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Epibiotic relationships in the Antarctic benthos

JULIAN GUTT[1] and THOMAS SCHICKAN

Alfred Wegener Institute for Polar and Marine Research, Columbusstraße, D-27568 Bremerhaven, Germany
[1]E-mail: jgutt@awi-bremerhaven.de

Abstract: On the high Antarctic shelf, 374 different epibiotic relationships of the megafauna were photographically registered and statistically analysed. These comprised 47 different epibiotic and 96 substratum taxa and had obvious differences in abundance and presence in three different benthic assemblages. Six abundant obligatory relationships in which the epibiont occurred almost exclusively on one type of substratum had highly specialized epibionts. For an additional eight relationships, a statistical test revealed that the epibionts preferred specific living and elevated mineral substrata. Most of these relationships are interpreted as commensalism (*sensu* Odum) in which the suspension feeding epibiont profits from the elevated position. Here it has better access to food compared with life on the sediment. The evolution of a rich and mainly sessile epifauna on parts of the high Antarctic shelves and the successful development of epibiotic behaviour in other species are suggested as a major reason for the high species richness in the benthic fauna. The results provide evidence that the Antarctic megabenthos is more biologically accommodated than physically controlled.

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Introduction

Intraspecific relationships, both trophic and behavioural, seem to significantly structure Antarctic benthic communities since physical conditions are comparatively stable below the littoral zone (Dayton *et al.* 1970, 1994). The introduction of underwater photography to Antarctic benthic research established that some species tend to use others as substrata. The first photographs from the Ross Sea by Bullivant (1959, 1961) showed crinoids which settled on sponges, while, more recently, Dearborn *et al.* (1986) described the ophiuroid *Astrotoma agassizii* as an epibiont on gorgonarians. Such descriptions lead to the term "multi-storied assemblages" (Knox & Lowry 1977). As a consequence, Dayton (1984) concluded that the structure of benthic communities in the Antarctic is considerably affected by species which serve as a biogenous habitat or as a substratum for others. Previously Hedgpeth (1971) had even compared the Antarctic benthos with reef communities off southern California. Later Gutt (1991) and Gutt & Ekau (1996) classified Antarctic holothurians and fish on the basis of such behaviour while Kunzmann (1996) described the role of sponges as substrata for other invertebrates. Such relationships investigated so far in high Antarctic shelf areas relate only to small, selected groups of animals so that no general conclusions about the relevance of epibiotic relationships can yet be drawn. Barnes & Clarke (1995) investigated for the first time epibiotic relationships at the community level in the sublittoral zone of Signy Island.

The overall approach of this study was to broaden the knowledge base by investigating all macro-epibiotic relationships of which most contribute to the "multi-storied assemblages". The study had two main objectives. The first was to record all such relationships and determine the dominant species and higher taxa that are involved, as they can be regarded as key taxa for the Antarctic benthos. Second, was to find significant preferences of epibionts for living substrata. The use of elevated mineral substrata such as large stones, gravel, or bryozoan debris that can provide a similar advantage to the epibionts as living substrata was also considered. The results should help our understanding of the present complex and diverse high Antarctic benthos and its development over millions of years.

Underwater photography was chosen as it is the method which is least selective and also covers a sufficiently large sample area. The study was carried out on the unusually deep shelves (< 500 m) of the south-eastern Weddell Sea and the easternly adjacent Lazarev Sea because the benthos of this region is faunistically the best known in the high Antarctic. The primary production is likely to be influenced by the pattern of variable surface ice cover while the resulting food input to the benthos is obviously affected by unpredictable weather conditions and by the complex and thus so far poorly understood near-bottom current (Gleitz *et al.* 1994, Gutt *et al.* in press). Our results were calculated separately for the three major benthic assemblages which were classified according to Gutt & Starmans (1998) based on the same photographic material used for this study.

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Material and methods

The photographs were taken from 55 stations sampled between 1985 and 1991 during the expeditions ANT III/3, ANT VI/3, ANT VII/4, and ANT IX/3 of RV *Polarstern* (Hempel 1985, Fütterer 1989, Arntz *et al.* 1990, Bathmann *et al.* 1992). At each station 26–82 photographs were taken which covered an area from 28.8–100.8 m^2. The size of the vertically photographed area ranged from 0.56–1.20 m^2 (± 3%) per frame. The median of the areas photographed per station was 63.6 m^2. 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. The techniques of underwater photography are described in more detail by Gutt & Starmans (1998).

All photographically distinct animals resting on other organisms were counted and identified. The most abundant taxa with epibiotic behaviour were included in the statistical analysis described below. They were also counted when resting on mineral substrata (sediment and elevated structures). All organisms acting as a substratum were also identified to the lowest practical taxonomic level. The relationships between epibionts and substrata were classified into three groups:

1) "Abundant obligatory relationships": absolute abundance (n) ≥ 15, presence ≥ 15% (on both living and elevated mineral substrata), ≥ 90% of the epibiotic specimens found on only a single taxon of substratum organism.

2) "Abundant facultative relationships": absolute abundance (n) ≥ 35, presence ≥ 15% (on both living and elevated mineral substrata), > 10% of the epibiotic specimens found on various substratum taxa.

3) "Rare relationships": all others.

Only "abundant facultative relationships" in which the epibiont was identified to the family, genus, or species level were considered for the statistical analysis. Crinoidea spp. was also included because virtually all specimens of this group were of a single species, *Pomachocrinus kerguelensis*. The living and elevated mineral substrata were classified into the following groups and estimated as % cover of the sea-floor:

a) Living substrata:
   - *Thouarella* spp., *Dasystenella acanthina*, Gorgonaria (THO)
   - Hexactinellida, Porifera (HEX)
   - other Porifera (POR)
   - Bryozoa (BRY)
   - other living sessile organisms, mainly ascidians, pterobranchs, gorgonarians other than *Thouarella* spp. or *D. acanthina* (OTH)

b) elevated mineral substrata
   - small stones (<10 cm) and debris (*SSD*)
   - large stones (>10 cm) (*LST*)

c) sediment (*SED*)

Firstly the relationship between the living plus elevated mineral substrata (in % sea-floor cover) and the use of these substrata by the epibionts was checked for homogeneity using a 2x2 contingency table test (χ^2-test, $P<0.05$; Sachs 1984). In all cases the zero-hypothesis of a random occurrence of supposed epibionts on living and elevated mineral substrata was rejected and so the data were explored further using a kx2 contingency table test ($P<0.05$; Sachs 1984) to determine if the epibionts showed specific substratum preferences and do not only prefer any elevated substrata. This test gives no evidence as to which of the substrata were preferred. Parameters were excluded if the cover of the sea-floor by the substratum was <5%, and if the absolute abundance of the epibiont on one single substratum (n) was <5.

Gutt & Starmans (1998) classified the megabenthos of the same stations and underwater photographs used here into six faunal assemblages by cluster analysis and Multidimensional Scaling based on 144 531 specimens belonging to 313 taxa. In order to find zoogeographical differences in the epibiotic relationships these six station groups were combined into three main assemblages of at least approximately equal size of the sea-floor area examined (Fig. 1). According to the feeding types of the taxa with highest abundances and presences and the statistically determined key taxa these are called assemblages of "Suspension Feeders" (SF), "Suspension and Deposit Feeders" (SD), and "Deposit feeders" (DF).

Results

In terms of absolute and relative abundance, presence and number of substratum and epibiotic taxa, most epibiotic relationships occurred in the SF assemblage, followed by SD, and DF (Table I). Highest presence values had the demosponge *Iophon radiatus* encrusting on the ophiuroids *Ophiurolepis* spp., the Crinoids and the holothurian Cucumariidae spp. on the gorgonarians *Thouarella* spp., *Dasystenella acanthina* and on the bryozoan *Cellarinella* sp. 1, respectively, the bivalve *Lissarca notorcadensis* on the pencil sea urchin *Notocidaris* sp. 1, and Porifera spp. (?) on the sea urchins *Sterechinus* spp (Table II). In addition to most of these relationships the gastropod *Margarella* sp. 1 on the glass sponges of the *Rossella / Scolymastra* group and the crinoids

Table I. Details of stations and assemblage classification.

assemblage	SF	SD	DF
number of stations	31	13	11
area (m^2)	1738	780	785
number of different relationships	343	99	10
number of relationships (presence >10%)	46	32	2
relative abundance of relationships (n/100 m^2)	247	100	10
number of epibiotic taxa	47	27	9
number of substratum taxa	96	42	8

SF (suspension feeders), SD (suspension and deposit feeders), DF (deposit feeders).

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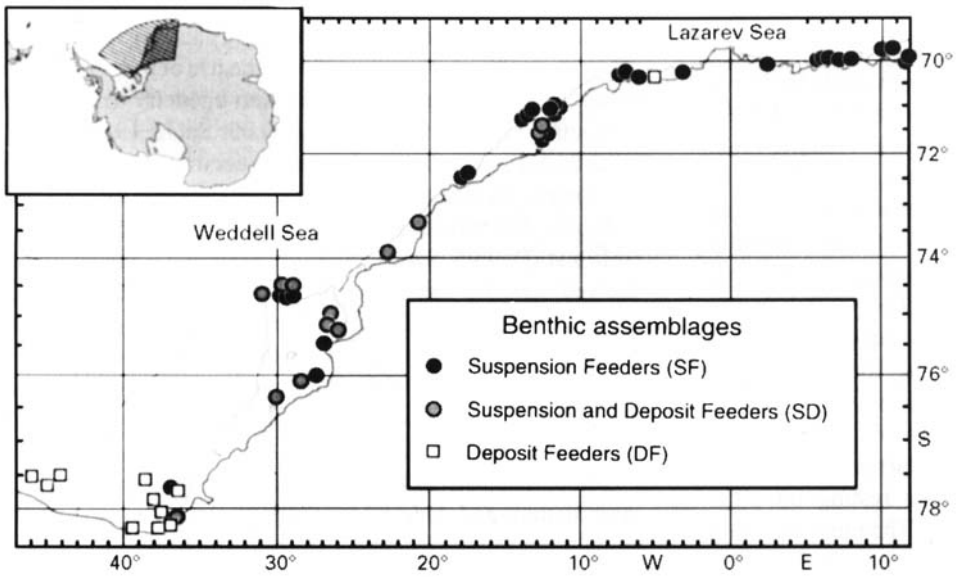


Fig. 1. Map of stations investigated by underwater photography. Classification of benthic assemblages changed after Gutt & Starmans (1998).

on the glass sponge *Rossella racovitzae* were also highly abundant. The epibionts which used the greatest diversity of different living substrata (Crinoidea spp., Cucumariidae spp., the holothurian *Abyssocucumis liouvillei*) and the organisms which serve as substrata for the greatest number of taxa (*R. racovitzae*, *Cellarinella* sp. 1, the compound ascidian *Synoicium* spp.) are listed in Tables III & IV.

The differences between the three assemblages were even more obvious if a coarse taxonomic level was considered (Table V). In this case the most frequent group of epibionts were echinoderms, while the substratum organisms belonged to several different taxonomic groups particularly bryozoans, glass sponges, demosponges, gorgonarians and echinoids. Among the three coarse classes of substrata, the living and the elevated mineral substrata were encountered far more frequently in assemblage SF than in SD (Fig. 2). In assemblage DF living substrata were almost absent and elevated mineral substrata comprised 8.2% of the area examined.

The ratios between the two classes of substrata (sediment, living substrata plus elevated mineral substrata) and the ratios

Table II. Epibiont/substratum percentage presence and numerical abundance data.

	Assemblage	Epibiont	Substratum taxon	
highest presences (%)	SF	*Iophon radiatus* (DEM)	*Ophiurolepis* spp. (OPH)	71.0%
		Cucumariidae spp. (HOL)	*Cellarinella* sp. 1(BRY)	58.1%
		Crinoidea spp. (CRI)	*Dasystenella acanthina*	51.6%
			Thouarella spp. (GOR)	
	SD	Crinoidea spp. (CRI)	*Cellarinella* sp. 1 (BRY)	53.8%
		Crinoidea spp. (CRI)	*Dasystenaella acanthina*	46.2%
			Thouarella spp. (GOR)	
		Lissarca notorcadensis (BIV)	*Notocidaris* sp. 1 (ECN)	38.5%
	DF	*Iophon radiatus* (DEM)	*Ophiurolepis* spp. (OPH)	27.3%
		Porifera spp. (?)	*Sterechinus* spp. (ECN)	18.2%
		all other relationships		9.1%
highest abundances (n/100 m^2)	SF	*Iophon radiatus* (DEM)	*Ophiurolepis* spp. (OPH)	33.4
		Crinoidea spp. (CRI)	*Cellarinella* sp. 1 (BRY)	12.6
		Margarella sp. 1 (GAS)	*Rossella nuda* (HEX)	12.2
	SD	*Lissarca notorcadensis* (BIV)	*Notocidaris* sp. 1 (ECN)	47.9
		Crinoidea spp. (CRI)	*Cellarinella* sp. 1 (BRY)	7.3
		Crinoidea spp. (CRI)	*Dasystenella acanthina*	5.5
			Thouarella spp. (GOR)	
	DF	Porifera spp. (?)	*Sterechinus* spp. (ECN)	7.6
		Iophon radiatus (DEM)	*Ophiurolepis* spp. (OPH)	1.4
		Crinoidea spp. (CRI)	*Rossella racovitzae* (HEX)	0.3

ACT (Actiniaria), ASC (Ascidiacea), BIV (Bivalvia), BRY (Bryozoa), CRI (Crinoidea), DEC (Decapoda, Crustacea), DEM (Demospongiae, Porifera), ECN (Echinoidea), GAS (Gastropoda), GOC (Gorgonocephalidae), GOR (Gorgonaria), HEX (Hexactinellida, Porifera), HOL (Holothuroidea), POR (Porifera), OPH (Ophiuroidea), PIS (Pisces), POC (Polychaeta)

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Table III. Epibionts on the widest range of substrata.

Assemblage	Epibiont	No. of substratum taxa
SF	Crinoidea spp. (CRI)	53
	Cucumariidae spp. (HOL)	32
	Abyssocucumis liouvillei (HOL)	30
SD	Crinoidea spp. (CRI)	31
	Ophiuroidea spp. (OPH)	14
	Cucumariidae spp. (HOL)	11
DF	Ophiuroidea spp. (OPH)	2
	all others	1

between the use of these substrata did not belong to one statistical population for any of the relationships (2x2 contingency table test; Fig. 2). Thus, all these epibionts showed a clear preference for living on a substratum elevated above the sea floor.

The kx2 contingency table test revealed that the proportion of the various elevated mineral and living substrata and their use by the epibionts were not homogeneous and hence the epibionts selected specific substrata. The only exception was the Crinoidea spp. in assemblage SF. In both assemblages considered for the analysis (SF and SD) the gorgonians *Thouarella* spp., *Dasystenella acanthina*, the hexactinellids, and the demosponges were disproportionally used by epibionts compared to their low sea floor cover. The abundant bryozoans were clearly preferred only by the holothurian *Taeniogyrus contortus* and avoided by Gorgonocephalids, the holothurians *Psolus dubiosus* and *Abyssocucumis liouvillei* (in assemblage SF). Other sessile organisms favoured colonization by gorgonocephalids and *Psolus dubiosus* while the holothurians *Ekmocucumis steineni*, Cucumariidae spp. and *Taeniogyrus contortus* were proportionately rare. On elevated mineral substrata small stones and debris (*SSD*) were not preferred by any epibionts and large stones (*LST*) were only favoured as a habitat by *Psolus dubiosus*. A statistical analysis for the "abundant obligatory relationships" (Table VI) was not necessary.

Table IV. Substrata with most diverse epibionts.

Assemblage	Substratum taxa	No. of epibiotic taxa
SF	*Rossella racovitzae* (HEX)	23
	Cellarinella sp. 1 (BRY)	16
	Synoicium spp. (ASC)	13
DF	*Dasystenella acanthina*	
	Thouarella spp. (GOR)	8
	Rossella racovitzae (HEX)	7
	Cellarinella sp. 1 (BRY)	7
DF	*Primnoella* spp. (GOR)	2
	Rossella racovitzae (HEX)	2
	all others	1

Table V. Most common epibiotic relationships (presence >20% or abundance >10/m²) on high taxonomic level.

Assemblage	epibiont	*n*	Substratum taxa	*n*	Presence (%)	Abundance (*n*/m²)
SF	HOL	6	BRY	14	80.6	65.4
	DEM	1	OPH	1	71.0	33.4
	CRI	1	BRY	15	61.3	24.3
	CRI	1	GOR	5	58.1	3.7
	HOL	6	HEX	6	51.6	17.7
	HOL	3	GOR	5	48.4	7.8
	CRI	1	DEM	12	45.2	1.8
	CRI	1	HEX	6	41.9	4.3
	HOL	5	ECN	2	38.7	13.1
	ACT	1	GAS	1	35.5	0.9
	HOL	6	DEM	13	29.0	4.9
	BIV	1	ECN	3	20.0	16.4
	POR	1	ECN	3	20.0	2.0
	HOL	3	ASC	9	25.8	1.4
	ASC	5	BRY	6	22.6	5.9
	DEC	1	BRY	6	22.6	1.0
	GAS	1	HEX	1	16.1	12.2
	HOL	5	*SED*		74.2	12.9
	CRI	1	*SSD*		64.5	27.2
	HOL	4	*SSD*		45.2	10.7
	CRI	1	*SED*		35.5	5.5
	CRI	1	*LST*		35.5	6.8
	HOL	3	*LST*		35.5	2.3
	PIS	1	*SED*		32.3	1.5
SD	CRI	1	BRY	13	53.8	12.4
	CRI	1	GOR	3	46.2	7.0
	CRI	1	HEX	5	46.2	4.2
	HOL	3	HEX	4	46.2	2.9
	OPH	1	GOR	3	46.2	2.9
	HOL	3	BRY	6	38.5	1.8
	BIV	1	ECN	1	38.5	47.9
	ACT	1	GAS	1	30.8	1.2
	DEM	1	OPH	1	30.8	1.4
	HOL	2	GOR	4	30.8	3.6
	OPH	1	POC	2	30.8	0.6
	CRI	1	DEM	3	23.1	0.5
	CRI	1	POC	2	23.1	0.5
	GOC	1	HEX	3	23.1	0.4
	OPH	1	ASC	2	23.1	0.8
	OPH	1	BRY	3	23.1	1.0
	POR	1	ECN	2	23.1	0.9
	CRI	1	*SED*		92.3	13.1
	CRI	1	*LST*		38.5	1.2
	HOL	4	*SED*		38.5	6.3
	PIS	1	*SED*		38.5	1.3
DF	DEM	1	OPH	1	27.3	1.4

SED (sediment), *LST* (large stones), *SSD* (small stones and debris), for all other abbreviations see Table I. (*n* = number of taxa)

Discussion

The most obvious result was the difference in the richness, abundance and presence of different epibiotic relationships in the three main mega-benthic assemblages. There are no studies in other ecosystems with a similar comprehensive broad-scale approach and using a comparable method. Nevertheless, we assume that in the rich suspension feeding

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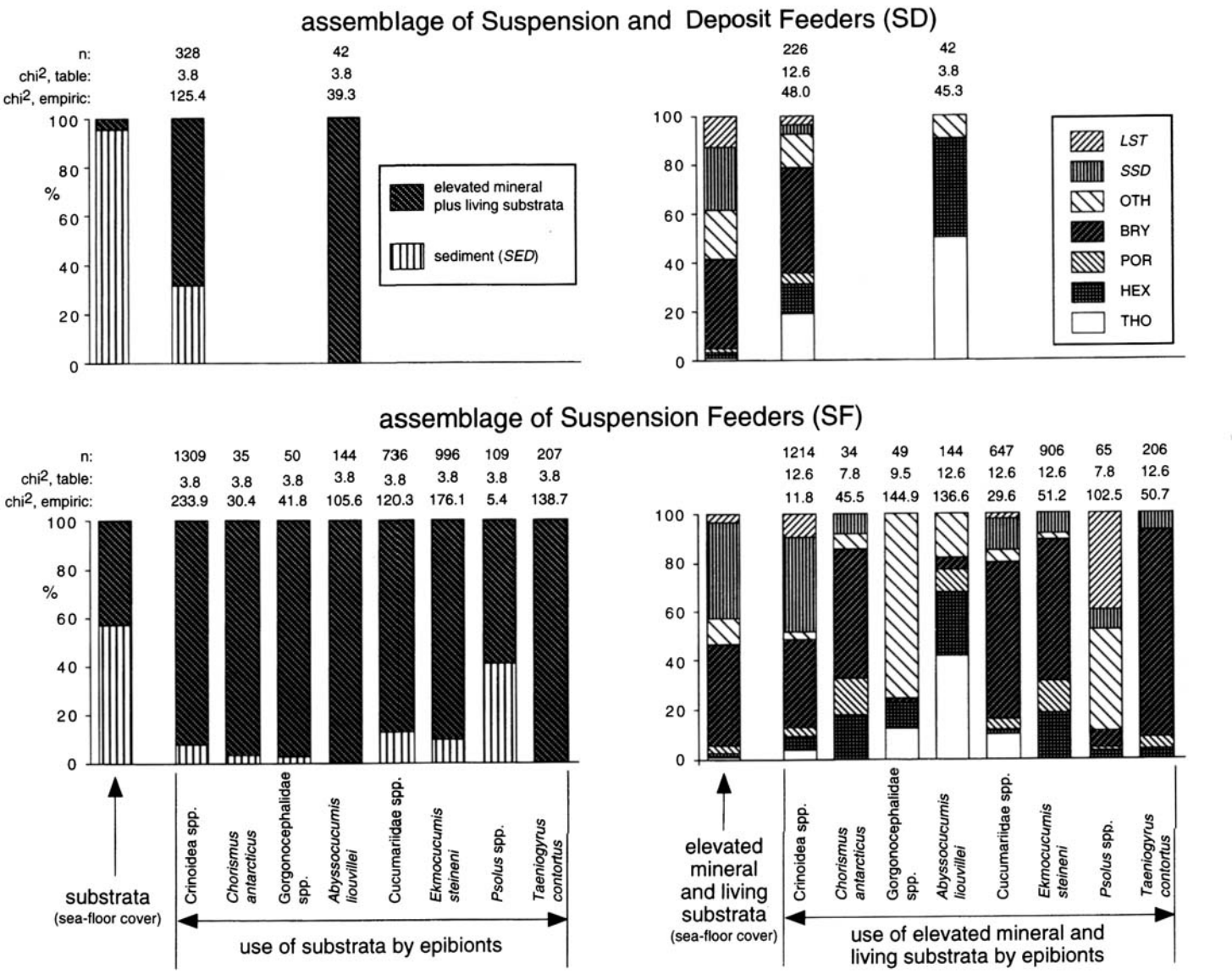


Fig. 2. Availability and use of the substrata by abundant facultative epibionts. The general preference for elevated substrata (2x2 contingency table test, left part of the figure) and the preference for specific elevated mineral and living substrata (k×*n* contingency table test, right part of the figure) was checked by comparing the proportions of the left columns ("substrata" and "elevated mineral and living substrata", respectively) with each of the other columns ("use of substrata by epibionts" and "use of elevated mineral and living substrata by epibionts", respectively). *SED* (sediment), *LST* (large stones), *SSD* (small stones and debris), OTH (other living substrata), BRY (Bryozoa), POR (Porifera), HEX (Hexactinellida, Porifera), THO (*Thouarella* spp. and/or *Dasystenella acanthina*, Gorgonaria).

Table VI. Obligatory relationships ($n \geq 15$, presence≥15%, >90% of the epibiotic specimens on one taxon of substratum organism; values for rare substratum organisms included). Spines of the cidarid echinoids*Homocidaris* spp. and *Notocidaris* sp. 1 and sp. 2 considered as one substratum. For abbreviations see Table I.

Assemblage	Epibiont		Substratum taxon		Presence (%)	Abundance (n)	Abundance (n/100 m^2)
SF	*Iophon radiatus*	DEM	*Ophiurolepis* spp.	OPH	71.0	581	33.4
	Isosicyonis alba	ACT	*Harpovoluta charcoti*	GAS	35.5	15	0.9
	Margarella sp. 1	GAS	*Rossella nuda*	HEX	16.1	212	12.2
	Echinopsolus acanthocola	HOL	*Cinachyra antarctica*	DEM	3.2	1	<0.1
			Gorgonaria sp. 5	DEM	3.2	1	<0.1
			Homocidaris spp.	ECN	3.2	10	0.6
			Notocidaris sp. 1	ECN	35.5	207	11.9
	Lissarca notorcadensis	BIV	*Rossella racovitzae*	HEX	3.2	11	0.6
		BIV	*Homocidaris* spp.	ECN	9.7	75	4.3
		BIV	*Notocidaris* sp. 1	ECN	19.4	187	10.8
		BIV	*Notocidaris* sp. 2	ECN	6.5	23	1.3
SD	*Lissarca notorcadensis*	BIV	*Notocidaris* sp. 1	ECN	28.5	374	47.9
DF	Porifera spp. (?)	POR	*Sterechinus* spp.	ECN	18.2	60	7.6

assemblage SF there are more such biological relationships than in most other benthic shelf systems worldwide, with the exception of coral reefs. The low frequency of epibiotic relationships within the DF assemblage is probably similar to many other shelf communities, that are mainly dominated by soft bottom with variable proportions of coarser fractions, as found in our study area. However, it must be noted that most stations belonging to the assemblage DF are deeper than 500 m and are, therefore, considered to be situated on the upper continental slope. The role of epibiotic relationships in the rich assemblages of the high Antarctic benthos may still be underestimated in our study for the following reasons:

1. we considered only the organisms which were larger than *c.* 5 mm. It is known that among the smaller animals there are various taxa which interact by epibiotic behaviour with others (e.g. Kunzmann 1996).
2. It is believed that several epibionts were visually hidden in the three-dimensional microhabitats of the rich assemblage, and thus were not registered.
3. Not all animals were determined to the species level.

In order to use our results for a better understanding of the development of the high Antarctic benthos, the epibiotic relationships can be classified according to Odum (1971). The complete range of interactions stretches from negative for the epibiont and the substratum organisms (concurrence) through to a tight positive relationship (mutualism/symbiosis). Most of the abundant facultative relationships can be considered as commensalism in which one animal profits and the other is not affected. The filter-feeding holothurians (*Abyssocucumis liouvillei, Ekmocucumis steineni, Cucumariidae, Echinopsolus acanthocola, Psolus dubiosus*) climb up different structures such as stones, sponges or spines of pencil sea urchins. The bivalve *Lissarca notorcadensis* uses the same substratum, spines of pencil sea urchins (see also Brey *et al.* 1993), as *E. acanthocola* (Gutt 1990) and small cucumariide holothurians. Crinoids were sometimes observed in high numbers resting on large sponges. We assume that the position within a range of several centimetres to a few decimetres above the sea floor, where Cacchione *et al.* (1978) observed a sharp increase of current, is advantageous for these epibionts since they feed off drifting particles, living organisms included. A similar behaviour has also been observed by Birkeland (1989) in coral-reefs. Since these epibionts were frequently observed on other animals, there are no indications of a defence mechanism in the substratum organisms. Especially for the crinoids a one-sided advantage is obvious because in the rich assemblage SF they apparently did not prefer any of the elevated mineral or living substrata. On the other hand, it is possible that among the rare relationships with a filter feeding epibiont the substratum taxon is also profiting. Another positive effect for the epibionts is a better opportunity to attach to either vertical, smooth and slightly rough surfaces e.g. glass sponge or filigrane structure of the gorgonians *Thouarella* spp., *Dasystenella acanthina* or bryozoans. The alternative would be the patchily dispersed and, in some areas, rare stones. Two other epibionts, the shrimp *Chorismus antarcticus* and the holothurian *Taeniogyrus contortus*, can be considered to participate in a relationship which represents a transitional stage between commensalism and proto-cooperation in which both animals profit from a non-obligatory co-ocurrence. They both occasionally occurred on the sediment and feed on organic material deposited between the branches of bryozoan colonies and the surface of sponges. Thus, we assume that the substratum organisms profit from the relationships by being cleaned, notably with the more selective behaving *Taeniogyrus contortus*. A similar kind of interaction seems to exist between the gastropod *Margarella* and the glass sponges of the *Rossella/Scolymastra* group. However, this must be considered as a transitional stage between commensalism and parasitism. *Margarella* sp. 1 cleans but

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also feeds on the sponges, thus having both a positive and a negative effect on its host. The sea urchin *Sterechinus* spp. covers itself with the Porifera spp. (?) which can be interpreted as proto-cooperation, in which the guest is protected against predators. The sponge *Iophon radiatus* was never found encrusting on substratum organisms other than the ophiuroids *Ophiurolepis* spp. According to Dearborn *et al.* (1973) it is mainly *O. gelida* being encrusted. The positive effects might be the same as those described for the latter example, but because this relationship is obligatory for the epibiont this represents a transitional stage between proto-cooperation and mutualism. The same is true for the association between the actinian *Isosicyonis alba* and the gastropod *Harpovoluta charcoti* -assuming the same positive effects exist as described for various ectosymbioses between actinians and molluscs or hermit crabs found mainly in tropical waters (Shick 1991). In most cases, the host is protected against sedimentation, early life stages cannot be destroyed by the bioturbation of deposit feeders (Dayton & Oliver 1980) and the epibiont profits from resuspended organic material as a food source if the host is vagile.

An unknown number of the rare epibiotic relationships might be due to chance. These can be considered as neutralism without benefit for the epibiont and the substratum organism or they represent amensalism if the host develops a behaviour to get rid of the epibiont; this we did not observe. The result that all abundant facultative relationships showed a preference for elevated mineral or living substrata leads to the conclusion that among the many rare relationships mainly positive effects, at least for the epibionts, probably exist.

A few of the rare relationships seem to display a clear epibiotic behaviour. The largely plankton feeding ophiuroid *Astrotoma agassizii* (Dearborn *et al.* 1986) has a very patchy distribution in the study area (maximum: 50/100 m^2, Starmans 1997); this gorgonocephalid clearly prefers the gorgonians *Thouarella* spp., *Dasystelella acanthina* and glass sponges as substratum. It is rarely seen on large boulders, in contrast to the other gorgonocephalids statistically analysed (see above). A similar attachment was described by Warner (1982) for tropical species. A glass sponge was also recorded to serve as substratum for the asteroid *Labidiaster annulatus*, where it apparently reached a favourable position to catch krill or small fish, a behaviour described earlier by Dearborn (1977). The isopods of the family Arcturidae were mostly observed on *Thouarella* spp. and/or *Dasystenella acanthina*. They rarely occurred on ascidian stalks, other gorgonians or on more voluminous organisms, such as hemichordates or glass sponges. Actinians, which are generally known to attach with their pedal disc on smooth surfaces such as stones, were photographed on filigrane bryozoans of the genus *Cellarinella*. They are even known (unpublished results) to climb thin stalks of sponges or ascidians. Compound ascidians, of which the majority settled on the sediment surface, were also photographed on a variety of other organisms mainly bryozoans (107 cases), solitary ascidians (47 cases), and glass sponges (23 cases). An unexpected association was presented by mainly small demosponges of the *Cinachyra barbata / Tetilla leptoderma* group living on glass sponges and specimens of the *C. barbata / Tetilla leptoderma* group itself. The behaviour of several fish species which use large barrel-shaped sponges, stalked ascidians or stalked sponges is shown by Ekau & Gutt (1991). This is referred to as a "sit-and-wait" strategy by Hubold (1991) and interpreted as a "sit-observe-and-hide" strategy by Gutt & Ekau (1996). Among these rare relationships the epibionts seem to profit from life on other animals due to a greater accessibility of food.

During the development of the high Antarctic benthos, environmental conditions supported the development of many sessile suspension feeders which have contributed to a diverse benthic system (Bullivant 1967, White 1984, Picken 1985). As a consequence, additional ecological niches can be occupied by additional species that develop either an unspecified preference for an elevated position, or that display a very specific ecological demand in terms of biogenic substratum preference. The simultaneous development of both processes over millions of years have contributed to the high species richness in the Antarctic macrobenthos.

Odum (1971) generalized that advanced developmental stages of an ecosystem are characterized by a high number of positive interspecific relationships. If this is true, for the high Antarctic megabenthos we can state that the investigated assemblages represent an advanced stage because of the many cases of commensalism. However, it is not a highly developed system at a stage of climax, if such a stage exists at all, because both types of symbiosis, mutualism and proto-cooperation, were found to be rare or weakly developed. Our data, in conjunction with the stable physical conditions, confirm the applicability of Sanders' (1968) time-stability hypothesis for the Antarctic benthos since it displays a diverse fauna of specialists with a highly elaborated behaviour in a predominantly biologically accommodated community (Sanders 1979).

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