

Circumpolar overview and spatial heterogeneity of Antarctic macrobenthic communities

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Abstract The geographical coverage of a comprehensive dataset on Antarctic macrobenthic communities is provided for the first time. Since the sampling methods applied since the 1950s vary considerably, a robust analysis was carried out. The results show firstly, that all main types of communities, especially suspension and mobile or infaunal deposit feeders, can occur everywhere. Thus, their biogeography is hardly predictable and assumed to be shaped by complex biological interactions. Secondly, the often-mentioned dominance of communities composed of suspension feeders and associated fauna can be confirmed.

Keywords Biogeographic pattern · Macrobenthic classification · Suspension feeders · Infauna · Mobile deposit feeders

Introduction

Antarctic benthic communities have been the subject of scientific investigations since the 1950s. Remarkable early

faunistic surveys included those of Bullivant (1967) in the Ross Sea and Arnaud (1974) off Adelie Land in East Antarctica. Comprehensive functional studies started with the outstanding work of Dayton et al. (1974) in McMurdo Sound and continued until recently. Corresponding information on macrobenthic systems published between 1956 and 2010 was compiled, uploaded at <http://ipt.biodiversity.aq/resource.do?r=macrobenthos>, and published by Gutt et al. (2013). Such spatially explicit information was attributed to discrete and overlapping community types classified to the best of expert knowledge (Gutt 2007) and modified in Turner et al. (2009). This approach was carried out despite marked differences in methods, quantity of results, taxonomic resolution and geographical coverage between the surveys.

The first aim of this study using the existing classification was to provide an overview of the geographical coverage of published information on macrobenthic communities. The second aim was to show the potential of such community studies if acquisition and analyses of faunistic and ecological data were to be standardised.

The data compiled by Gutt et al. (2013) are complex, georeferenced and valuable. Thus, the availability of this information alone leads us to the third aim of this study, despite being of different nature and collected by different methods. We carried out a coarse spatial analysis, in which we (1) mapped the number of macrobenthic communities within equal-sized (3° of latitude by 3° of longitude) spatial units (=cells), (2) identified for each spatial cells the community within the highest abundance of occurrence, and (3) checked a possible correlation between the abundance and dominant types of communities and water depth.

Because this approach covers the macrobenthos as a whole, the results can provide a valuable basis for further studies on applied and fundamental science, e.g. on ecosystem functioning (see, e.g., Dayton et al. 1974; Gutt 2006; Cummings et al. 2010), biodiversity (Clarke and Johnston

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2003; Gutt et al. 2010) or climate change (Barnes and Peck 2008; Brandt and Gutt 2011; Barnes et al. 2009).

We do not claim to cover all material on Antarctic macrobenthic biogeography, especially since it is difficult to decide which data are suited for this approach and which are not. However, this study is based on the most comprehensive dataset of this kind in the world. Some of the data are historic, very comprehensive and descriptive, while some newer data cover only a certain proportion of the macrobenthos or have a low taxonomic resolution but are important to understand benthic processes. We tried to consider as much published information as possible, covering the period from March 1956 to February 2010, of which the metadata were published by Gutt et al. (2013). By undertaking this study, we hope to motivate the scientific community to contribute to this continued growing dataset with newly published results.

Material and methods

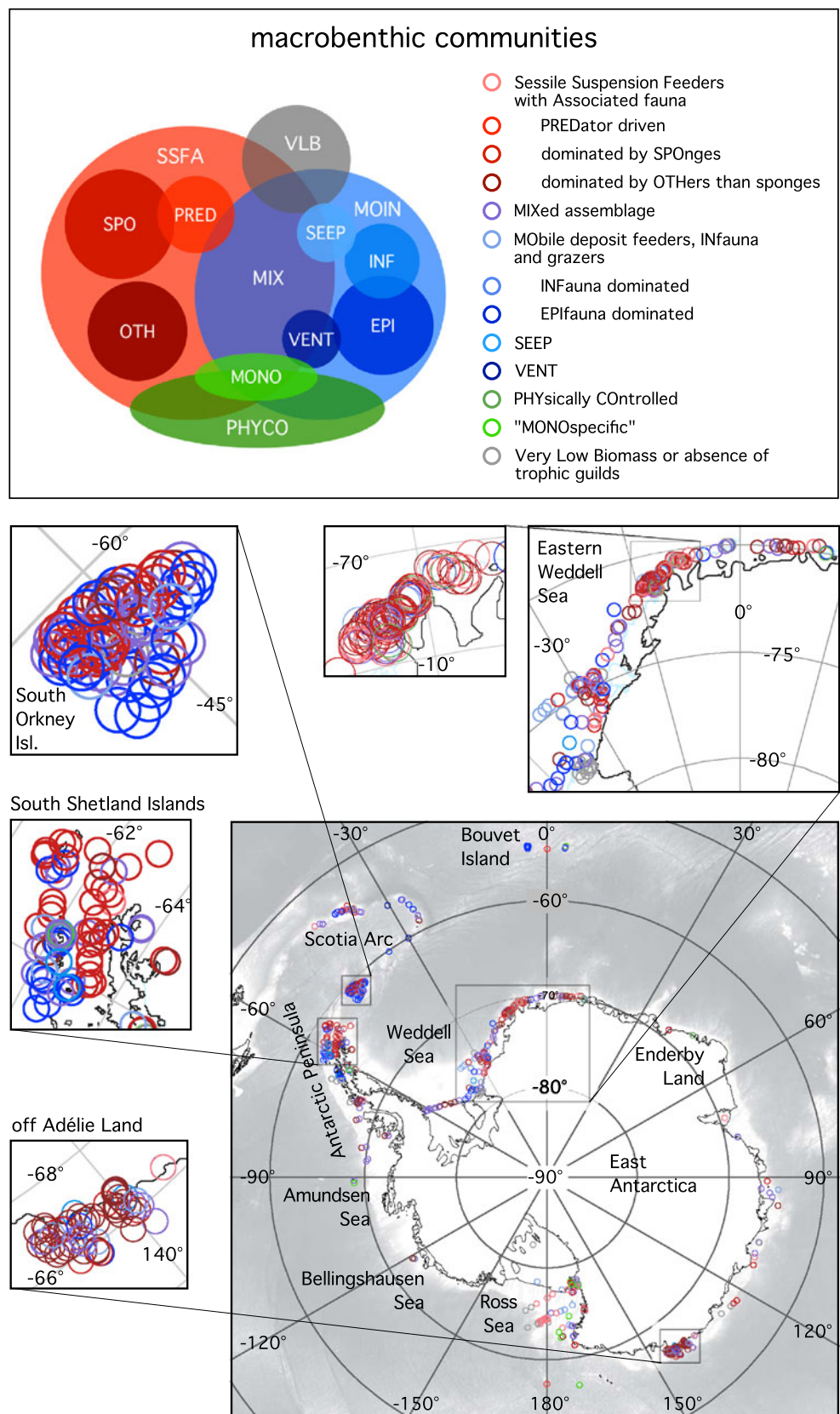
For all three analyses, 861 data points from approximately 90 single datasets were used (<http://ipt.biodiversity.aq/resource.do?r=macrobenthos>, and Gutt et al. 2013). The biological information stems from various sampling gear, stationary grabs and corers, towed trawls and dredges, as well as direct observations, e.g. by scuba diving, sea-bed videos and photography. The sites of these investigations were mainly situated on the shelf and unevenly distributed around the Antarctic continent. MS Access and ArcGIS were used to carry out numeric analyses and to prepare the maps. In a first step, the numbers of communities per spatial cell were counted. Cell size of 3° of latitude by 3° of longitude was selected to get a sufficient spatial resolution and a sufficient average number of records per cell for the analysis. Their residuals resulting from a regression between number of samples (x) and number of communities (per spatial cell, y) were calculated to reduce bias from regionally varying sampling efforts. A semi-log model (number of samples on x -axis transformed) was applied because it achieved a better regression ($y=1.57x+0.92$, $r^2=0.74$) than correlations without any transformation ($r^2=0.57$) or with a log–log transformation ($r^2=0.68$). In the second attempt, the most abundant community per spatial cell was simply displayed. No decision was made when only one community per cell occurred (“Single”) and when no true dominance existed and more than one community had the same abundance (“Equal”). Thirdly, we correlated the number of depth bins in 100-m depth increments with the number of community types per cell and the log number of records with the depth bins per cell (=depth range of the cell). We also calculated the mean water depth for the three supra-communities. The Shannon Index was used to calculate the diversity of community types per depth bins.

Results and discussion

The basic information in Figs. 1 and 2 shows that results on macrobenthic communities exist from all around the continent and some islands but with a high regional patchiness. The Antarctic Peninsula area together with the Scotia Arc, especially the South Shetland and South Orkney Islands, the southeastern Weddell Sea, the eastern Ross Sea and the area off Adelie Land have a high density of data, whilst information is still very scarce from the Amundsen/Bellingshausen Seas and off Enderby Land in East Antarctica. Surveys that focus on these areas are being undertaken, but analyses have not yet been completed. Most obvious is the missing of community information from the deep sea, where recent successful expeditions have taken place, but, due to the high richness of known and undescribed species, community analyses require much time and, due to the generally low abundances, a modified approach.

A first biological generalisation is that all abundant communities can occur everywhere around the continent. This can even be observed for relatively small areas with high sampling effort (Fig. 1). The patterns seem to have a fractal nature where the complexity does not decrease if one zooms in. In such a case, it is difficult to find more specific generalisations; the patterns seem to be non-predictable. A conclusion from this is that mainly small-scale biological processes and interactions shape the communities. It has already been shown that environmental parameters that usually shape benthic communities worldwide, such as sediment grain size and water depth, have relatively little influence on the Antarctic benthos, whilst some Antarctic-specific factors, such as sea-ice cover and ice-shelves are at least partly efficient (Cummings et al. 2010). Among the biological processes structuring the communities especially dispersal, predations, competition, trophic commensalism, and symbioses, the formation of favourable or unfavourable micro-niches by engineering organisms are potentially important (Gutt 2006). In addition, small-scale physical impacts exist, such as iceberg scouring and anchor ice, which lead to the coexistence of different successional stages and small-scale bottom topography, shaping complex bottom near-current regimes and causing locally extreme sediment conditions (see, e.g., Smale and Barnes 2008; Barnes and Conlan 2007). However, such patchiness at a scale of several meters transect length (for examples, see Brandt and Gutt 2011) is not well represented in most of the results used for this study, neither those with towed gear like trawls and dredges that integrate biological information over a long distance nor video-transects, which have not been analysed with a high spatial resolution. For stationary samples, e.g. from box corers or single sea-bed photos, such bias cannot be excluded, but remain exceptional. Other generally large-scale environmental parameters also contribute to the

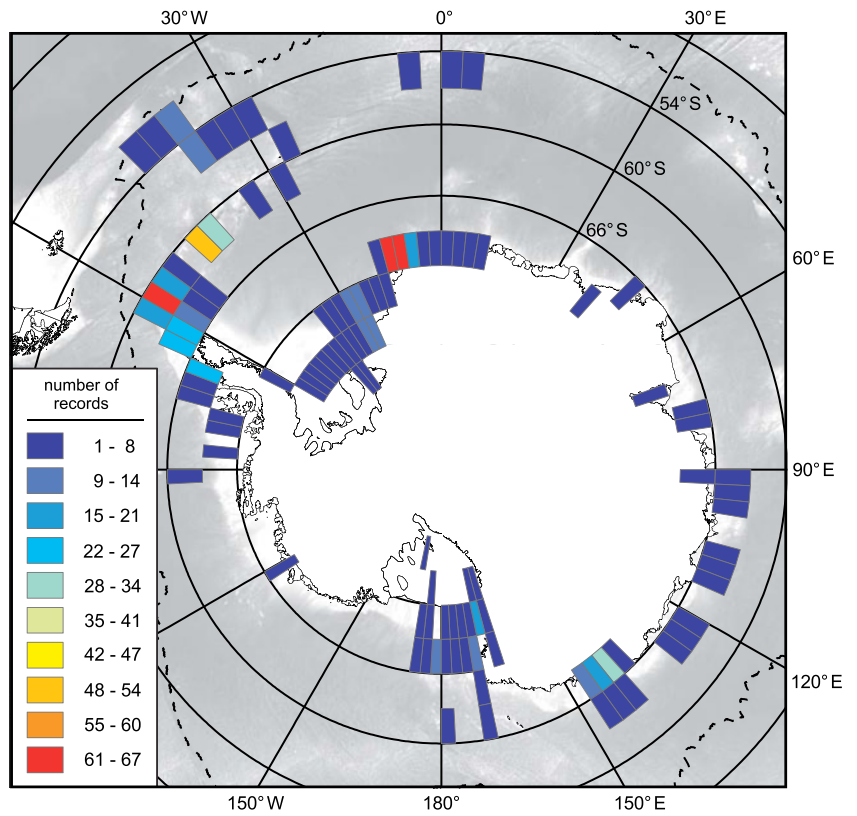
Fig. 1 Classification (after Gutt 2007 and Turner et al. 2009) and geographical coverage of Antarctic macrobenthic communities



macrobenthic pattern, but, based on our limited state of knowledge, the effect of most such parameters is obscured

by other factors and, therefore, a significant impact cannot be identified.

Fig. 2 Number of records of Antarctic benthic communities per spatial cell



A second simple generalisation is that the unquantified assumption of a dominance of suspension feeding communities on the Antarctic shelves, and of their circumpolar

occurrence (see, e.g., Dayton 1990), can be confirmed if a large spatial scale is considered. A total of 391 of all records belonged to supra-community “Sessile suspension feeders and

Fig. 3 Dominant types of Antarctic macrobenthic communities per spatial cells

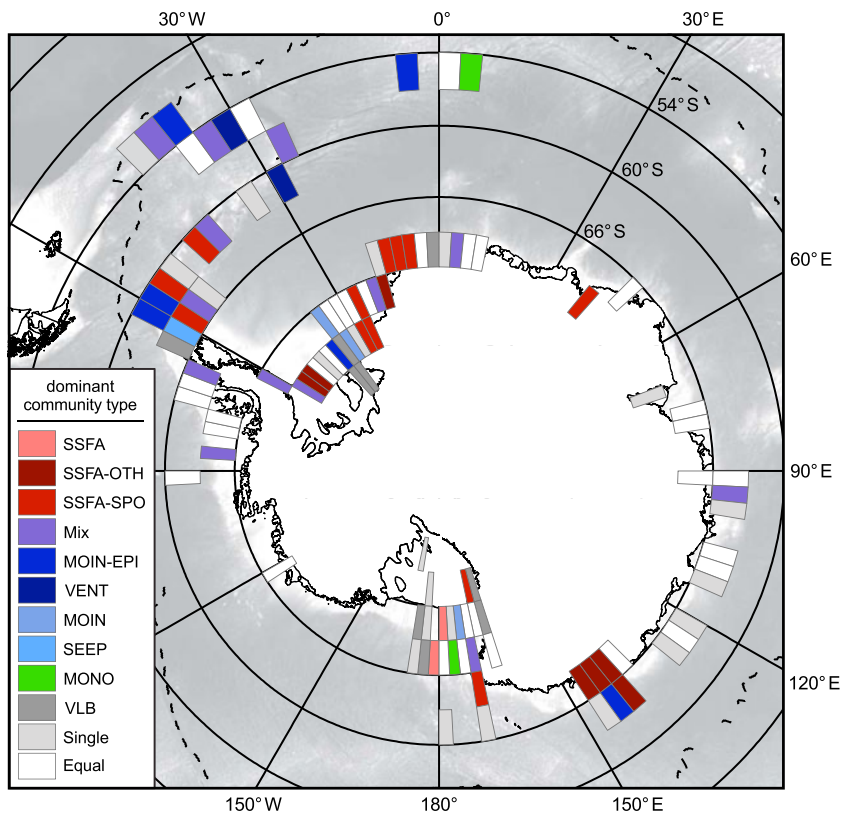
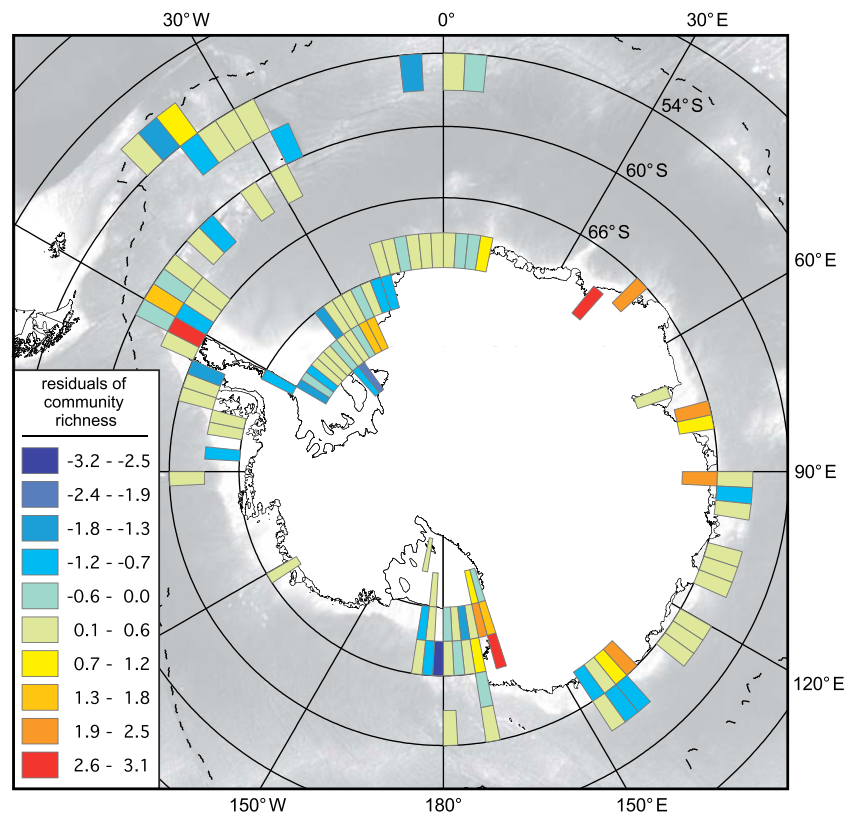


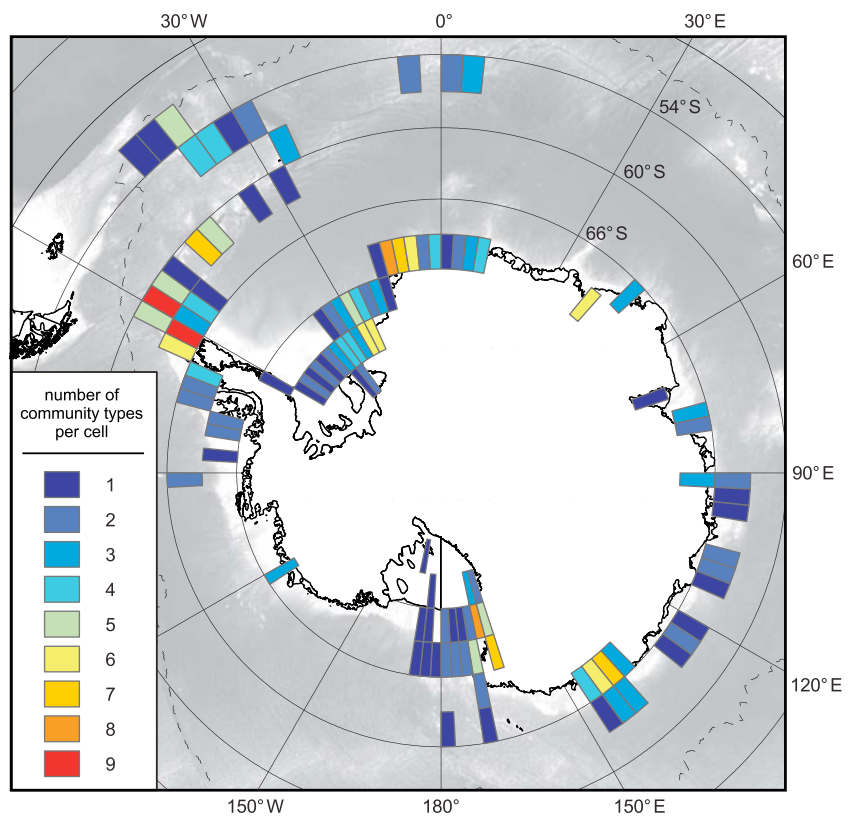
Fig. 4 Richness of Antarctic macrobenthic communities per spatial cell, expressed as residuals of the expected number of community types at a given number of records



associated fauna”, which was also dominant within many cells (Fig. 3). However, despite their general existence, they never dominate the northern areas along the Scotia Arc and around

Bouvet Island. The impression that this community type is only dominated by sponges and not also by others (see, e.g., Barthel and Gutt 1992) might have been inspired by the

Fig. 5 Richness of Antarctic macrobenthic communities per spatial cell, expressed as absolute number of community types



statement of the Antarctic being the “kingdom of sponges” (Koltun 1968), but seems to be wrong.

A total of 166 records belonged to the “opposite” community “Mobile deposit feeders, infauna and grazers” and 167 to the “Mixed assemblage”. It is also not a surprise that seeps as well as vents and “monospecific” assemblages were rare. Cells dominated by very low biomass comprised only 7.5 % of all cells.

Residuals, used as a proxy for the number of communities per spatial cell, show a quite even pattern (Fig. 4). The dominance of low values of the absolute abundances of community types per cell (Fig. 5) is mostly biased by the low sampling effort within most cells. Both maps show that some areas have above-average heterogeneity, at the tip of the Antarctic Peninsula, in the eastern Weddell Sea, at several sites in East Antarctica and in the Ross Sea.

A depth dependency of the community types did not become obvious. The larger the depth range within one cell (x), the larger its number of community types (y): where ($y=0.02x+8.14$, $r^2=0.62$, $n=9$). Also, depth bins with a high number of records (y) had a high number of community types (x) ($y=0.62x+0.77$, $r^2=0.71$, $n=110$). The numbers of records decrease with depth, but, for water depths <900 m, the maximum number of community types (11) was almost reached by <30 records, whilst the maximum per depth bin was 176. Also, the diversity did not show a clear trend. Values for water depth <600 m covered only a narrow range between 6.25 and 8.41, and varied much more but irregularly at greater depths.

The approach applied here follows the principle that the coarser the method, the more robust the study is against methodological bias. More detailed analyses, however, are difficult because of methodological weaknesses, mainly resulting from the classification of communities by expert best knowledge. The situation could be considerably improved by standardising data acquisition. The easiest approach would be to define key groups of animals as well as key environmental parameters and to consider biomass as the most important parameter. For example, scientists and scientific observers working in the Southern Ocean are required to report to the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) when they encounter a threshold density of Vulnerable Marine Ecosystem indicator taxa which consists of 29 taxonomic groups of benthic invertebrate megafauna (see <http://www.ccamlr.org/en/document/publications/vme-taxa-classification-guide>). Challenges would arise from the integration of results from different methods, e.g. providing images and true material, which could be solved by introducing well-defined proxies, e.g. sea-floor cover to be converted to biomass. Also, information from methods covering different spatial scales and spatial resolutions, e.g. trawls, videotransects and stationary grabs, has to be merged in a statistically sound way.

Finally, we can conclude that a huge amount of information on macrobenthic communities around the Antarctic

continent is available, which has gaps in data quality and geographical coverage. The heterogeneity of communities is high at intermediate and local spatial scales. A big step forward in the research on structural and functional issues of the macrobenthos is feasible if data acquisition could be standardised in a generally accepted way. The results and conclusions can contribute to the design of advanced research programmes such as SCAR’s new biology programme “Antarctic Thresholds—Ecosystem Resilience and Adaptation” (AnT-ERA), provide a temporal base-line for climate change studies, confirm or falsify text-book generalisations, e.g. of the dominance of sessile suspension feeders, and can serve as a source of information for conservation issues, e.g. the establishment of Marine Protected Areas (MPAs).

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