Antarctic Science 7 (3): 227–234 (1995)

Sponges of the Lazarev and Weddell Sea, Antarctica: explanations for their patchy occurrence

JULIAN GUTT[1,3] and VLADIMIR M. KOLTUN[2]

[1]Alfred Wegener Institute for Polar and Marine ResearchColumbusstraβe, D-27568 Bremerhaven, Germany
[2]Zoological Institute, Universitetskaja Emb. 1, St. Petersburg 199034, Russia
[3]Reprint requests and correspondence

Abstract: Seventy-three sponge species were caught at 23 stations on the continental shelf of the Lazarev and Weddell Sea (Atlantic sector of the Southern Ocean). *Tedania tantula* was the most often found species amongst the 63 demosponge species caught and among the five hexactinellid species *Rossella racovitzae* was most common. The stations were classified according to their species inventory, and so the individual stations of the resulting four groups were rather uniformly dispersed over the entire investigation area. The species composition of adjacent stations varied considerably. There was no discernible relationship between the biological set of data and any combination of the available environmental characteristics of the stations. The sponge fauna of the, so far very poorly investigated, Lazarev Sea did not differ considerably from that of the adjacent Weddell Sea. The only species to be recorded for the first time on the Antarctic continental shelf were *Homaxinella flagelliformis* and *Hyrtios arenosa*. Small scale environmental events such as iceberg scouring, or biological characteristics such as extremely slow growth and budding reproduction are thought to generate the patchy distribution pattern.

Received 13 December 1994, accepted 30 May 1995.

Key words: Antarctic, Weddell Sea, Lazarev Sea, sponges, distribution

Introduction

The macrobenthic shelf fauna of some high Antarctic areas is dominated by a variety of sessile suspension feeders (Bullivant 1967, Arnaud 1977, White 1984, Picken 1985, Gutt 1991a). Sponges can contribute the highest proportion of biomass in some regions such as parts of the Weddell and Ross Seas (Beliaev & Ushakov 1957, Koltun 1968 and 1970, Dayton *et al.* 1974, Barthel & Gutt 1992, Gerdes *et al.* 1992; for review see Koltun 1969 and 1976, Sarà *et al.* 1992, Dayton *et al.* 1994). Around the Antarctic Peninsula (Jazdzewski *et al.* 1986, Mühlenhardt-Siegel 1988) and in the West Antarctic (unpublished result) sponges are less abundant. Comparable investigations in the coastal areas of the East Antarctic are scarce. Little is known about the ecological role of sponges, apart from the few comprehensive studies of Dayton (1972, 1978, 1989), Dayton *et al.* 1974, and Kunzmann (1992). However, the sponge dominated benthic assemblages are known to be the richest in species and life forms in the Antarctic (Voß 1988). A variety of different life forms (Barthel *et al.* 1991) form a variable micro habitat for other organisms (Kunzmann 1992), or serve as food for highly specialized predators such as nudibrancs (Wägele 1989) and asteroids (Dayton *et al.* 1974). When sponges die, they generate, over long periods of time, spicule mats which are substrates for other animals, even for sponges (Koltun 1966, Barthel 1992). With this background, sponges sampled during an ecological faunistic survey, mostly conducted in the Lazarev Sea with a few additional stations in the Weddell Sea, were analysed with regard to the following aspects.

a) Which sponges were most often present at the study site?

b) Could different species assemblages be distinguished?

c) To what degree is the sponge fauna of the Lazarev Sea similar to that of the adjacent Weddell Sea and other areas?

d) Could the distribution pattern of the sponges be explained by any measured physical parameter?

Material and methods

The material was sampled during the expedition ANT XI/3 with RV *Polarstern* in 1991 at 15 stations using a modified 3 m wide Agassiz-trawl and at eight stations by a commercial bottom-trawl, in water depths between 119 and 830 m (Fig. 1, Table I). A 20 l subsample was taken from the catches from which all sponges individuals and fragments were sorted out. The identification of species was carried out on the basis of spicule preparation using light microscopy. More details about the stations including a list of all benthic taxa caught was given by Arntz *et al.* (1992).

Because the material contained a certain amount of fragments, only presences were considered for the data analysis. Species which were caught at only one station were excluded from the community analysis because a common

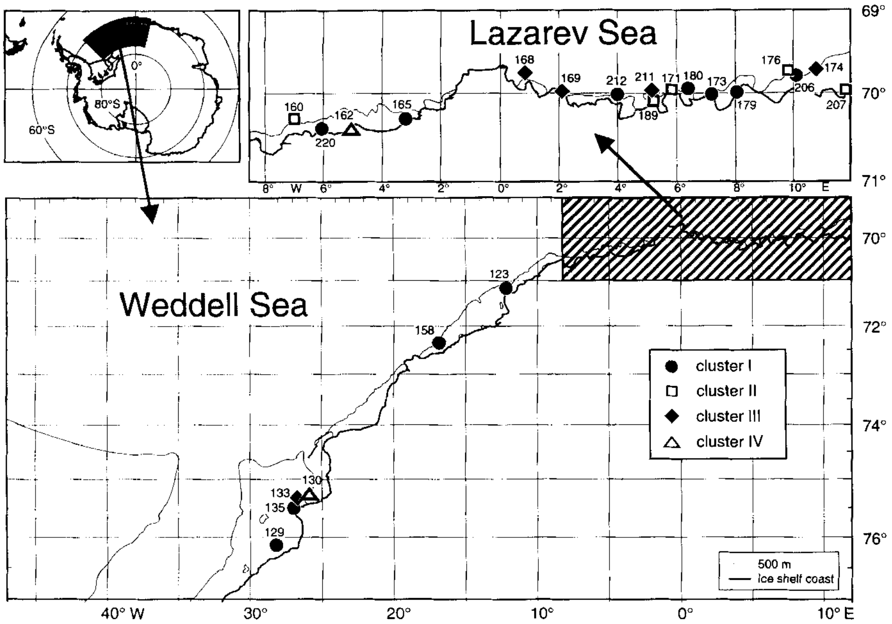

Fig.1. Station map. The stations are classified according to the cluster analysis (see Fig. 2).

presence of two species at one station due to chance, would lead to an erroneous high similarity between the species clusters. Similarity matrices were calculated on the basis of a station-species matrix using the Jaccard-index. A classification was calculated for both stations and species. The results for the stations are shown in a dendrogram; for the species and stations the order and grouping of the cluster analysis were used for the community table. The

Table I. List of stations with environmental parameters.

Station	Distance to shelf edge =500m depth contour (km)*	Distance to ice shelf coast (km)	Depth (m)	Longitude
123	0.5	16.5	400	12.2°W
129	23.5	23.0	315	28.4°W
130	73.0	12.5	561	25.8°W
133	67.5	23.5	424	26.6°W
135	91.0	4.0	221	26.9°W
158	-1.0	27.5	623	16.9°W
160	-1.0	18.0	830	7.1°W
162	22.0	0.5	429	5.0°W
165	10.0	3.5	206	3.3°W
168	9.0	14.5	498	0.8°E
169	-9.0	0.5	560	2.1°E
171	-3.0	3.0	813	5.8°E
173	4.5	0.5	228	7.1°E
174	0.5	25.5	432	10.7°E
176	-3.5	20.7	734	9.9°E
179	11.5	1.0	181	8.0°E
180	0.5	15.0	282	6.3°E
189	0.5	6.0	477	5.2°E
206	0.5	19.0	343	10.0°E
207	42.0	1.0	208	11.8°E
211	-5.5	18.0	661	5.1°E
212	-5.5	11.5	607	3.9°E
220	11.0	0.5	119	6.1°W

*negative values indicate stations deeper than 500m (beyond the shelf edge).

Multidimensional Scaling (MDS) as a method of ordination shows the similarities between all single stations to each other on a two-dimensional scale (Field *et al.* 1982).

The relationship between the four available physical and the biological data was calculated after Clarke & Ainsworth (1993). Corresponding to the biological similarity matrix for all pairs of stations (see above) a similar set of data was generated on the basis of the physical factors at each station sampled using the Euclidean distance. Finally a Spearman-rank correlation was calculated between the ranked similarity matrices of the biological and physical data for all possible combinations of the physical parameters.

Results

A total of 73 species were identified of which five belonged to the Calcarea, five to the Hexactinellida, 13 species were tetractinomorphe and 50 ceractinomorphe Demospongiae. In the Weddell Sea 39 species were recorded and 65 in the Lazarev Sea. These are given in Table II where the 23 stations and 45 species are ordered according to the results of the cluster analysis. The 28 species which were found only once are listed separately. The highest presence of 65.2% (15 stations) was recorded for *Tedania tantula*. *Tetilla leptoderma*, *Suberites caminatus*, *Cinachyra antarctica*, and *Rossella racovitzae* were found at more than 50% of the stations. The highest number of species per station was 22 at station 169, whereas average values were *c.* 10.

The classification of the stations according to their species inventory resulted in four distinct clusters I–IV at a 5% similarity level (dendrogram, Fig. 2). In contrast, the ordination (MDS-plot, Fig. 3) does not show such a clear grouping with the exception of station 130. If, however, the information of the dendrogram is superimposed, the general image of the classification is recognizable. One conspicuous

Table II. Species-station matrix based on presences. Stations and species (presence > 4.3%) listed according to cluster analysis, Jaccard index, complete linkage. Species not considered in the cluster analysis are listed in the lower part. CA: Calcalrea, HE: Hexactinellida, TE: Tetractinomorpha, CE: Ceratinomorpha.

	Station no	220	212	165	206	158	129	135	180	123	179	173	211	133	174	169	168	207	189	176	171	160	162	130	Presence
	Depth (m)	119	607	206	343	623	315	221	282	400	181	228	661	424	432	560	498	208	477	734	813	830	429	561	(%)
Cluster		I	I	I	I	I	I	I	I	I	I	I	II	II	II	II	II	III	III	III	III	III	IV	IV	
A *Myxilla mollis* Ridley & Dendy, 1886	CE													x								x			8.7
A *Lissodendoryx flabellata* Burton, 1929	CE													x								x			8.7
A *Scolymastra joubini* Topsent, 1910	HE						x							x											8.7
A *Tentorium semisuberites* (Schmidt, 1870)	TE												x	x											8.7
A *Gellus sp.*	CE								x					x		x									13.0
A *Tedania oxeata* Topsent, 1916	CE													x						x				x	13.0
A *Inflatella coelosphaeroides* (Koltun, 1964)	CE				x								x	x		x									17.4
A *Pseudosuberites nudus* Koltun, 1964	CE												x	x		x	x								17.4
A *Artemisina plumosa* (Hentschel, 1914)	CE				x								x	x	x	x	x						x		30.4
A *Tedania charcoti* Topsent, 1908	CE				x									x		x		x	x						21.7
B *Tetilla leptoderma* Sollas, 1886	TE				x	x	x				x	x	x		x	x		x	x	x	x	x	x		60.9
B *Cinachyra antarctica* (Carter, 1872)	TE		x	x		x	x			x	x	x	x					x	x	x	x	x			56.5
B *Rossella nuda* Topsent, 1901	HE			x									x					x			x	x	x	x	30.4
B *Haliclona sp.*	CE					x															x	x			12.0
B *Suberites caminatus* (Ridley & Dendy, 1887)	TE		x	x					x	x		x	x	x	x	x	x			x	x	x			56.5
B *Isodictya setifera* (Topsent, 1901)	CE								x	x						x	x	x		x	x	x			34.8
B *Cinachyra barbata* Sollas, 1886	TE		x		x					x			x			x	x					x			30.4
B *Bubaris antarctica* Koltun, 1954	CE												x							x		x			12.0
C *Rossella antarctica* Carter, 1872	HE			x	x			x										x							17.4
C *Phorbas areolata* (Thiele, 1905)	CE			x	x																				8.7
C *Microxina benedeni* (Topsent, 1901)	CE				x		x										x								13.0
D *Isodictya erinacea* (Topsent, 1916)	CE		x	x									x			x		x	x			x			30.4
D *Myxilla asigmata* Topsent, 1901	CE		x	x												x									13.0
D *Leucetta floridana* (Haeckel, 1872)	CA		x				x						x												13.0
D *Sphaerotylus schoenus* Kirkpatrick, 1908	TE		x						x	x			x												17.4
E *Leucetta sp.*	CA				x	x																			8.7
E *Plocamia gaussiana* Hentschel, 1914	CE		x			x																			8.7
E *Ectyodoryx sp.*	CE					x										x									8.7
F *Rossella racovitzae* Topsent, 1901	HE		x	x	x	x	x	x	x	x	x	x	x	x				x							56.5
F *Polymastia invaginata* Kirkpatrick, 1907	TE		x		x	x	x						x	x	x	x									34.8
F *Tedania tantula* (Kirkpatrick 1908)	CE	x	x	x	x	x	x	x	x			x			x	x	x			x		x	x		65.2
F *Monosyringa longispina* (Lendenfeld, 1907)	TE	x							x	x	x	x	x		x	x									34.8
F *Inflatella belli* (Kirkpatrick, 1907)	CE	x		x		x			x		x				x		x				x				34.8
F *Mycale magellanica* (Ridley, 1881)	CE	x											x												8.7
F *Axociella flabellata* (Topsent, 1916)	CE	x			x																				8.7

https://doi.org/10.1017/S0954102095000320 Published online by Cambridge University Press

	Station no	220	212	165	206	158	129	135	180	123	179	173	211	133	174	169	168	207	189	176	171	160	162	130	Presence
	Depth (m)	119	607	206	343	623	315	221	282	400	181	228	661	424	432	560	498	208	477	734	813	830	429	561	(%)
Cluster		I	I	I	I	I	I	I	I	I	I	I	II	II	II	II	II	III	III	III	III	III	IV	IV	
G *Rossella sp.*	HE	x														x			x	x					17.4
G *Hyrtios arenosa* (Thiele, 1905)	CE															x			x						8.7
G *Oxymycale acerata* (Kirkpatrick, 1907)	CE												x		x	x				x					17.4
G *Phorbas glaberrima* (Topsent, 1917)	CE						x								x	x									13.0
H *Latrunculia apicalis* Ridley & Dendy, 1886	TE										x							x							8.7
H *Haliclona dancoi* (Topsent, 1902)	CE															x		x							8.7
H *Mycale gaussiana* Hentschel, 1914	CE																	x					x		8.7
H *Isodictya kerguelensis* (Ridley & Dendy, 1886)	CE						x					x						x							13.0
H *Ectydoryx anacantha* Hentschel, 1914	CE								x								x	x							13.0
H *Pseudosuberites hyalinus* (Ridley & Dendy, 1887)	CE									x					x			x							13.0
Leucetta gelatinosa (Jenkin, 1908)	CA			x																					4.3
Leucetta primordialis var. leptoraphis (Jenkin, 1908)	CA				x																				4.3
Achromorpha truncata (Topsent, 1901)	CA																	x							4.3
Plakina trilopha (Schulze, 1862)	TE			x																					4.3
Stylocordyla borealis (Loven, 1868)	TE										x														4.3
Suberites montiniger Carter, 1880	TE													x											4.3
Sphaerotylus borealis antarcticus Kirkpatrick, 1908	TE									x															4.3
Haliclona spongiosissima (Topsent, 1908)	CE																				x				4.3
Gellius flagellifer Ridley & Dendy, 1887	CE						x																		4.3
Vagocia arcuarius (Topsent, 1913)	CE													x											4.3
Halichondria sp.	CE											x													4.3
Isodictya toxophila Burton, 1932	CE												x												4.3
Mycale tridens Hentschel, 1914	CE		x																						4.3
Cercidochela lankesteri Kirkpatrick, 1907	CE									x															4.3
Hoplakithera dendyi Kirkpatrick, 1908	CE																					x			4.3
Biemna chilensis Thiele, 1905	CE															x									4.3
Tylodesma sp.	CE															x									4.3
Myxilla australis (Topsent, 1901)	CE											x													4.3
Iophon aceratus Hentschel, 1914	CE																	x							4.3
Iophon unicornis Topsent, 1907	CE					x																			4.3
Lissodendoryx sp.	CE																	x							4.3
Iotrochota somovi (Koltun, 1964)	CE																	x							4.3
Ectyodoryx antarctica (Hentschel, 1914)	CE																	x							4.3
Ectyodoryx ramilobosa (Topsent, 1916)	CE												x												4.3
Ectyodoryx nobilis (Ridley & Dendy, 1886)	CE																						x		4.3
Clathria pauper Broensted, 1926	CE													x											4.3
Pseudanchinoe toxifera (Topsent, 1913)	CE													x											4.3
Homaxinella flagelliformis (Ridley & Dendy, 1886)	CE														x										4.3
number of species	73	6	12	12	14	11	10	3	9	10	7	9	20	17	11	22	9	19	6	9	8	13	6	2	

difference between the results of both methods is the closer relationship of station 162 to part of cluster III than to station 130. The information about the geographical position of the station clusters is given in Fig. 1. Cluster I is represented everywhere in the entire study area. The stations of clusters II and III are mostly concentrated in the eastern Lazarev Sea; in cluster IV one station is in the Lazarev Sea and one in the Weddell Sea. Examples for the sponge fauna of two clusters are shown by three *in situ* photographs (Fig. 4), which were analysed under faunistic-ecological by Gutt & Starmans (in press).

The relationship between the sponge distribution pattern and the physical parameters: distance between station and shelf edge (=500 m depth contour), distance between station and ice shelf coast, water depth, and longitude (Table I) did not show any remarkable relationships either when single physical parameters were considered or when they were combined. The highest coefficient for a single parameter was 0.270 for the correlation between biological data and the distance between the station sampled and the shelf edge (500 m depth contour). The combination of the distance between the station and the shelf break and the geographical longitude of the station reached a correlation factor of 0.304. (Generally values of 0.7 indicate a good relationship between the physical and biological data.)

Discussion

The 63 demosponges recorded in the entire area of investigation are 31% of all species known from the Antarctic coastal areas listed by Sarà *et al.* (1992). The four hexactinellids which were identified to the species level are a similar percentage of the 13 hexactinellid species recorded so far from water depth < 1000 m in the Antarctic (Barthel & Tendal 1994). The presented data provide good evidence for a large scale circumpolar distribution of the Antarctic sponge fauna (Koltun 1969) since they fill the previously little studied gap in the eastern part of the Atlantic sector. Of the 50 demosponges found in the Lazarev Sea only two have been recorded previously in this area. From the Weddell Sea 17 out of the total of 22 species which we found have been recorded. This discrepancy is a reflection of the different levels of research effort in both areas. In four of the eight Antarctic sectors defined by Sarà *et al.* (1992) 49 species (79%) from the Weddell and Lazarev Sea (this study) were also present. The only species found for the first time in the Antarctic were *Homaxinella flagelliformis* and *Hyrtios arenosa*. They were both previously caught off subantarctic Islands. Compared with the Demospongiae both, the Hexactinellida and Calcarea, were represented by only a few species. The hexactinellid species, however, showed mainly intermediate to high values for presence, whereas the calcarean species were generally rare. This confirms earlier observations about the significant role hexactinellid sponges have in the high Antarctic benthic system (Arnaud 1977, Barthel 1992,

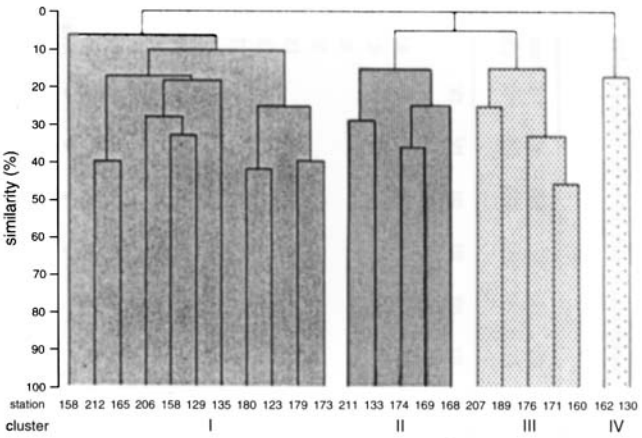

Fig. 2. Dendrogram of the stations according to their sponge species inventory. Jaccard index, complete linkage, cophenetic coefficient: 0.53.

Barthel & Tendal 1994).

Barthel *et al.* (1990), in preliminary observations in the Weddell Sea, suspected that not all sponge species which occur in a limited area were caught by the sampling method employed. They identified *c.* 150 species from 15 catches distributed over an area of similar size to that of the Lazarev Sea. The main reason for the difference in species between both investigations was because we sorted a subsample whilst Barthel *et al.* (1990) checked the entire catch for sponges. Another argument for this effect of sorting procedure are our low values for the most present species

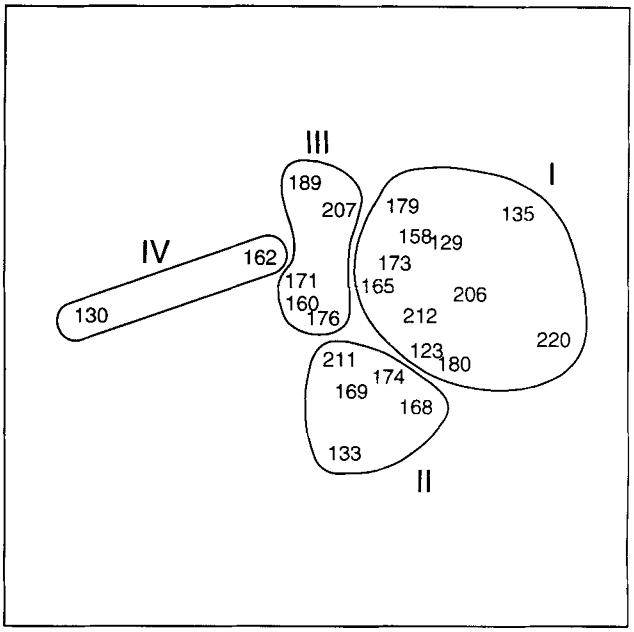

Fig. 3. Plot of the Multidimensional Scaling, based on a similarity matrix established by the Jaccard index; stress: 0.229. The stations are encircled according to the result of the cluster analysis (dendrogram).

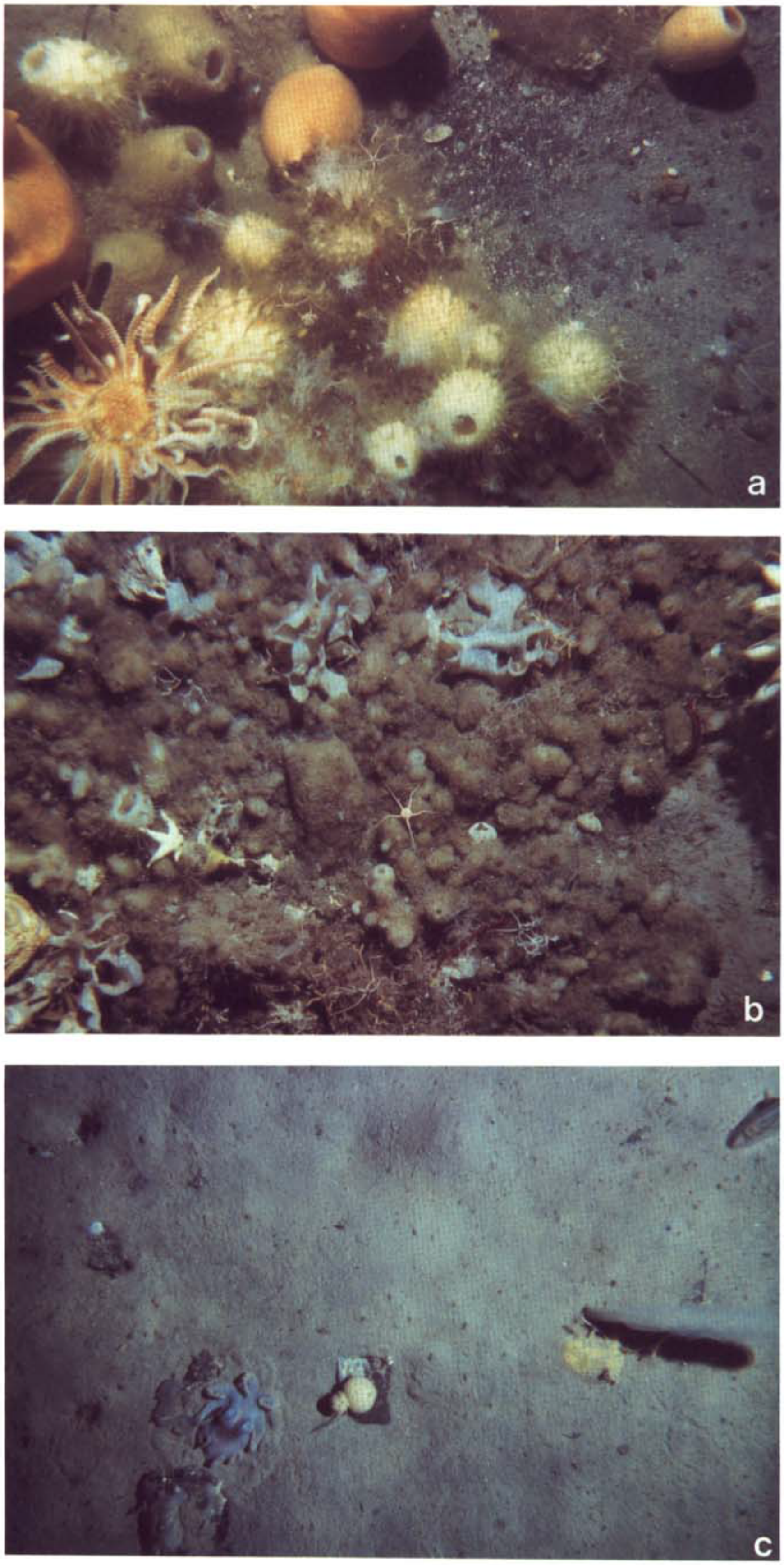

Fig. 4. Underwater-photographs (area: 0.5 m^2). **a.** Cluster I, station 165 (Lazarev Sea). Rich epibenthic assemblage. *Scolymastia joubini* or *Rossella nuda* with smooth, yellowish surface (upper and left margin). Three green-grey specimens of *R. antarctica* (upper left corner) and many spiny, near white specimens of *R. racovitzae*. Many dendrochirote (*Ekmocucumis steineni* and *Staurocucumis liouvillei*) and one dark red apodide (*Taeniogyrus contortus,* centre) holothurian, and one *Labidiaster annulatus* (asteroidea) on the sponges. **b.** Cluster I, station 135 (Weddell Sea). Sediment almost totally covered by small specimens of *Rossella racovitzae* with different bryozoans (*Reteporella gelida*, *Phylactella lyrulata*, *Cellarinella* sp.), dark red apodide holothurians (*Taeniogyrus contortus*), ophiuroids and asteroids (*Diplasterias brucei*, left margin) in between. **c.** Cluster IV, station 162. Poor epibenthic assemblage. Two small specimens of *Tedania vanhoeffeni* on a stone (centre), octopode, compound ascidian (right margin), elasipode deep-sea holothurian (c.f. *Peniagone vignioni*, upper left corner).

https://doi.org/10.1017/S0954102095000320 Published online by Cambridge University Press

(65.2%) and the high number of sponges which occurred only once in the material collected. Therefore, we cannot conclude that the sponge fauna of the Lazarev Sea is less rich in species than that of the Weddell Sea. An additional reason for the low presences might be a high degree of patchiness in the spatial dispersion pattern of sponges as has already been described for other benthic sessile suspension feeders by Gutt (1991a & b) and Gutt & Starmans (in press). Barthel *et al.* (1990) also found an extremely poor overlap between the species composition of adjacent stations. This phenomenon apparently also exists in the Lazarev Sea as can be seen in the community table (Table II).

Despite this spatial variability a classification by cluster analysis was possible. The stations of most clusters were evenly dispersed over the entire investigation area. Even the four southern-most stations in the Weddell Sea belong to three different clusters. This general finding also holds true for the only cluster (II) which was restricted to the Lazarev Sea since in this area it had the broadest west–east extension. For the result of the ordination, the MDS-plot indicated a continuum in species composition rather than distinct assemblages. Barthel & Gutt (1992) in the Weddell Sea also only found a weak regional classification which was explained by water depth and sediment grain size. Abundances varied within the resulting station clusters by a factor of 20. In the study of Gutt and Starmans (in press) which considered the entire macrobenthic epifauna of the Lazarev Sea not one sponge belonged to the key species which contributed best to a separation of distinct clusters. Nevertheless, a significant role of sponges, especially the hexactinellids, for other benthic organisms is known (Voß 1988, Gutt, 1991b, and Kunzmann 1992). However, Voß (1988) also found stations with very low abundances of sponges which belonged to the species assemblage generally characterized by a dominance of sponges.

Another indication for the variable and patchy occurrence of sponges is that no common characteristics could be found for species belonging to one species cluster. This was possible in comparable studies for other animal groups e.g. holothurians (Gutt 1991a) or shrimps (Gutt *et al.* 1994) concerning their feeding type and preference of a special habitat respectively. However, it has to be considered that our knowledge about environmental demands of Antarctic sponges is still very poor.

The findings of this study and the few other studies mentioned above can be briefly summarized: The sponge fauna of the Weddell and Lazarev Sea is highly variable in terms of space. Sponges play a significant role for the entire benthic system, although a clear classification on the basis of the available information is not possible. This leads to the conclusion that physical conditions which generally lead to a separation of faunal assemblages (Gutt & Starmans in press) either do not shape the local sponge composition as they effect other taxa or their influence on sponges is of a different nature. Also, biological characteristics of single sponge species and intraspecific interactions can be more important for the growth of sponge populations than the physical parameters (Dayton 1974). However, the patchiness observed on a smaller scale than analysed in this study (Barthel & Gutt 1992, unpublished results of J. Gutt) indicate that the effect of small scale changes in environmental conditions e.g. iceberg scouring, are more obvious in sponge populations than in other taxa. Because most sponges grow extremely slowly, and because therefore a long life span can be assumed, the distribution pattern of these sessile animals reflects the environmental conditions of a much longer period than faster growing Antarctic invertebrates. For example, iceberg scouring which happened a long time ago may not show any influence on representatives of other taxonomic groups, whilst this small scale effect is still visible in the dispersion pattern of several sponges. However, the general question remains as to whether or not this hypothesis can be applied to the majority of sponge species. If the many species differ in their biology and ecological demands, which is not proven, their distribution pattern can also be influenced by biological factors such as reproduction mode. Budding as a main reproduction type (e.g. from *Rossella racovitzae*, Dayton 1979) in combination with a resulting slow dispersion and slow growth can lead to a highly patchy distribution so that adjacent stations can be dominated by different species. Another conclusion based on the fact that until 12000 years ago this habitat was covered by shelf ice due to the glaciation period is possible. The time elapsed since then might not yet have been long enough for all benthic groups to inhabit all locations with suitable environmental conditions. Due to the especially slow growth at least part of the sponge fauna would then be still in a stage more separate from an ecological equilibrium than taxa which are more uniformly distributed or which are clearly restricted to certain species assemblages due to their environmental demands.

Acknowledgements

Thanks are due to D. Thomas, P. Dayton and one anonymous referee for critical comments. This is publication no. 818 of the Alfred-Wegener-Institute.

References

Arnaud, P.M. 1977. Adaptations within the Antarctic Marine Benthic Ecosystem. *In* Llano, G.A., *ed. Adaptations within Antarctic Ecosystems. Proceedings of the third SCAR Symposium on Antarctic Biology.* Houston: Gulf Publishing Co., 135-157.

Arntz, W., Gerdes, D., Gorny, M., Gutt, J., Schanz, A., & Steinmetz, R. 1992. Preliminary subsample evaluation from AGT and GSN catches. *In* Bathmann, U., Schulz-Baldes, M., Fahrbach, E., Smetacek, V. & Hubberten, H.W., *eds. Berichte zur Polarforschung*, **68**, 193-196.

Barthel, D. 1992. Do hexactinellids structure Antarctic sponge associations? *Ophelia*, **36**, 111-118.

Barthel, D. & Gutt, J. 1992. Sponge associations in the eastern Weddell Sea. *Antarctic Science*, **4**, 137-150.

BARTHEL, D. & TENDAL, O.S. 1994. Antarctic Hexactinellida *In* WÄGELE, J.W. & SIEG. L., *eds. Synopses of the Antarctic Benthos. In* FRICKE R., *ed. Theses Zoologicae,* Vol. 23. Königstein: Koeltz Scientific Books, 154 pp.

BARTHEL, D., GUTT J. & TENDAL, O.S. 1991. New information on the biology of Antarctic deep-water sponges derived from underwater photography. *Marine Ecology Progress Series*, **69**, 303-307.

BARTHEL, D., TENDAL, O. & PANZER, K. 1990. Ecology and taxonomy of sponges on the eastern Weddell Sea shelf and slope communities. *In* ARNTZ, W., ERNST, W. & HEMPEL, G., *eds.* The expedition Antarktis VII/4 (Epos leg 3) and VII/5 of RV "Polarstern" in 1989. *Berichte zur Polarforschung*, **68**, 120-129.

BELIAEV, G.M. & USHAKOV, P.V. 1957. Some regularities in the quantitative distribution of the benthic fauna in Antarctic waters. [Dokladay Akademy NAUK SSSR, **112**, 137-140, Translation (1957)]. *The American Institute of Biological Sciences*, **112**, 116-119.

BULLIVANT, J.S. 1967. Ecology of the Ross Sea benthos. *Bulletin of the New Zealand Department of Scientific and Industrial Research*, **176**, 49-78.

CLARKE, K.R. & AINSWORTH, M. 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series*, **92**, 205-219.

DAYTON, P.K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. *In* PARKER, B.C., *ed. Proceedings of the Colloquium on Conservation Problems in Antarctica*. Lawrence, Kansas: Allen Press Inc., 81-96.

DAYTON, P.K. 1978. Observations of growth, dispersal and population dynamics of some sponges in McMurdo Sound, Antarctica. *In* LEVI, C. & BOURY-ESNAULT, N., *eds.* Sponge Biology. *Colloques internationaux du Centre national de la recherche scientifique*, No. 291, 271-282.

DAYTON, P.K. 1989. Oceanographic climate shifts cause interdecadal variation in populations of an Antarctic sponge and its predators. *Science*, **245**, 1484-1486.

DAYTON, P.K., MORDIDA, B.J. & BACON, F. 1994. Polar marine communities. *American Zoologist*, **34**, 90-99.

DAYTON, P.K., ROBILLIARD, G.A., PAINE, R.T. & DAYTON, L.B. 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecological Monographs*, **44**, 105-128.

FIELD, J.G., CLARKE, K.R. & WARWICK, R.M. 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series*, **8**, 37-52.

GERDES, D., KLAGES, M., ARNTZ W.E., HERMAN, R.L., GALÉRON, J. & HAIN, S. 1992. Quantitative investigations on macrobenthos communities of the south-eastern Weddell Sea shelf based on multibox corer samples. *Polar Biology*, **12**, 291-301.

GUTT, J. 1991a. Are Weddell Sea holothurians typical representatives of the Antarctic benthos? - A comparative study with new results. *Meeresforschung*, **33**, 312-329.

GUTT, J. 1991b. On the distribution and ecology of holothurians on the Weddell Sea shelf (Antarctica). *Polar Biology*, **11**, 145-155.

GUTT, J., EKAU, W., GORNY, M. 1994. New results on the fish and shrimp fauna of the Weddell Sea and Lazarev Sea (Antarctic). *Proceedings of the NIPR Symposium on Polar Biology*, **7**, 91-102.

GUTT, J. & STARMANS, A. In press. Macrobenthic structure and biodiversity in the Lazarev Sea (Antarctic): indications for the ecological role of physical parameters and biological interactions. *Deep-Sea Research.*

JAZDZEWSKI, K., JURASZ, W., KITTEL, W., PRESLER, E., PRESLER, P. & SICIŃSKI, J. 1986. Abundance and biomass estimates of the benthic fauna in Admiralty Bay, King George Island, South Shetland Islands. *Polar Biology*, **6**, **5-16**.

KOLTUN, V.M. 1966. Sponges of the Antarctic. I. Tetraxonida and Cornacuspongida. *Biological Reports of the Soviet Antarctic Expedition (1955–58)*, Vol. 2. Translated by the Israel Program for Scientific Translations, Jerusalem 1966, 1-116.

KOLTUN, V.M. 1968. Spicules of sponges as an element of the bottom sediments of the Antarctic. *In Symposium on Antarctic Oceanography, Santiago, Chile, 13–16 September 1966*. Cambridge: W. Heffer & Sons Ltd., 121-123 p.

KOLTUN, V.M. 1969. Porifera. *Antarctic Map Folio Series*, **11**, 13-14.

KOLTUN, V.M. 1970. Sponges of the Arctic and Antarctic: A faunistic review. *Symposia of the Zoological Society of London*, **25**, 285-297

KOLTUN, V.M. 1976. Porifera — Part I: Antarctic sponges. *In British Australian New Zealand Antarctic Research Expedition 1929–31. Reports-Series B (Zoology and Botany)*, IX (4), 153-198.

KUNZMANN, K. 1992. *Die mit ausgewählten Schwämmen (Hexactinellida und Demospongiae) aus dem Weddellmeer, Antarktis vergesellschaftete Fauna.* Ph.D thesis, University of Kiel, 108 pp. [Unpublished.]

MÜHLENHARDT-SIEGEL, U. 1988. Some results on quantitative investigations of macrozoobenthos in the Scotia Arc (Antarctica). *Polar Biology*, **8**, 241-248.

PICKEN, G.B. 1985. Marine Habitats-Benthos. *In* BONNER, W.N., WALTON, D.W.H., *eds. Key Environments Antarctica*. Oxford, New York: Pergamon Press, 154-172.

SARÀ, M., BALDUZZI, A., BARBIERI, M., BAVESTRELLO, G. & BURLANDO, B. 1992. Biogeographic traits and checklist of Antarctic demosponges. *Polar Biology*, **12**, 559-585.

VOß, J. 1988. Zoogeographie und Gemeinschaftsanalyse des Makrozoobenthos des Weddellmeeres (Antarktis). *Berichte zur Polarforschung*, **45**, 1-145.

WÄGELE, H. 1989. Diet of some Antarctic nudibranchs. *Marine Biology*, **100**, 439-441.

WHITE, M.G. 1984. Marine benthos. *In* LAWS, R.M., *ed. Antarctic Ecology*. Vol. 2. London: Academic Press, 421-461.