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Julian Gutt, Anna Fricke, Nuria Teixidó, Michael Potthoff, Wolf Arntz. Mega-epibenthos at Bouvet Island (South Atlantic): a spatially isolated biodiversity hot spot on a tiny geological spot. *Polar Biology*, 2006, 29 (2), pp.97-105. 10.1007/s00300-005-0012-6 . hal-00093811

HAL Id: hal-00093811

<https://hal.science/hal-00093811>

Submitted on 14 Nov 2022

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Mega-epibenthos at Bouvet Island (South Atlantic): a spatially isolated biodiversity hot spot on a tiny geological spot

Julian Gutt, Anna Fricke, Nuria Teixido, Michael Potthoff, Wolf E. Arntz

Abstract Mega-epibenthic diversity was analysed using a seabed photography at four stations off Bouvet Island and one station at the Spiess Seamount in the South Atlantic. Surprisingly, the intermediate-scale diversity within the area of investigation was not lower compared to that on the Patagonian shelf and only moderately lower than that on the Antarctic continental shelf. This result is incompatible with Mac Arthur and Wilson's Island Biogeography Theory describing species richness as a function of immigration of new species into an area and its extension. The relatively high species number and the very small extension of the Bouvet shelf compared to the much larger continental shelves of the other two areas can be explained by long-range dispersal of marine benthic animals in the Antarctic Circumpolar Current and high habitat heterogeneity. The observed uncoupling of intermediate-scale from large-scale background species diversity on the Antarctic shelf raises the question whether in these benthic systems an upper capacity limit for diversity exists.

Introduction

The area of investigation at Bouvet Island and Spiess Seamount, South Atlantic (Fig. 1) is geologically active, since it is located at the southern end of the Mid-

Atlantic Ridge where the African, Antarctic and South American lithospheric plates meet. It is situated in the Antarctic Circumpolar Current south of the Antarctic Convergence. Nothing is known about macro- or megabenthic assemblages at water depths < 600 m and their biodiversity at this "most isolated piece of land on the earth's surface" (NN, 1997). Based on the single zoogeographical findings, the Bouvet area is faunistically assigned rather to Antarctic islands and even to the continental shelf rather than to the Subantarctic Islands (Knox 1977; De Broyer and Jazdzewski 1993).

The core question of this study was whether the benthic fauna might follow the island biogeography theory (Mac Arthur and Wilson 1967) resulting in very low species richness due to extreme geographic isolation and small spatial extension or whether environmental factors such as habitat heterogeneity or physical disturbance led to a different result. To answer this question, the megabenthic community and its diversity were analysed. The results were to be compared with those from the high latitude Antarctic shelf almost 2,000 km to the south and from the Patagonian shelf situated at a distance of 4,400 km to the west (Fig. 1, Table 1), which have been published in a different context (Gutt and Starman 1998; Gutt et al. 1999) and have been recalculated to achieve the best possible compatibility. Seabed photography was used because the objective of this study demands a quantitative faunistic coverage, and because the seafloor is locally characterized by hard substrata and a rough topography, which is difficult to sample with dredges and corers. Consequently, the results presented here mainly refer to the mobile and sessile epifauna.

Materials and methods

Areas of investigation

Bouvet Island (54°24'S 003°21'E) is an almost entirely glaciated volcano rising from over 2,500-m water depth

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Fig. 1 Maps of areas of investigation with stations at Bouvet Island/Spiess Seamount

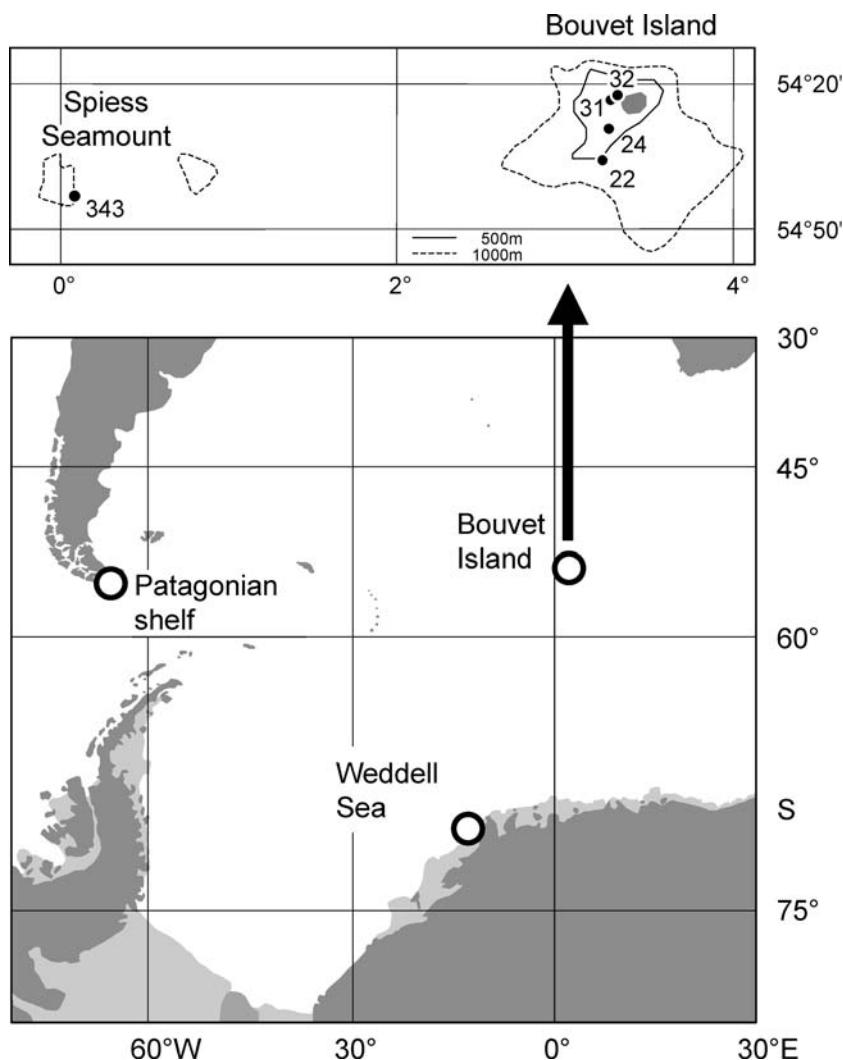


Table 1 Station list

Region, station	Latitude (S)	Longitude	Depth (m)	Transect length (m)
Bouvet Island + Spiess Seamount, ANT XXI/2				
PS65_22	54°36.3'	003°12.6' E	540	256
PS65_24	54°29.7'	003°14.0' E	245	205
PS65_31	54°23.1'	003°16.1' E	130	427
PS65_32	54°22.6'	003°17.5' E	115	340
PS65_343	54°43.9'	000°07.1' E	481	550
Weddell Sea, ANT VII/4				
PS14_274	71°37.00'	012°11.38' W	225	740
PS14_278II	71°29.75'	012°30.85' W	458	?
PS14_280	71°40.93'	012°06.46' W	107-166	?
PS14_306	71°07.32'	011°41.36' W	206	390
Patagonian shelf, ANT XIII/4				
PS40_110	55°26.35'	066°15.76' W	100	112
PS40_112	55°44.33'	066°14.68' W	430	320
PS40_113	55°44.41'	066°17.15' W	182	375
PS40_116	55°26.95'	066°09.11' W	180	410

Positions of the beginning of the photographic transect listed. Transect lengths refer to distance between first and last photograph during expeditions ANT VII/4 and ANT XIII/4 and to the total of minute-wise distances (per station) during ANT XXI/2

(Baker and Tomblin 1964). It is at least 1 million years old (Prestvik and Winsnes 1981), 9.5×7.0-km large and is surrounded by a relatively even slope, typical of volca-

noes, which is steeper and more irregular in the east than in the north- and south-western parts where sampling took place (Fjørtoft 1981). Icebergs run aground in

shallow water especially at the southern coast (personal observation). The distance between the coastline and the 400-m depth contour ranges between 5 km and 20 km. The area < 500-m deep around Bouvet is not larger than 800 km². The maximum distance between the Bouvet stations was 26 km (excl. Spiess Seamount). South of Bouvet Island Foldvik et al. (1981) measured an average current velocity of 6.7 cm/s east–northeast, and a local maximum of 50 cm/s in the middle of the water column above 585-m depth. Perissinotto et al. (1992) assumed that the ≤ 7 times greater phytoplankton summer productivity on the shelf, compared to offshore waters, is a result of reduced surface temperature and salinity due to meltwater and, consequently, to a stabilization of the water column. This seems to support a krill stock (Fevolden 1980) and, at higher level in the food web, relatively large stocks of fur and elephant seals (Kirkman et al. 2000, 2001) as well as Adélie, chinstrap and macaroni penguins, cape pigeons, silver-grey fulmars and snow petrels (Holdgate et al. 1968). The Spiess Ridge, approximately 200 km west of Bouvet Island, has a minimum water depth of 320 m, and has been described as a short and thick volcanic ridge or a large volcanic seamount (Ligi et al. 1997). The sampling site is situated ≤ 5 km south of its central caldera and has extremely uneven bottom topography.

Seabed photography

A vertically orientated 70-mm deep-sea camera (Photo-sea PS70D with two strobes Photo-sea PS 3000SX, Kodak Ektachrome 64 film) was used at four stations at Bouvet Island and one on the Spiess Seamount. It was triggered at approximately evenly spaced time intervals by a bottom contact switch at constant distance to the sea-floor resulting in an area per photograph of 1 m². In order to obtain equal sample sizes representing 63 m² the first 63 photographs per station were selected for the analyses.

Data base

Data from the Patagonian and Weddell Sea shelves (Table 1) were recalculated using the same criteria as for the Bouvet samples except for the Weddell Sea samples where the area per photograph was smaller. In order to achieve high comparability, all photos from this dataset were reconsidered resulting in an area photographed per station ranging between 41 m² and 44 m². The area photographed on the Patagonian shelf was the same as at Bouvet Island. In the Weddell Sea, the most distant stations were 64 km and on the Patagonian shelf 33 km apart from each other. The entire Patagonian shelf between 40 °S and 55 °S can roughly be estimated to be 1 Mio km²; the entire Weddell Sea shelf is 4.6 Mio km² large (Clarke and Johnston 2003).

Identification of taxa

All visible obviously living organisms ≥ 5 mm were identified to the lowest possible taxonomic level and counted. Animals that could not be identified were called IND. For Polychaeta sp. 6 (POL06), the seafloor cover was estimated in percent and in the calculations used as a proxy of true abundances since individuals could not be counted. Colonial taxa, e.g., compound ascidians were counted as individuals. Infaunal taxa were also considered when only part of their body was visible. Abundances were standardized to $n/100$ m².

Community and biodiversity analysis

Bray Curtis-similarities were calculated after fourth root transformation and excluding rare taxa, which were present at a single station with $n < 5$ (cluster *r* in Table 2) and organisms identified to a coarse taxonomic level (bulk groups = cluster *b* in Table 2). In a next step, the multi-dimensional scaling (MDS) was applied in order to visualize the similarities between stations. Classifications (dendrograms) were performed to show in a community table, which species groups characterize different station groups.

For diversity analyses, taxa identified to a coarse taxonomic level were omitted. To cover a broad variety of diversity information Shannon diversities, equitability (Pielou 1977), as well as expected number of taxa at a standardized sample (rarefaction; Hurlbert 1971) were calculated and cumulative dominance plots were created. Calculations were carried out for all five single stations (alpha-diversity) as well as for pooled abundances from the four Bouvet stations and pooled abundances from the four stations on the Patagonian and Weddell Sea shelf (intermediate scaled diversity). Beta-diversity or species turnover was determined by Bray–Curtis (faunistic) similarities between the single stations for all three large study areas. In addition, the faunistic composition is shown as proportions of abundances of individuals per higher systematic unit. A similar classification of abundances per two pooled photographs and a cumulative dominance plot were used to show the effect of iceberg scouring. Abundances of the taxa HYD01 and CRU + PAN inside and outside the iceberg scour were compared with each other by the Mann–Whitney test.

Results

A total of 20,387 individuals belonging to 145 taxa were counted on 315 photographs (~ 315 m²) from five stations resulting in a total relative abundance of $6,472n/100$ m². Most abundant at single stations were *Dendrochirotidasp.* 5 (DEN05) with $5,357n/100$ m², *Bivalvia* sp. 1 (BIV01) with $4,841n/100$ m², and *Ophiuroidea* sp. 3 (OPH03) with $2,549n/100$ m² at stations 32, 343, and 22,

Table 2 Community table with taxa and stations grouped according to the cluster analysis. Abundances as $n/100\text{ m}^2$

Cluster	Taxon	Stations				
		31	32	24	22	343
A	POL08	269.8	0.0	0.0	0.0	0.0
A	POR01	268.3	0.0	0.0	0.0	0.0
A	BRA01	44.4	0.0	0.0	0.0	0.0
A	IND22	85.7	0.0	0.0	0.0	0.0
A	BRY09	0.0	44.4	0.0	0.0	0.0
A	ALC03	0.0	12.7	0.0	0.0	0.0
A	POL05	0.0	12.7	0.0	0.0	0.0
A	ACT06	0.0	220.6	3.2	0.0	0.0
A	BIV02	0.0	1222.2	0.0	0.0	0.0
A	DEN05	0.0	331.7	0.0	0.0	0.0
A	AST06	46.0	19.0	0.0	0.0	0.0
A	GAS01	12.7	22.2	0.0	4.8	0.0
A	IND17	31.7	33.3	0.0	4.8	0.0
A	ACT01	1.6	6.3	0.0	0.0	0.0
A	AST05	4.8	7.9	1.6	0.0	0.0
A	GAS02	15.9	11.1	4.8	0.0	0.0
A	IND03	9.5	7.9	9.5	0.0	0.0
A	DEN04	2446.0	5357.1	0.0	0.0	0.0
A	HYD04	536.5	47.6	7.9	0.0	0.0
A	OPH01	63.5	1030.2	203.2	0.0	0.0
B	HYD01	7.9	42.9	1111.1	52.4	0.0
B	HYD02	1.6	0.0	100.0	7.9	0.0
B	ACT03	0.0	61.9	4.8	0.0	9.5
B	POR09	0.0	4.8	38.1	1.6	0.0
B	AST01	0.0	1.6	9.5	1.6	0.0
B	ASC01	0.0	1.6	7.9	12.7	0.0
B	POL03	0.0	4.8	1.6	0.0	0.0
B	POL01	0.0	4.8	12.7	0.0	0.0
B	POL02	0.0	3.2	4.8	0.0	0.0
B	POL04	0.0	14.3	46.0	0.0	0.0
B	POL07	0.0	14.3	101.6	0.0	0.0
B	DEC01	0.0	27.0	22.2	0.0	0.0
B	DEC02	0.0	25.4	4.8	0.0	0.0
B	NUD01	3.2	0.0	6.3	0.0	0.0
B	AST03	0.0	0.0	7.9	0.0	0.0
B	IND16	0.0	0.0	7.9	0.0	0.0
B	BRY08	0.0	0.0	11.1	0.0	0.0
B	BRY12	0.0	0.0	9.5	0.0	0.0
B	NUD02	0.0	0.0	9.5	0.0	0.0
B	BRY05	0.0	0.0	9.5	0.0	0.0
B	IND21	0.0	0.0	19.0	0.0	0.0
B	POR06	0.0	0.0	17.5	0.0	0.0
B	HYD03	0.0	0.0	17.5	0.0	0.0
B	SAS01	0.0	0.0	17.5	0.0	0.0
B	SCL01	0.0	0.0	28.6	0.0	0.0
B	BRY06	0.0	0.0	28.6	0.0	0.0
B	GOR02	0.0	0.0	36.5	0.0	0.0
B	GOR03	0.0	0.0	33.3	0.0	0.0
B	OPH07	0.0	6.3	317.5	0.0	0.0
B	POL06	0.0	0.0	579.4	0.0	0.0
B	OPH08	0.0	0.0	1281.0	0.0	0.0
B	CRU02	0.0	0.0	874.6	0.0	0.0
B	GOR01	0.0	0.0	90.5	0.0	0.0
B	BRY07	0.0	0.0	71.4	0.0	0.0
B	BRY11	0.0	0.0	225.4	0.0	0.0
B	AMP01	0.0	0.0	177.8	0.0	0.0
B	ASC03	0.0	0.0	144.4	0.0	0.0
C	ALC01	0.0	0.0	25.4	631.7	0.0
C	POR02	0.0	0.0	14.3	868.3	0.0
C	OPH02	0.0	0.0	0.0	496.8	0.0
C	OPH03	0.0	0.0	0.0	2549.2	0.0
C	ACT02	1.6	0.0	0.0	1.6	0.0
C	GAS04	0.0	0.0	0.0	20.6	0.0
C	APO01	0.0	0.0	0.0	23.8	0.0

Table 2 (Contd.)

Cluster	Taxon	Stations				
		31	32	24	22	343
C	IRR01	0.0	0.0	0.0	39.7	0.0
C	IND01	0.0	0.0	0.0	33.3	0.0
C	IND08	0.0	0.0	0.0	30.2	0.0
C	OPH05	0.0	0.0	0.0	7.9	0.0
C	BRY04	0.0	0.0	0.0	7.9	0.0
C	GAS03	0.0	0.0	0.0	12.7	0.0
C	DEN07	0.0	0.0	0.0	15.9	0.0
C	IND18	0.0	0.0	3.2	1.6	0.0
C	AST04	0.0	0.0	1.6	1.6	0.0
C	PAN01	0.0	0.0	1.6	1.6	0.0
C	BRY03	0.0	0.0	1.6	3.2	0.0
C	DEN02	0.0	0.0	1.6	3.2	0.0
C	DEN08	0.0	0.0	1.6	3.2	0.0
C	CRI01	0.0	0.0	3.2	3.2	0.0
C	ISO01	0.0	0.0	4.8	3.2	0.0
C	ASC02	0.0	0.0	1.6	33.3	0.0
C	ALC02	0.0	0.0	4.8	20.6	0.0
C	BRY01	0.0	0.0	4.8	36.5	0.0
D	BIV01	0.0	0.0	1.6	434.9	4841.3
D	OPH04	0.0	0.0	0.0	58.7	1833.3
D	ACT04	0.0	0.0	0.0	0.0	7.9
D	BRY14	0.0	0.0	0.0	0.0	9.5
D	GAS05	0.0	0.0	0.0	0.0	103.2
D	ASC04	0.0	0.0	0.0	0.0	176.2
D	IND13	0.0	0.0	0.0	0.0	144.4
D	POR07	0.0	0.0	0.0	0.0	31.7
D	DEN06	0.0	0.0	0.0	0.0	61.9
D	POR08	0.0	0.0	0.0	0.0	69.8
D	OPH09	0.0	0.0	0.0	0.0	42.9
D	CRU01	0.0	0.0	0.0	0.0	55.6
D	ECH01	0.0	0.0	0.0	0.0	49.2
D	HYB01	0.0	0.0	0.0	0.0	50.8
D	BRY02	0.0	0.0	1.6	11.1	42.9
D	ACT05	0.0	0.0	42.9	0.0	6.3
D	SCL02	0.0	0.0	4.8	0.0	34.9
r	POR03	0.0	0.0	0.0	1.6	0.0
r	POR04	0.0	0.0	0.0	1.6	0.0
r	POR05	0.0	0.0	0.0	4.8	0.0
r	PEN01	0.0	0.0	4.8	0.0	0.0
r	CNI01	0.0	0.0	0.0	0.0	1.6
r	CNI02	0.0	0.0	3.2	0.0	0.0
r	BRY10	0.0	0.0	0.0	0.0	1.6
r	BRY13	0.0	0.0	1.6	0.0	0.0
r	POP01	0.0	0.0	1.6	0.0	0.0
r	MOL01	0.0	1.6	0.0	0.0	0.0
r	POL09	0.0	0.0	3.2	0.0	0.0
r	PAN02	0.0	0.0	6.3	0.0	0.0
r	CRU03	0.0	0.0	1.6	0.0	0.0
r	CRU04	0.0	3.2	0.0	0.0	0.0
r	DEC03	0.0	0.0	0.0	0.0	3.2
r	DEC04	0.0	0.0	0.0	0.0	3.2
r	DEN01	0.0	0.0	0.0	3.2	0.0
r	DEN03	0.0	0.0	4.8	0.0	0.0
r	DENSP	0.0	0.0	0.0	6.3	0.0
r	OPH06	0.0	0.0	0.0	6.3	0.0
r	AST02	0.0	0.0	3.2	0.0	0.0
r	AST07	1.6	0.0	0.0	0.0	0.0
r	AST08	0.0	0.0	0.0	0.0	1.6
r	PIS01	0.0	0.0	0.0	0.0	1.6
r	IND02	0.0	0.0	3.2	0.0	0.0
r	IND04	0.0	0.0	0.0	0.0	1.6
r	IND05	0.0	0.0	1.6	0.0	0.0
r	IND06	0.0	0.0	1.6	0.0	0.0
r	IND07	1.6	0.0	0.0	0.0	0.0
r	IND09	0.0	0.0	1.6	0.0	0.0

Table 2 (Contd.)

Cluster	Taxon	Stations				
		31	32	24	22	343
r	IND10	0.0	0.0	0.0	1.6	0.0
r	IND11	1.6	0.0	0.0	0.0	0.0
r	IND12	0.0	0.0	0.0	1.6	0.0
r	IND14	0.0	0.0	4.8	0.0	0.0
r	IND15	0.0	4.8	0.0	0.0	0.0
r	IND19	0.0	0.0	1.6	0.0	0.0
r	IND20	0.0	0.0	0.0	6.3	0.0
r	IND23	0.0	0.0	3.2	0.0	0.0
b	HYBSP	7.9	28.6	115.9	77.8	0.0
b	BRYSP	0.0	0.0	0.0	0.0	69.8
b	PANSP	7.9	206.3	96.8	14.3	0.0
b	OPHSP	1.6	0.0	3.2	0.0	0.0
b	ASTSP	0.0	0.0	11.1	1.6	0.0
b	ASCSP	0.0	0.0	1.6	1.6	0.0
b	PISSP	66.7	71.4	34.9	1.6	1.6
b	IND24	25.4	41.3	57.1	3.2	0.0
	total	3965.1	8957.1	6206.3	5574.6	7657.1

r rare taxa, *b* bulk groups. Highest abundances in bold. *ACT* Actinaria, *ALC* Alcyonaria, *AMP* Amphipoda, *APO* Apodida (Holothuroidea), *ASC* Ascidiacea, *AST* Asteroidea, *BIV* Bivalvia, *BRA* Brachiopoda, *BRY* Bryozoa, *CRI* Crinoidea, *CRU* Crustacea (others than Decapoda), *DEC* Decapoda (Crustacea), *DEN* Dendrochiroidea (Holothuroidea), *ECH* Echinoidea, *GAS* Gastropoda, *GOR* Gorgonaria, *HYB* Hydrozoa/Bryozoa, *HYD* Hydrozoa, *IND* undetermined, *IRR* Irregularia (Echinoidea), *ISO* Isopoda, *MOL* Mollusca, *NUD* Nudibranchia, *OPH* Ophiuroidea, *PAN* Pantopoda, *PEN* Pennatularia, *PIS* Pisces, *POL* Polychaeta, *POP* Polyplacophora, *POR* Porifera, *SAS* synascidians, *SCL* Scleractinia

A number followed by one of these abbreviations indicates a taxon at the species level, if "SP" is followed the name indicates a higher systematic unit (bulk group)

respectively. *Hydrozoa* sp. 1 was the only identified non-bulk taxon being present at all five stations; 64% of the taxa were found only at one station.

Community analysis

The reduced dataset comprised of 99 taxa and provided the basis for the MDS-plot with the grouping from the classification superimposed (Fig. 2). It shows a faunistic gradient from stations 31 and 32 to stations 24, 22, and 343 (for sea-bed photographs see Thatje et al. 2005). In the community table (Table 2) the reason for the similarity between stations 31 and 32 becomes obvious, i. e., the common occurrence of several taxa from group A at both stations. Taxon cluster B is characterized by some species, which co-occur at stations 32 and 24; the weak similarity between stations 22 and 24 is mainly based on taxa from cluster C. The faunistically most isolated station 343 is almost exclusively characterized by species from cluster D of which only two species (*BIV02* and *OPH04*) occur with considerable abundances also at station 22. The grouping of taxa does not reflect their affiliation to higher systematic units or life forms, instead almost all higher systematic groups are represented in all taxa clusters by different species with the exception

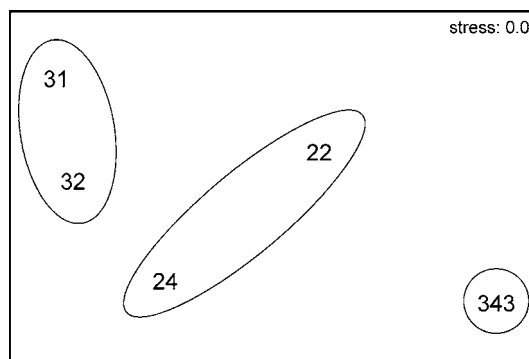


Fig. 2 Multi-dimensional scaling plot of Bouvet Island/Spiess Seamount stations according to their species inventory. Grouping from classification (dendrogram) at 10% Bray-Curtis similarity superimposed

of polychaetes grouped in cluster B, and consequently at stations 32 and 24, but not at stations 22 and 343. Ascidians are almost absent at stations 31 and 32 and, consequently, are missing in cluster A. In this species, cluster also crustaceans are missing, although they occur at stations 32, 24 and 343.

Diversity

Station- (alpha-) diversities were highest at station 24; all other stations did not differ considerably from each other except variations in abundance (Fig. 3). Gamma-diversity in the Bouvet samples was slightly higher than at the Patagonian sampling sites. On the Weddell Sea shelf true diversities (J' and H') were slightly higher than at Bouvet Island, dominance patterns were most even (Fig. 4), species numbers (S and ES) highest, and abundances lowest. In all three areas, the number of rare taxa, those present at a single station with an absolute

diversity *s.l.*

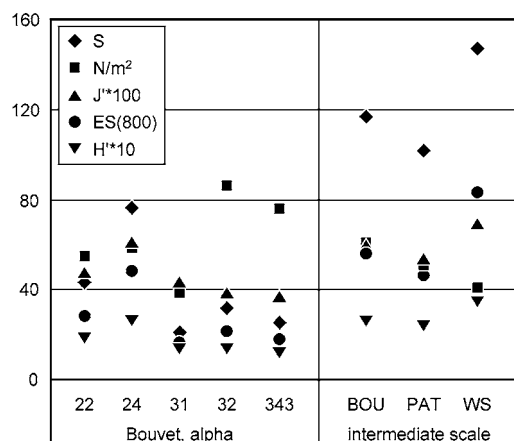


Fig. 3 Local (alpha) diversity at Bouvet Island (Spiess Seamount incl.), left and intermediate scale diversity at the three large areas of investigation, right. *BOU* Bouvet Island (Spiess Seamount excl.), *PAT* Patagonian shelf, *WS* Weddell Sea. Transformations of standard algorithms (*10 and *100) applied in order to use the same diversity scale

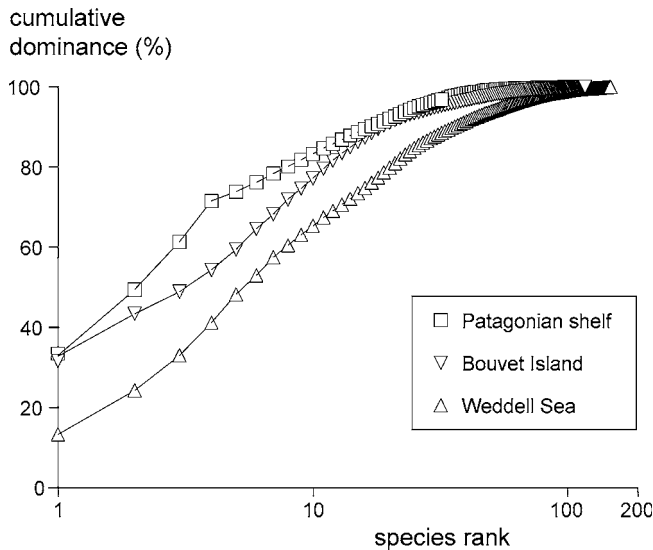


Fig. 4 Cumulative dominance plots of pooled data from four stations at each of the large investigation areas (Bouvet samples excl. Spiess Seamount)

abundance < 5 , ranged between 38 and 45. Beta diversity (=species turnover or intermediate scaled faunistic heterogeneity) was highest at Bouvet Island, had a high variation on the Patagonian shelf and was lowest at the Weddell Sea sampling sites (Fig. 5).

Faunistic composition

Relative abundances in all three investigation areas were similar (Fig. 6). A coarse systematic classification demonstrates that large systematic groups were most evenly represented in the Weddell Sea samples, whereas, the

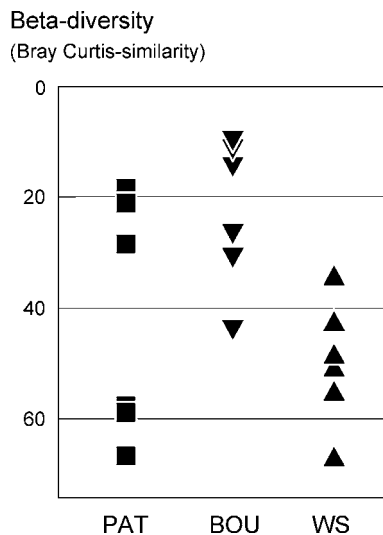


Fig. 5 Faunistic heterogeneity, beta-diversity or taxa turnover expressed as Bray Curtis-similarities between four stations at each of the three large areas of investigation. *PAT* Patagonian shelf, *BOU* Bouvet Island (Spiess Seamount excl.), *WS* Weddell Sea

Bouvet samples (incl. Spiess Seamount) were dominated by echinoderms and molluscs, and the Patagonian samples by ascidians and molluscs, the latter being extremely poor at the Weddell Sea site. At station 24, an approximately 65-m long portion of the photographic transect clearly represented a former iceberg scour, characterized by the abrupt change in the assemblage composition within a few metres from one photograph to the next (Fig. 7). Abundances of all bulk taxa were much lower inside the scour than outside with three exceptions. In contrast, values for *Hydrozoa* sp. 1, crustaceans and pantopods were significantly higher inside the scour than outside ($P < 0.05$). The dominance pattern outside the scour was more even than inside it (Fig. 8). Pooled data from both inside and outside the scour did not show a considerable difference when compared to the undisturbed situation. Along with the exception of one specimen of *Crustacea* sp. 1 and one of undetermined sp. 6 no other taxa were found exclusively in the scour.

Discussion

Due to the geological isolation of Bouvet Island and the Spiess Seamount, this area is an appropriate place to study selected aspects of local and regional benthic ecosystem structure and functioning. In order to obtain the quantitative results with a feasible effort in such a remote area and to come up with general conclusions the study focussed on diversity and community structure at a local and intermediate spatial scale. It is assumed that the mega-epibenthos has been representatively covered by the method applied and by the taxa identified. Also by using this approach, a large-scale comparison was possible allowing for conclusions on the effect of large-scale processes on small and intermediate-scale benthic structures.

The most surprising result was the intermediate-scaled taxa diversity and taxa richness at Bouvet Island and Spiess Seamount not being (much) poorer than that of the much larger adjacent areas on the Patagonian and Weddell Sea shelves. Consequently, Mac Arthur and Wilson's island biogeography theory, mainly developed for terrestrial islands, cannot be applied to this marine system. Two explanations for this finding are possible. If this fauna is actually isolated, a high proportion of endemic species should have evolved. Such a situation is known from southwest Pacific (Richer de Forges et al. 2000), but not from Atlantic sea-mounts (Piepenburg and Müller 2004). Theoretically, the fauna can also represent a unique relict fauna from the past glaciation period. If detailed taxonomic studies and genetic analyses do not confirm this hypothesized high endemism, it can be concluded that the Antarctic Circumpolar Current links benthic assemblages over large distances of deep water, which thus would not act as barriers between isolated habitats. Since faunistic overlap between Subantarctic

Fig. 6 Coarse faunistic composition at the three large areas of investigation (IND = undetermined organisms). *BOU* Bouvet Island (incl. Spiess Seamount), *PAT* Patagonian shelf, *WS* Weddell Sea

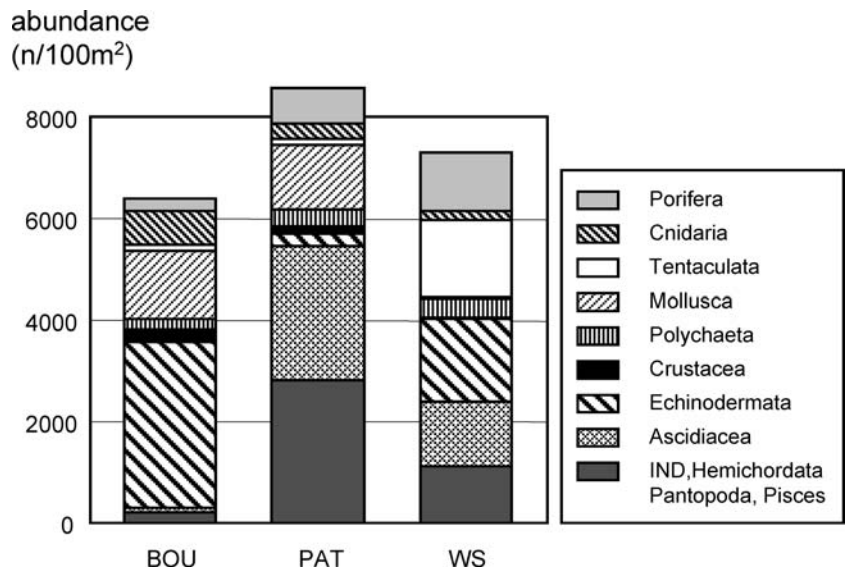
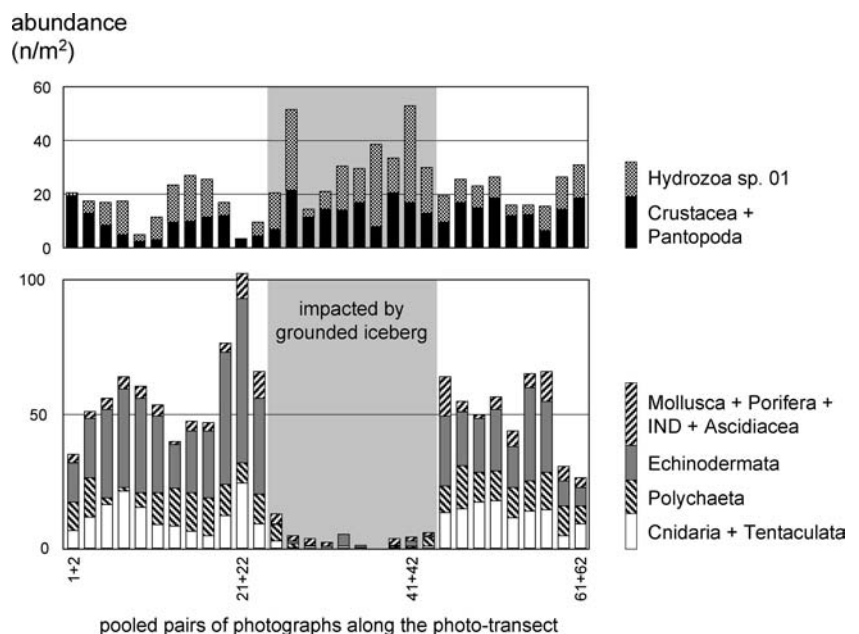


Fig. 7 Abundances of coarse taxa groups in a stage of recolonization after iceberg impact (*centre*) and undisturbed sections along the photographic transect at station 24 (IND = undetermined organisms)



islands, the continental shelves of Antarctica as well as New Zealand and South America is known from zoogeographical studies (Beu et al. 1997) this explanation of a restricted isolation seems most likely.

However, why does the small area of Bouvet shallow waters not lead to a reduced number of taxa as, e.g., as it could be concluded from Rosenzweig's (1995) assumption that the number of species and specimens can be positively correlated? The reason might be the low number of sampling sites. More samples could result in relatively low total species numbers at Bouvet and much higher values on the continental shelf. However, the number of rare species should have been much higher on the two large continental shelves if their total number of species within the investigated spatial scale had been comparably higher (Chao and Lee 1992). However, this

was not found. The intermediate-scale diversity in the Antarctic has a large-scale background of an estimated total number of 17,000 species (Gutt et al. 2004), to be considered as a result of evolutionary processes, which is not possible at Bouvet Island due to the small extension of its shelf and slope. From this, we can conclude that, in contrast to the findings of Bond and Chase (2002), the analysed intermediate scaled species richness at the Antarctic sampling site is largely independent from its evolutionary background. It seems to be primarily determined or reduced, respectively, by specific adaptations to recent regional or local ecological conditions and biological interactions such as competitive displacement. If two such systems, one with a species-rich and the other with a species-poor background reveal a similar number of species at intermediate spatial scales,

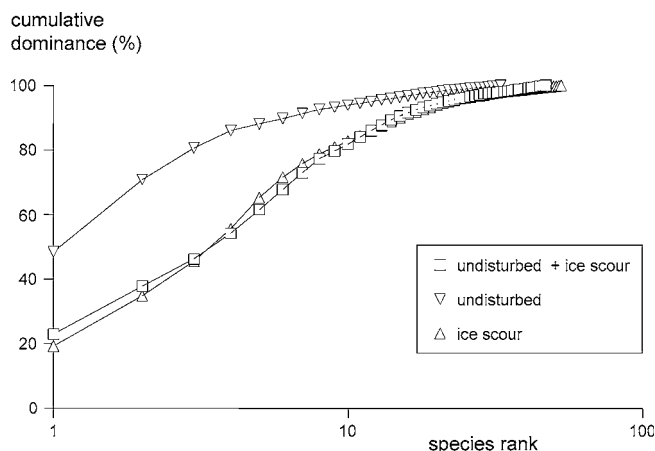


Fig. 8 Cumulative dominance plots of an undisturbed assemblage (first 20 photographs of transect), recolonization stage after iceberg scouring (first 20 photographs of former iceberg scour), and a combination of undisturbed and disturbed assemblage (first ten photographs of transect plus first ten photographs of former iceberg scours)

the question arises whether the investigated exposed deep benthic shelf habitats might have a generally limited capacity for mega-epibenthic species richness and diversity.

An alternative explanation is that a permanent import of species by long-range dispersal leads to a persistence of the unexpected high number of species at Bouvet Island, many of which would become extinct in an isolated situation if they are inferior in competition (Pielou 1975). However, it can be assumed that this mechanism is also (if not even more) effective on the high Antarctic shelf (Gutt 2005). Environmental heterogeneity might be another important factor to explain the relatively high number of benthic species at Bouvet Island. Iceberg scouring did not turn out to be of high relevance in this context. The community table and the high beta diversities, however, provide hints that taxa belonging to the same higher systematic group avoid competition among each other since they do not obviously co-occur, i. e. they belong to different taxa clusters. Consequently many of them can persist at a larger spatial scale. Off Bouvet, a broad variation of different sediments exists (personal observation) due to the volcanic origin of the island such as black sand (stations 22, 24 and 343) with patches of pebbles (stations 31 and 32), soft sediments (station 32), ripple marks created by high currents (station 31) and predominant volcanic rocky hard substrata (station 343). Some of these features provide clear evidence for significant differences in current velocity, which has also been identified as a main driver for habitat heterogeneity at the Jasper Seamount in the northeast Pacific (Genin et al. 1986) and Kolbeinsey Ridge in the North Atlantic (Piepenburg and Juterzenka 1994).

A comparison at a coarse level of ecological or systematic guilds shows an intermediate position of the Bouvet benthos between South America and Antarctica.

Typical of the high Antarctic shelf benthos and Bouvet Island are cnidarians, underrepresented in the four selected stations in the Weddell Sea, and echinoderms, bryozoans and ascidians more abundant in the Antarctic. The occurrence of lithodid crabs resembles the South American fauna and that of Subantarctic islands, while these decapod crustaceans are not a typical element of the high Antarctic fauna despite their rare and local occurrence at Antarctic Islands or even on the continental shelf (Klages et al. 1995; Thatje and Arntz 2004). The Bouvet fauna has a high abundance of gastropods and bivalves in common with that on the Patagonian shelf. The relatively high primary productivity supporting higher components of the food web does obviously not reduce benthic invertebrate diversity, as predicted by a modification of the productivity–diversity–hypothesis (Huston 1994), but may even support it if food is not a critical resource for deposit and suspension feeders, leading to competitive displacement. Several of the above mentioned animal groups can be considered as belonging to the shelf fauna, but further detailed studies are necessary to clarify to which degree an exchange with the deep sea may also have led to the surprisingly high number of taxa at Bouvet Island and Spiess Seamount.

Acknowledgements Thanks are due to K. Linse, M. Varela, DKA Barnes and E Rodriguez for taxonomic identification support. Detailed transect data (position, depth), photographs and abundances per photograph are available at <http://www.pangaea.de/PangaVista?query=@Ref26493>

References

- Baker PE, Tomblin JF (1964) A recent volcanic eruption on Bouvetøya, South Atlantic Ocean. *Nature* 494:1055–1056
- Beu AG, Griffin M, Maxwell PA (1997) Opening of Drake Passage gateway and late Miocene to Pleistocene cooling reflected in Southern Ocean molluscan dispersal: evidence from New Zealand and Argentina. *Tectonophysics* 281:83–97
- Bond EM, Chase JM (2002) Biodiversity and ecosystem functioning at local and regional spatial scales. *Ecol Lett* 5:467–470
- Chao A, Lee S-M (1992) Estimating the number of classes via sample coverage. *JASA* 87:210–217
- Clarke A, Johnston NM (2003) Antarctic marine benthic diversity. *Oceanogr Mar Biol* 41:47–114
- De Broyer C, Jazdzewski K (1993) Contribution to the marine biodiversity inventory. A checklist of the Amphipoda (Crustacea) of the Southern Ocean. *Doc Trav Inst R Sci Nat Bel* 73:1–154
- Fevolden SE (1980) Krill off Bouvetøya and in the southern Weddell Sea with a description of larval stages of *Euphausiocrystallorophias*. *Sarsia* 65:149–162
- Fjortoft JH (1981) Hydrographic surveying around Bouvetøya. *Norsk Polarinstitutt Skrifter* 175:13–15
- Foldvik A, Gammelsrød T, Tørresen T (1981) Measurements of ocean current and bottom pressure near Bouvetøya, January–March 1979. *Norsk Polarinstitutt Skrifter* 175:105–112
- Genin A, Dayton PK, Lonsdale PF, Spiess FN (1986) Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. *Nature* 322:59–61
- Gutt J, Starmans A (1998) Structure and biodiversity of megabenthos in the Weddell and Lazarev Seas (Antarctica): ecological role of physical parameters and biological interactions. *Polar Biol* 20:229–247

- Gutt J, Helsen E, Arntz W, Buschmann A (1999) Biodiversity and community structure of the mega-epibenthos in the Magellan region (South America). *Sci Mar* 63(Supl 1):155–170
- Gutt J, Sirenko BI, Smirnov IS, Arntz WE (2004) How many macrobenthic species might inhabit the Antarctic shelf? *Antarct Sci* 16:11–16
- Gutt J (2005) Coexistence of macro-zoobenthic species on the Antarctic shelf: an attempt to link ecological theory and results. *Deep Sea Res II* (in press)
- Holdgate MW, Tilbrook PJ, Vaughan RW (1968) The biology of Bouvetøya. *Br Antarct Surv Bull* 5:1–7
- Hurlbert HS (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52:577–586
- Huston MA (1994) Biological diversity. Cambridge University Press, Cambridge
- Kirkman SP, Wilson W, Klages NTW, Bester MN, Isaksen K (2000) Diet and estimated food consumption of Antarctic fur seals at Bouvetøya during summer. *Polar Biol* 23:745–752
- Kirkman SP, Hofmeyr GJG, Bester MN, Isaksen K (2001) Counts of southern elephant seals, *Mirounga leonina*, at Bouvet Island. *Polar Biol* 24:62–65
- Klages M, Gutt J, Starman A, Bruns T (1995) Stone crabs close to the Antarctic Continent: *Lithodes murrayi* Henderson, 1888 (Crustacea; Decapoda; Anomura) off Peter I Island (68°51'S, 90°51'W). *Polar Biol* 15:73–75
- Knox GA (1977) The Antarctic Polychaete fauna: Its characteristics, distribution patterns, and evolution. In: Llano GA (ed) Adaptations within Antarctic ecosystems. Proceedings of the 3rd SCAR symposium on Antarctic biology. Washington DC, Smithsonian Institution, Washington DC, Gulf Publishing Co., Houston, pp 1111–1131, 26–30 August 1974
- Ligi M, Bonatti E, Bortoluzzi G, Carrara G, Fabretti P, Penitenti D, Gilod D, Peyve AA, Skolotnev S, Turko N (1997) Death and transfiguration of a triple junction in the South Atlantic. *Science* 276:243–245
- Mac Arthur RH, Wilson EO (1967) The theory of Island biogeography. Princeton University Press, Princeton
- NN (1997) The Antarctic Pilot. The Hydrographer of the Navy (publ). Taunton, Somerset, England
- Piepenburg D, Müller B (2004) Distribution of epibenthic communities on the Great Meteor Seamount (NE Atlantic) mirrors pelagic processes. *Arch Fish Mar Res* 51:55–70
- Piepenburg D, Jutenzenka K von (1994) Abundance, biomass and spatial distribution pattern of brittle stars (Echinodermata: Ophiuroidea) at the Kolbeinsey Ridge North of Iceland. *Polar Biol* 14:185–194
- Prestvik T, Winsnes TS (1981) Geology of Bouvetøya, South Atlantic. *Norsk Polarinstitutt Skrifter* 175:41–69
- Perissinotto R, Laubscher RK, McQuaid CD (1992) Marine productivity enhancement around Bouvet and the South Sandwich Islands (Southern Ocean). *Mar Ecol Prog Ser* 88:41–53
- Pielou EC (1975) Ecological diversity. Wiley, New York
- Pielou EC (1977) Mathematical ecology. Wiley, New York
- Richer de Forges B, Koslow JA, Poore GCB (2000) Diversity and endemism of the benthic seamount fauna in the southwest Pacific. *Nature* 405:944–947
- Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge
- Thatje S, Arntz WE (2004) Antarctic reptant decapods: more than a myth? *Polar Biol* 27:195–201
- Thatje S, Linse K, Avila C, Ballesteros M, Barnes DKA, De Broyer C, Gutt J, Isla E, Raupach M, Rauschert M, Rodriguez E, Teixidó N, Arntz WE (2005) Missing link in the Southern Ocean: sampling the marine benthic fauna of remote Bouvet Island. *Polar Biol* (this volume)