of sessile animals. It has been postulated that high abundances of detritus feeders can cause an elevated mortality of juvenile suspension feeders (Dayton and Oliver 1980). This can change a benthic community to a deposit feeder-dominated composition (Thayer 1979; Dayton 1984), as described by Dayton et al. (1974) in McMurdo Sound. A bias of our results due to the long period of sampling can not be excluded. However, rapid growth has so far only been observed for very few litoral species (Dayton 1978; Rauschert 1991); therefore, we assume that the entire megabenthic communities did not change significantly within the 6 years that data were collected.

Physical disturbance

At station XI 175 (70°00.7′S 11°44.0′E), even though belonging to SFR, the fauna was poor and bryozoan debris almost completely covered the sediment. This probably reflects a heavy impact on the benthos through a natural disturbance that eradicated most, if not all, macrobenthic organisms. The extinction of the benthos could have been directly caused by a grounded iceberg, by a dramatic change in the near-bottom current caused by a grounded iceberg or the breaking off of a piece of the shelf-ice coast. A first attempt to estimate quantitatively and qualitatively the effect of iceberg scouring on benthic communities has been made by Gutt et al. (1996). During the time prior to this investigation only a few sessile species have grown in this area and several errant taxa have invaded. The hypothesis of a natural catastrophe is supported by the fact that the station belongs to the richest cluster SFR. The inventory of species here revealed only an impoverished composition of the other stations that belong to this cluster. In addition to some abundant errant taxa, sessile animals that were much more abundant at this station than elsewhere in the study area were *Latrunculia apicalis* (DEM) and Demospongia spp. Specimens of these species were considerably smaller than the individuals at other stations. A first conclusion is that these primary colonizers grow rapidly. Dayton (1978), however, found only intermediate growth rates for *Latrunculia apicalis* in McMurdo Sound. Thus, a second conclusion is that an important factor shaping benthic structure is the successful recruitment and survival of early life stages. This station could be an example of a low level of persistence on a small spatial scale (station), embedded in a relatively stable and undisturbed system (Hedgpeth 1971; Dayton 1972; Dayton 1990), which is the assemblage SFR.

The most significant differences between SFD and the above-mentioned station group were the low abundances and numbers of taxa, as well as the dominance of stony sediments (Fig. 4b). Besides the ubiquitous ophiuroids, sessile suspension feeders were most abundant. In contrast, the relative proportion of motile deposit feeders (mainly echinoderms) was much higher in DFS whose stations were also situated mainly in the southernmost Weddell Sea. Echinoids, and especially the elasipode holothurians, were so patchily dispersed (see also Gutt and Piepenburg 1991) that they could not serve as good key species. Two species of Ceriantharia were more evenly distributed and thus they appeared to be characteristic of this station group. They belong to the semi-infauna like *Chiridota weddellensis* (HOL), an indicator of SDF. This may be the reason why the Ceriantharia prefer a benthic assemblage with only a few other sessile organisms.

Biological interactions

In addition to physical factors, biological interactions influence species diversity and spatial dispersion patterns (Sanders 1968, 1979; Dayton and Hessler 1971; Grassle and Sanders 1973). The correlation between the abundances of large sponges and the number of other megabenthic species gives evidence of the ecological role of these sponges. If the reason for this correlation was only favourable conditions for benthic organisms in general, we would also expect a correlation between intermediate and small sponges and other species, which did not exist. So called "multi-storied assemblages" have been used to describe Antarctic benthic communities, but have never been verified (Bullivant 1967; Andriashev 1968; Knox 1970; Dearborn et al. 1973; Barthel 1992). Only Kunzmann (1996) studied how hexactinellid sponges serve as hosts for small commensals. Dayton et al. (1970) hypothesized that within a stable environment and homogenous substratum biological interactions can be most important for the evolution and maintenance of benthic communities. Therefore, this correlation can be considered as an indicator for stable physical conditions over evolutionarily relevant time scales.

Relationship between the physical and biological data

The distribution of the shelf megabenthos could best be explained by a combination of most of the physical parameters measured, the best single one being the SW-NE gradient. This confirms the weakness of the depth zonation and a more pronounced patchiness and indicates that most relevant parameters for the shelf fauna have only been measured indirectly. One of such parameters is the bottom-near current because it transports the food of the suspension and detritus feeders (see also Genin et al. 1986). Above the narrow shelf of the southeastern Weddell Sea, a coastal current is known which diverges on the wider shelf in the Halley Bay area, where the velocity is probably reduced. An additional factor is the current direction. A water mass that is enriched by organic particles can flow under the ice and support a rich assemblage there. An oligotrophic current floating from beneath the ice shelf may result in a much poorer benthos (Dayton and Oliver 1977; Barry and Dayton 1988). We assume this to be the reason for the extreme scarcity at station 376 (DFP) and for the more patchy distribution at the ice shelf coast compared to off-shore areas (Pasternak and Gusen 1960). In addition, the current velocity determines the sediment grain size. If the stations on the upper continental slope (> 500 m deep) were included in the BIOENV analysis, the depth gradient became more obvious, which indicates an ecological boundary.

Comparison with other studies in the area

The benthic species assemblage "EAST", discriminated by both Voß (1988) and Piepenburg et al. (1997) in the Weddell Sea, corresponds with our clusters SFR and SFP. The division into two related clusters is due to our additional deeper stations and our quantitative approach. The assemblage "SOUTH" (Voß/Piepenburg et al.) is situated in both studies off Halley Bay. The assemblage "TRENCH" (Voß/Piepenburg et al.) is similar to our clusters SFD, the deep stations of DFS, and DFP. A similar pattern has also been found for single systematic groups such as holothurians (Gutt 1991a), fish and shrimps (Gutt et al. 1991; Gutt et al. 1994), and sponges (Barthel and Gutt 1992; Gutt and Koltun 1995); however, the classification for the sponges was weak. Benthic community analyses on a coarser taxonomic level and based on trawl and corer sampling respectively (Galéron et al. 1992; Gerdes et al. 1992), partly coincide with our results.

Comparison with other Antarctic areas

In the Ross Sea Bullivant (1967) discriminated two "Minor Assemblages" besides others. The "McMurdo Sound Glass Sponge Assemblage", similar to our cluster SFR, is characterized by the dominance or special role of the sponges *Rossella* spp. and *Cinachyra* spp., echinoderms, molluscs, polychaetes and pycnogonids. The "McMurdo Sound Mixed Assemblage", dominated by demosponges, gorgonarians, bryozoans, echinoderms and polychaetes, corresponds to our clusters SFP and SDF. This supports the judgement of Dell (1972) that these "Minor Assemblages" are more widespread on the Antarctic shelfs than suggested by Bullivant (1967). Studies of the benthos at the Antarctic Peninsula based on grab samples show a different image. Polychaetes, molluscs and crustaceans are the predominating taxa, e.g. on soft bottom at Haswell Island (Lowry 1975), whereas bryozoans and sponges are rare and make up only a maximum of 26% of the biomass in Admiralty Bay (King George Island) and west of the Antarctic Peninsula (Jazdzewski et al. 1986; Mühlenhardt-Siegel 1988). At Greenwich Island (South Shetland Islands) polychaetes compose up to 61% of the total macrobenthic abundance (Gallardo et al. 1977).

Comparison with the shelf and slope at 75°N

At two shelf stations off northeast Greenland, the study of Meyer and Piepenburg (1996) depicted low numbers of taxa (22 and 50) compared with our clusters SDF and SFR. One extremely high abundance value off Greenland ($234/m^2$) was due to the mass occurrence of one polychaete as we found for a bryozoan ($330/m^2$). At the other shallow station Meyer and Piepenburg (1996) found a lower abundance ($26/m^2$) than our medians (31 and 75/100 m^2, SDF and SFR). Our medians for diversity (approximately 2.5) were inbetween the extremely varying values on the Greenland shelf (0.57 and 3.49); our evenness values were similar to the higher value off northeast Greenland (0.63). The deeper shelves of the Weddell and Lazarev Seas (SFP and partly DFS) had approximately twice as many taxa as the north polar upper slope, similar average abundances, but lower diversity and thus lower evenness values. The key species off northeast Greenland represented a variety of taxa from both groups, sessile suspension feeders and motile animals. From this we can confirm the general statement of a higher number of taxa in the Antarctic than in the Arctic, but we cannot confirm the hypothesis of a higher diversity in Antarctic waters. Also an assumed difference in the occurrence of sponges and other suspension feeders cannot be found; however, it seems that in the Arctic sponges are more patchily distributed or concentrated at greater depth (approximately 770 m) than in the Antarctic.

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Appendix

Short description of unidentified species mentioned in the text and Tables 3 and 4

Actiniaria sp. 5: column and disc grey-white, but white around the mouth opening, ≥3 cm in diameter, length of column apparently less long, tentacles translucent grey, half as long as disc diameter.
Ampeliscidae sp. 1: only the tubes visible consisting of sediment material, approximately 4 cm long and 1 cm in diameter, ending in a tip, sometimes branched.
Cellarinella sp. 1: dichotomic branched colonies, branches flattened with pale yellow tips.
Ceriantharia sp. 1: buried in soft sediment, tentacular crown a few centimetres above substratum, ~24 white marginal tentacles, labial tentacles short and white, in the centre of the disc a red dot (actinopharynx?).
Ceriantharia sp. 3: like Ceriantharia sp. 1 but dark-grey marginal tentacles.
Sedentaria sp. 1 and 2: tubes consisting of sediment material, 4–6 cm long, 2 cm in diameter. Sp. 2 mainly vertically sticking in the sediment, rarely lying on the sediment; sp. 2 tube sticking with one end obliquely in the sediment, down so that the opening at the other end is pointing to the sediment.
Synascidians sp. 12: yellow, < 1 cm in diameter, up to ~20 zooids, mainly on hard substratum (biogenic and terrigenous)

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