

Review

High Latitude Antarctic Benthos: A “Coevolution” of Nature Conservation and Ecosystem Research?

Julian Gutt*

*Alfred Wegener Institute for Polar and Marine Research
Columbusstraße, D-27568 Bremerhaven, Germany*

Abstract : Due to international law the Antarctic is currently the best protected large ecosystem on earth, providing the opportunity for scientific research into processes of both regional and global importance. However, it is impossible to carry out research activities without minor disturbances to the environment. The Weddell Sea with its shelf inhabiting fauna can be considered to be representative for the entire Antarctic shelf with exceptions. It has generally escaped major anthropogenic impact but it is the only area in the high latitude Antarctic where long-term research fishing has been carried out. There are two main results combining aspects of nature conservation and benthos research. Firstly, the use of dredges has clearly decreased over the last two decades, whilst the use of non-invasive underwater photography and video has significantly increased. Secondly, during the same period icebergs destroyed an area of the seafloor and its fauna more than 2000-times greater than the area affected by research trawls. The increased use of imaging methods, Remotely Operated Vehicles (ROV) and other modern instruments, as well as statistically based and coordinated sampling strategies can contribute to both a better understanding of ecosystem function and to an ongoing reduction in anthropogenic impact.

Key words : trawling, imaging methods, ROV, icebergs, disturbance, environmental awareness.

1. Introduction

One of the most significant changes related to activities taking place in the Antarctic is a quite recent increase in environmental awareness and corresponding consequences. Before this, some positive steps had already been taken, such as the protection of formerly exploited species, the introduction of protected areas and self-imposed restrictions especially to activities for peaceful purposes only (Rothwell 1996, 1998). The “Protocol of Environmental Protection to the Antarctic Treaty” (“Madrid Protocol”), which governs all areas of environmental and natural protection came into force in 1998, long after similar laws relating to other continents and their coastal waters (for further information, see Francioni and Scovazzi 1996). As a consequence, the waters south of 60°S now represent a vast, legally controlled habitat which is the one area on earth best protected against any human impact.

Given this background, the following questions concerning links between nature conservation and research in the high latitude antarctic benthic system arise:

- Which information originating from ecological research is essential for nature conservation in the Antarctic?
- What are the consequences of increased environmental awareness and legislation for ecosystem research on the seafloor?
- What is the best way forward and are there any areas which need to be reconsidered?

Since the benthos seems not to be tightly matched in time with primary production (Gutt 2000; Barnes and Clarke 1995), which is assumed to be most affected in case of climate changes, only direct mechanical disturbances will be considered here. The benthos around the tip of the Antarctic Peninsula has been affected for decades by commercial fishing, which has had a far greater impact than any research activity but, however, is not the subject of this paper. Thus, all calculations, data and discussions

*Corresponding author. E-mail : gutt@awi-bremerhaven.de

are restricted to the high latitude Antarctic, using examples from the Weddell Sea shelf.

2. Nature conservation needs research

Any reliable assessment of the value and importance of the biota within a specific area requires both basic and specific ecological information. Out of all the marine subsystems, the benthos demands special attention because, unlike the plankton or nekton it is difficult or impossible to escape or reinvade after any disturbance. Thus, it is somehow in an especially endangered position. An important initial step in this context would be to compare the number of known species living in a large habitat with those in different areas. If the number of species new to science can be related to the sampling effort, or reliable species area curves can be drawn, it would then be possible to predict the total number of species. However, these have to be independent from the general preference of taxonomists or the commercial value of specific taxa. At present, only very unsatisfactory comparisons of this kind are possible. Assuming that the number of macrobenthic invertebrates reported from the antarctic shelf do not exceed 5,000 species (based on Gutt *et al.* 2000) it is questionable whether this habitat is really the rich system it is pointed out e.g. by White (1984). In fact, the much more intensively investigated but considerably smaller southern North Sea has less than 1,000 species (Rachor 1999), whereas, the total number of species inhabiting coral reefs is speculated to be 950,000, calculated from the 93,000 known species (Reaka-Kudla *et al.* 1997). That such figures can vary by one order of magnitude (for review see Arntz *et al.* 1997) is mainly due to a lack of sound data, as a result of non-comparative studies and false assumptions.

Another important point as far as nature conservation is concerned is the uniqueness of the biota. The proportion of endemic species varies between intermediate values of around 40 % for diatoms and macroalgae and high values of 90 % or even more for demersal fish, amphipods and pycnogonids (White 1984; Arntz *et al.* 1997). Consequently, any of these species which become extinct in the Antarctic are definitely lost on earth, but other, more cosmopolitan species are less endangered and thus less effort has to be put into their protection. On the other hand, the Antarctic can serve as a refuge for more widespread species which are under greater threat in other areas, since human influence here is relatively low. At present, both these considerations are more theoretical since on a worldwide

scale, not only the Antarctic but also adjacent seas, e.g. around South America, belong to the less anthropogenically affected areas. Furthermore, it is not only the presence or absence of a species, but also its spatial equitability on a global scale which plays an important role. Past research has revealed marked patchiness on all scales for both species as well as communities. Assemblages with many sessile suspension feeders appear to be richer in the total number of species than others, due to their three-dimensional structure (Gutt and Schickan 1998; Knox and Lowry 1977) and seem to concentrate in the high latitude Antarctic. Examples of micro-habitats being dominated by locally abundant species, which, are very rare over a larger scale, are polychaete reefs in Ellis Fjord (Kirkwood and Burton 1988) and large concentrations of the fast growing sponge, *Homaxinella* spp., in disturbed areas of the Ross and Weddell Seas (Dayton 1989; Gutt 2000; Dawber and Powell 1997). These types of species, together with their associated background fauna, are clearly in greater danger than circumpolar generalists. Such information is essential where areas, for example those, "with important or unusual assemblages of species, ... or only known habitat of any species" or "areas of particular interest to ongoing or planned scientific research" (Madrid Protocol, Annex V) are being considered as Antarctic Specially Protected Areas.

It may also be necessary to find out how resilient a system is even where there is little risk of species or assemblages becoming extinct. This is only possible if there is a wide range of information available on its diversity and function, as well as environmental conditions. Table 1 shows an initial attempt at classifying the benthos of the high latitude Antarctic in this way. There are a few important traits which indicate a high degree of resilience, one in particular being that the benthos is permanently exposed to natural disturbance. On the other hand, slow growth indicates a low degree of resilience. So far, little is known about other factors such as genetic variation, migration, early life history and whether high or low diversity contributes to the stability in a marine ecosystem (Pimm 1984). In addition, it has to be emphasized that most of the information available so far is either still very general or only detailed for a few species and thus, not necessarily representative of the broader taxonomic spectrum. To date best information on the resilience of the high latitude antarctic benthos can be provided, studying the results of natural disturbances. Shallow water here is rare and there is permanent exposure to ice abrasion (for review see Barnes 1999; Gutt 2001). The biota consist of

Table 1. Attempt to assess the resilience of the high antarctic benthos according to characteristics of species and the ecosystem function.

Low resilience	High resilience
close interspecific (epibiotic) relationships	food preference of filter feeders not specific
some specific ecological demands (stenoecy)	“match-mismatch” between water column and benthic processes not obvious
slow growth rates and long generation times (but exceptions exist)	system is adapted to physical damage but many other environmental variables are stable
few planktonic larvae	
short periods as meroplankton	
low capacity to disperse	
sessile or sedentary life mode	
many k-strategists	
high complexity (?)	

only very few species and life forms which are well adapted to these conditions. There must be a high resilience, since only those species which can reinvade or grow fast, e.g. some macroalgae, are generally present. However, two groups of researchers from England and Germany made the surprising discovery that even the much richer benthos found on the deeper shelf down to almost 500 m, is intensively disturbed by icebergs (Gutt *et al.* 1996; Peck *et al.* 1999). The fauna at these depths had previously been thought of as more sensitive to disturbance according to most of the characteristics listed in Table 1. Gutt and Starmans (2001) estimated that this impact on the deeper water benthos in the high latitude Antarctic actually ranks as the fifth most serious that any ecosystem on earth experiences. On average it is never possible for the fauna to approach its theoretical climax. It has been proposed by Gutt (2000) that the relatively small maximum size (never exceeding 1.3 m) of the hexactinellid sponge, *Scolymastra joubini*, found in the Weddell Sea is a long-term, large-scale consequence of iceberg scouring. Individuals of the same species are known to grow to a height of 2 m in areas which are probably more sheltered.

Only with detailed information on the biology of single species and physical conditions within a habitat more applied questions concerning nature conservation can be answered. Examples of such issues might be: Which activities have, “less than a” or “more than a minor or transitory impact”? What constitutes a “molestation”? What represents, “detrimental changes in the distribution, abundance or productivity of species or populations...” or, “...degradation of, or substantial risk to, areas of biological ... significance” to be avoided (Madrid Protocol, Article 8; Annex II, Article 1; Article 3). So far, only information of

some preliminary studies are available. Further specific ecological and field studies are required to provide comprehensive answers.

3. Changes in benthic ecosystem research

Research is possibly the only anthropogenic source of direct disturbance experienced by the high latitude antarctic benthos. Interestingly, the nature of such research activities changed considerably at exactly the same time as the above mentioned concept of antarctic environmental protection was first proposed. For example, the capacity of icebreaking research vessels increased and much effort was invested in preliminary faunistic surveys of formerly unknown areas (Bullivant 1967; Gutt 2000; Voss 1988; Faranda *et al.* 2000). Based on these initial results, further, more specific studies were carried out, however, with a much reduced sampling effort (for review see also Arntz 1998; Peck in press; Gutt and Starmans 2001). In addition, the contemporary focus on climate-related studies based on bulk parameters, led to a shift in research activities and any associated anthropogenic impact from the bottom to the water column (Arntz *et al.* 1999). On the other hand, advanced biodiversity research which developed from the idea of nature conservation, requires modern research strategies which providing taxonomically complete samples being representative of large areas.

Analysis of towed sampling gear and imaging methods used aboard the German research vessel, “Polarstern”, illuminates two important aspects where there is a “coevolution” of nature conservation and research. Between 1983 and 2000, international research initiatives (EPOS and EASIZ) and the national benthos research programme focussed on the shelf of the southeastern

Weddell Sea, between 30° and 7°W. Included in this area were a wide shelf area off Halley Bay in the southwest and Atka Bay in the northeast. Outside this area, the number of stations to the West was less than 4 and to the East, approximately 2 stations per 100 km of coast, respectively. Within the main investigation area, there were 14 stations per 100 km. Depths greater than 600 m were excluded since the slope differs considerably from the shelf and has, so far, been less intensively investigated. The areas covered by the trawls are detailed in Voss (1988) for years 1983/84 and Gutt (1988) for 1985. Values for all subsequent years were calculated as a simple function of the average trawling speed of 0.7 nm (nautical miles=1852 km h⁻¹) for Agassiz-trawls and 3 nm for bottom trawls, the width of the net (3 m for Agassiz-trawl and 24 m for bottom trawls) and the trawling time on the seabed. Values for the latter are listed in the cruise reports (Fütterer 1988; Schnack-Schiel 1987; Arntz and Gutt 1997; Arntz and Gutt 1999; Miller and Oerter 1990; Arntz *et al.* 1990; Bathmann *et al.* 1992). In 1989, an assumed average haul time of 20 minutes was used for the Agassiz-trawl. Benthopelagic trawls were only considered if they included material from the seafloor; their time

actually trawling on ground was divided by 2 because it was only occasionally in contact with the seafloor. Epibenthic sledges and small dredges were not included because they are almost irrelevant in this context, as are grabs. Due to a lack of detailed information it was necessary to estimate the area covered by six of the Agassiz-trawls, based roughly on other catches taken at the same time in the same area. As a result of these limitations, definitions and assumptions, 92 Agassiz-trawls and 52 bottom trawls, covering a total area of 2.04 km², have been considered. Fig. 1 shows how the catch effort has changed over time since 1983 (area covered by the trawls versus 2-year intervals), with a sharp decrease in Agassiz-trawls. During the same period the general effort, which could be expressed as the number of scientists participating in the expeditions and being engaged in benthos research, did not decrease. A large amount of biological samples is no longer necessary and short catches to obtain few living animals became more important instead. So far there has been no yet a similar change in bottom trawls, although it might be expected in the future.

The introduction of underwater photography to the Antarctic in the late fifties (Bullivant 1959, 1961) might have been initially due to scientific curiosity. It was later used in studies on quantitative ecology, the main advantages being that it is relatively non-selective, the organisms are studied in their natural habitat with little bias and abundances of larger organisms on a larger spatial scale can be evaluated, even for separate m². There has been an obvious increase in the use of underwater photography and video in the Weddell Sea as a result of the advantages and advances in modern technology (Fig. 1). The fluctuations, however, show that they are recognised only by few working groups as a useful tool for benthic ecosystem research. One clear advantage that trawls still have is that they provide true samples, which are necessary for most individual-based studies and those surveys which require a complete list of species for a defined area. In the late eighties, ROV's were successfully used by Japan, New Zealand, Germany, Italy, Spain and others for a variety of scientific purposes (see e.g. McInnes and Powell 1995; Bergström *et al.* 1990; Hamada *et al.* 1986), however, their main use was only to observe animals on the seafloor or in the water column. In advanced ecosystem research a finely balanced coexistence between both methodological approaches, sampling and imaging, will lead to the best possible success in the sense of the Madrid Protocol.

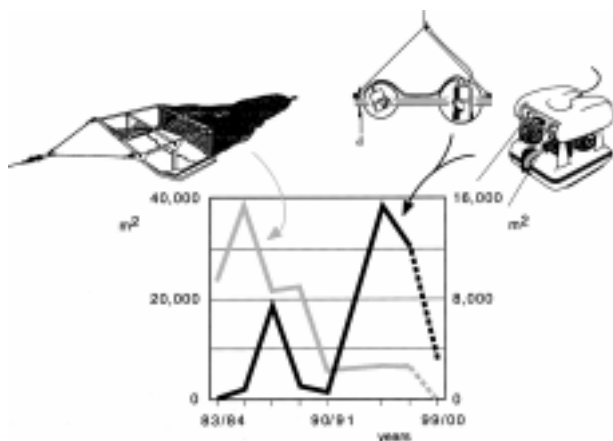


Fig. 1. Effort of Agassiz-trawls expressed as total area covered by all hauls (grey curve) and by the imaging methods underwater photography and video (black curve) on the deeper shelf of the south-eastern Weddell Sea. Data were pooled for 2 year periods because, on average, there was only a benthic programme every second year. Only activities giving scientific data were considered. Activities in 2000 were exceptionally short and hampered by bad weather. The peak in the use of imaging methods in 1985/86 was due to the introduction of ROV. This was then followed by lower values due to technical problems.

4. Natural versus anthropogenic impact

In antarctic benthos research there has been one especially important development as a result of in situ observations. For the first time, the natural damage of benthic communities on the deeper shelf by grounding icebergs was analyzed. Based on this study also a visually controlled sampling (Lee *et al.* 2001) and fishing at an obviously disturbed site was possible, only because this area was previously discovered by the ROV (Gutt 2001; Brenner *et al.* 2001). A simple comparison might help to clarify whether research activities harm the benthic ecosystem, which is generally seen as worth protecting, or whether their effect is insignificant. The calculations shown in Table 2 are based on the above mentioned 2.04 km² disturbed by towed sampling equipment, the total size of the investigation area, and the value for the impact by grounded icebergs (Gutt and Starman 2001). The final result is that the natural disturbance is, purely mathematically, >2,000 times more destructive than the research activities. This comparison does not touch on the fact that also the intensity of disturbance by trawling (proportion of the total amount of fauna which is destroyed according to Pickett and White 1985) is much lower than that of icebergs, which is close to 100 %. It has also to be noticed that the assumption of the recolonization period is at least 15 years and thus the entire calculation is a quite conservative one. Recently, iceberg disturbance has been looked at in the context of both the intermediate-disturbance hypothesis (Houston 1979) and the patchy dynamics concept (Pickett and White 1985). It might be possible that a certain frequency of disturbance creates and/or maintains a relatively high benthic biodiversity in the high latitude Antarctic. However, it should not be forgotten that also environmental stability plays an

Table 2. Comparison of natural and anthropogenic impact on the high antarctic benthos in the southeastern Weddell Sea. Values for proportions of area refer to the total area of investigation.

area of investigation: 38 × 690 km (shelf between 7° and 24°W)	
110 × 150 km (shelf off Halley Bay)	
total: 42,600 km ²	
icebergs:	research trawls:
7.6 % area in 15 years*	2.04 km ² in 19 years (82/83 until 00/01)
	2.15 km ² in 20 years
10.1 % area in 20 years	0.0050 % area in 20 years
ratio between disturbance by icebergs and research trawls:	
>2,000 : 1	

*after Gutt & Starman (2001)

important role to create and maintain, especially over an evolutionary time scale, communities being rich in species (Grassle and Sanders 1973).

5. Future perspective and conclusion

It seems possible that nature conservation and fundamental research could mutually benefit from continuing to develop side-by-side in the future (see also Estes and Peterson 2000). South polar specific international initiatives, such as EPOS, EASIZ and EVOLANTA, together with global programmes, serve as an umbrella under which many nations have agreed on common areas of research, focussing on life on the seafloor. A harmonized cooperation in different aspects, such as the area, depth, and time of an investigation, the environmental parameters measured and the taxonomic groups or single species studies can 1) reduce the anthropogenic impact and 2) optimize the scientific output.

In order to achieve these aims, the following may play a strategic role:

- use of modern information technology (internet and data banks) to exchange information and avoid unnecessary sampling or experiments,
- efficient sampling strategies (e.g. He and Legendre 1996),
- use of advanced statistics to evaluate how representative results are,
- increased use of non-invasive methods and visually controlled sampling,
- development of new, less disruptive methods (landers, low energy acoustics),
- joint use of expensive equipment by several working groups to reduce costs (ships, ROV, submersibles, AUV).

The biological parameter which is most urgent to be studied in this context is the speed of recolonisation after disturbances, which is closely related to growth rates and the early life history of a species. On the physical side, the disturbance regime (Sousa 1984) and its effect on the biota is not yet well understood for most marine systems and may well play a key role in their resilience. For a general relationship between stability and complexity, as well as diversity and ecosystem function, see Grime (1997), Holling (1973), Pimm (1984), Elmgren and Hill (1997), Lawton and Brown (1993), and Schwartz *et al.* (2000). Any comprehensive comparison between natural and anthropogenic impact should also include areas

within the Antarctic where fishing is relatively intensive. Not before such studies reach a certain stage they are truly relevant within a global concept of nature conservation. Such concepts are either descriptive and focus on the ethics and aesthetic aspects or corresponding calculations estimate the economic value of the world's ecosystems assuming that they contribute to human welfare (Costanza *et al.* 1997). A complete view of value of the high latitude antarctic ecosystem to the entire human race can only be achieved through dialogue between relevant social groups, scientists and politicians, economists and ethical groups as well as administrators and even insurance experts (see also Aust and Shears 1996).

After all, for any marine biologist working in the high latitude Antarctic there are two things which go hand-in-hand. They alone can contribute far more than in areas of greater economic importance to the conservation of this unique, diverse and pristine ecosystem, as stated in the Madrid Protocol, "...Antarctica as a natural reserve, devoted to peace and science." (Article 2) and, "The protection of the Antarctic environment ... and its value ... for ... scientific research ... shall be fundamental considerations in the planning and conduct of all activities in the Antarctic Treaty area." (Article 3). However, the scientist has to abide by certain rules aimed at protecting the biota in this area of scientific interest better than any other large ecosystem on earth.

References

- Arntz, W.E., J. Gutt, and M. Klages. 1997. Antarctic marine biodiversity: an overview. p. 3-14. In: *Antarctic Communities. Proc. 6th SCAR Biol. Symp., Venice 1994*, eds. by B. Battaglia, J. Valencia, and D.W.H. Walton. Cambridge University Press, Cambridge.
- Arntz, W.E. 1998. Marine ecology in Antarctica and its connections to "Global Change". p. 3-27. In: *Atti del 12° Congresso della Associazione Italiana di Oceanologia e Limnologia (Isola di Vulcano, 18-21 Settembre 1996)*. Vol. II, ed. by M. Picazzo. AIOL, Genova.
- Arntz, W.E., J.M. Gili, and K. Reise. 1999. Unjustifiably ignored: Reflections on the role of benthos in marine ecosystems. p. 105-124. In: *Biogeochemical Cycling and Sediment Ecology*, eds. by J.S. Gray, W. Ambrose, and A. Szaniawska. NATO ASI series, Kluwer, Dordrecht.
- Arntz, W. and J. Gutt. 1997. The expedition ANTARKTIS XIII/3 (EASIZ I) of "Polarstern" to the eastern Weddell Sea in 1996. *Ber. Polarforsch.*, 249, 1-148.
- Arntz, W.E. and J. Gutt. 1999. The expedition ANTARKTIS XV/3 (EASIZ II) of RV "Polarstern" in 1998. *Ber. Polarforsch.*, 301, 1-229.
- Arntz, W., W. Ernst, and I. Hempel. 1990. The expedition ANTARKTIS VII/4 (Epos leg 3) and VII/5 of RV "Polarstern" in 1989. *Ber. Polarforsch.*, 68, 1-214.
- Aust, A. and J.R. Shears. 1996. Liability for environmental damage in Antarctica. *Review of European Community & International Environmental Law*, 5, 312-320.
- Barnes, D.K.A. 1999. The influence of ice on polar near-shore benthos. *J. Mar. Biol. Ass. UK*, 79, 401-407.
- Barnes, D.K.A. and A. Clarke. 1995. Epibiotic communities on sublittoral macroinvertebrates at Signy Island, Antarctica. *J. Mar. Biol. Ass. UK*, 75, 689-703.
- Bathmann, U., M. Schulz-Baldes, E. Fahrback, V. Smetaček, and H.-W. Hubberten. 1992. The expeditions ANTARKTIS IX/1-4 of the research vessel "Polarstern" in 1990/91. *Ber. Polarforsch.*, 100, 1-403.
- Bergström, B.I., G. Hempel, H.-P. Marschall, A. North, V. Siegel, and J.-O. Strömberg. 1990. Spring distribution, size composition and behaviour of krill *Euphausia superba* in the western Weddell Sea. *Polar Rec.*, 26, 85-89.
- Brenner, M., B.H. Buck, S. Cordes, L. Dietrich, U. Jacob, M. Mintenbeck, A. Schröder, T. Brey, R. Knust, and W. Arntz. 2001. The role of iceberg scours in niche separation within the Antarctic fish genus *Trematomus*. *Polar Biol.*, 24, 486-496.
- Bullivant, J.S. 1959. Photographs of the bottom fauna in the Ross Sea. *N.Z. J. Sci.*, 2, 485-497.
- Bullivant, J.S. 1961. Photographs of antarctic bottom fauna. *Polar Rec.*, 68, 505-508.
- Bullivant, J.S. 1967. Ecology of the Ross Sea benthos. *N.Z. Dep. scient. ind. Res.*, 176, 49-78.
- Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R.V. O'Neill, J. Paruelo, R.G. Raskin, P. Suttom, and M. van den Belt. 1997. The value of the world's ecosystem services and natural capital. *Nature*, 387, 253-260.
- Dawber, M. and R.D. Powell. 1997. Epifaunal distributions at antarctic marine-terminating glaciers: influences of ice dynamics and sedimentation. p. 875-884. In: *The Antarctic Region: Geological Evolution and Processes*, ed. by C.A. Ricci. Terra Antarctica Publication, Siena.
- Dayton, P.K. 1989. Interdecadal variation in an antarctic sponge and its predators from oceanographic climate shifts. *Science*, 245, 1484-1486.
- Elmgren, R. and C. Hill. 1997. Ecosystem function at low biodiversity - the Baltic example. p. 319-336. In: *Marine Biodiversity: Patterns and Processes*, eds. by R.F.G. Ormond, J.D. Gage, and M.V. Angel. Cambridge University Press, Cambridge.
- Estes, J.A. and C.H. Peterson. 2000. Marine ecological research in seashore and seafloor systems: accomplishments and future directions. *Mar. Ecol. Progr. Ser.*, 195, 282-289.
- Faranda, F.M., L. Guglielmo, and A. Ionora. 2000. *Ross Sea Ecology*. Springer, Berlin. 604 p.
- Francioni, F. and T. Scovazzi. 1996. International law for

- Antarctica. Kluwer Law International, The Hague. 681 p.
- Fütterer, D.K. 1988. The expedition ANTARKTIS-VI of RV "Polarstern" in 1987/1988. *Ber. Polarforsch.*, 58, 1-267.
- Grassle, J.F. and H.L. Sanders. 1973. Life histories and the role of disturbance. *Deep-Sea Res.*, 20, 643-659.
- Grime, J.P. 1997. Biodiversity and ecosystem function: the debate deepens. *Science*, 277, 1260-1261.
- Gutt, J. 1988. Zur Verbreitung und Ökologie der Seegurken (Holothuroidea, Echinodermata) im Weddellmeer (Antarktis). *Ber. Polarforsch.*, 41, 1-87.
- Gutt, J. 2000. Some "driving forces" structuring communities of the sublittoral Antarctic macrobenthos. *Antarct. Sci.*, 12, 297-313.
- Gutt, J. 2001. On the direct impact of ice on marine benthic communities, a review. *Polar Biol.*, 24, 553-564.
- Gutt, J. and T. Schickan. 1998. Epibiotic relationships in the Antarctic benthos. *Antarct. Sci.*, 10, 398-405.
- Gutt, J. and A. Starmans. 2001. Quantification of iceberg impact and benthic recolonization patterns in the Weddell Sea (Antarctica). *Polar Bol.*, 24, 615-619.
- Gutt, J., A. Starmans, and G. Dieckmann. 1996. Impact of iceberg scouring on polar benthic habitats. *Mar. Ecol. Prog. Ser.*, 137, 311-316.
- Gutt, J., B.I. Sirenko, W.E. Arntz, S. Smirnov, and C. De Broyer. 2000. Biodiversity of the Weddell Sea: macrozoobenthic species (demersal fish included) sampled during the expedition ANT XIII/3 (EASIZ I) with RV "Polarstern". *Ber. Polarforsch.*, 372, 1-103.
- Hamada, E., H. Numanami, Y. Naito, and A. Taniguchi. 1986. Observation of the marine benthic organisms at Syowa Station in Antarctica using a remotely operated vehicle. *Mem. Nat. Inst. Polar Res.*, 40, 289-298.
- He, F. and P. Legendre. 1996. On species-area relations. *Am. Nat.*, 148, 719-737.
- Holling, C.S. 1973. Resilience and stability of ecological systems. *Ann. Rev. Ecol. Syst.*, 4, 1-23.
- Houston, M. 1979. A general hypothesis of species diversity. *Am. Nat.*, 113, 81-101.
- Kirkwood, J.M. and H.R. Burton. 1988. Macrobenthic species assemblages in Ellis Fjord, Vestfold Hills, Antarctica. *Mar. Biol.*, 97, 445-457.
- Knox, G.A. and J.K. Lowry. 1977. A comparison between the benthos of the Southern Ocean and the North Polar Ocean with special reference to the Amphipoda and the Polychaeta. p. 423-462. In: *Polar Oceans. Proceedings of the Polar Oceans Conference held at McGill University, Montreal, May 1974*, ed. by M.J. Dunbar. Arctic Institute of North America, Calgary, Alberta.
- Lawton, J.H. and V.K. Brown 1993. Redundancy in ecosystems. p. 255-270. In: *Biodiversity and Ecosystem Function*, eds. by E.-D. Schulze and H.A. Mooney. Springer, Berlin.
- Lee, H.J., D. Gerdes, S. Vanhove, and M. Vincx. Meiofauna response to iceberg disturbance on the Antarctic continental shelf at Kapp Norvegia (Weddell Sea). *Polar Biol.* (in press).
- McInnes, J.N. and R.D. Powell. 1995. Characterization of the glaci-marine grounding-line environment of Mackay Glacier Tongue, Antarctica, using a submersible remotely operated vehicle. *Antarct. J. US*, 30, 80-82.
- Miller, H. and H. Oerter. 1990. The expedition ANTARKTIS-V of RV "Polarstern" 1986/87 Report of Legs ANT-V/4-5. *Ber. Polarforsch.*, 57, 1-207.
- Peck, L.S., S. Brockington, S. Vanhove, and M. Beghyn. 1999. Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica. *Mar. Biol.*, 117, 235-241.
- Peck, L.S. in press. Ecophysiology of Antarctic marine ectotherms: limits to life. *Polar Biol.*
- Pickett, S.T.A. and P.S. White. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando. 472 p.
- Pimm, S.L. 1984. The complexity and stability of ecosystems. *Nature*, 307, 321-326.
- Rachor, E. 1999. Voraussetzungen für die Erhaltung der biologischen Vielfalt in Nord- und Ostsee einschließlich ihrer Küsten. p. 27-37. In: *Ziele des Naturschutzes und einer nachhaltigen Naturnutzung in Deutschland-Küsten und Randmeere*. Bundesumweltministerium, Bonn.
- Reaka-Kudla, M.L., D.E. Wilson, and E.O. Wilson. 1997. *Biodiversity II. Understanding and Protecting Our Biological Resources*. Joseph Henry Press, Washington DC, 551 p.
- Rothwell, D. 1996. *The Polar Regions and the Development of International Law*. Cambridge University Press, Cambridge. 498 p.
- Rothwell, D. 1998. Australian and Canadian initiatives in polar marine environmental protection: a comparative review. *Polar Rec.*, 34, 305-316.
- Schwartz, M.W., C.A. Brigham, J.D. Hoeksema, K.G. Lyons, M.H. Mills, and P.J. Van Mantgem. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia*, 122, 297-305.
- Schnack-Schiel, S. 1987. The Winter-Expedition of RV "Polarstern" to the Antarctic (ANT V/1-3). *Ber. Polarforsch.*, 39, 1-259.
- Sousa, W.P. 1984. The role of disturbance in natural communities. *Ann. Rev. Ecol. Syst.*, 15, 353-391.
- Voss, J. 1988. Zoogeographie und Gemeinschaftsanalyse des Makrozoobenthos des Weddellmeeres (Antarktis). *Ber. Polarforsch.*, 45, 1-145.
- White, M.G. 1984. Marine benthos. p. 421-461. In: *Antarctic Ecology. Vol. 2*, ed. by R.M. Laws. Academic Press, London.

Received Sep. 28, 2001

Accepted Dec. 17, 2001