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Antarctic macro-zoobenthic communities: a review and an ecological classification

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Abstract: A partly new classification of shelf inhabiting Antarctic macro-zoobenthic communities is proposed in this review. The main components are two core communities. One is dominated by sessile suspension feeders supported by food entrained in strong near-bottom currents. Variants of this community include assemblages without sponges, those that prefer sponge spicule mats as substratum and predator-driven systems. The second core community is dominated by the infauna and mobile epifauna and controlled by vertical phytodetritus flux and soft sediments. This community is obviously restricted to areas with low current velocity, particularly in areas that are sheltered due to a heterogeneous coastal and sea floor topography. In addition, in physically controlled shallow water a small number of representatives of all these ecological guilds can become very abundant. Between both core communities a broad range of mixed assemblages exists that can be explained by a gradient in environmental conditions and trophic amensalism. A concept is also proposed for the ecological functioning of systems with extremely low abundances within ecological guilds, such as those that occur under and close to ice shelves, which cannot satisfactorily be explained by trophic limitation. These extremely low abundances may result from a shift during ontogenesis from a state with predominantly mismatched environmental conditions and ecological demands of young recruits, to a state where a match occurs.

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Key words: deposit feeder, match, mismatch, near-bottom current, sediment, suspension feeder, trophic limitation

Introduction

The term "the Antarctic benthos" is frequently used in the marine biological literature and in scientific discussions when referring to life on the shelves of the Antarctic continent and adjacent islands. Interestingly, ecologists do not generalize like that in describing other ecosystems, e.g. they would not talk about "the tropical benthos" when they study mangroves or coral reefs despite a possible overlap between both. Similarly, in temperate seas one usually discriminates between hard and soft bottom communities. The application of such a traditional classification to the Antarctic macrobenthos has been attempted, for example, by Richardson & Hedgpeth (1977), Dayton (1990), Dayton *et al.* (1994), Clarke (1996), Cattaneo-Vietti *et al.* (2000a) and Barnes & Conlan (2007). However, the difficulties of this approach, due to physical and biological peculiarities (poorly sorted glacio-marine sediments and adaptation to "unusual" sediments), has already been recognized for the Antarctic by Gallardo (1987) and in an experimental approach by Wu & Shin (1997). In contrast to the concept of splitting the Antarctic benthos into distinct sub-systems, there are also good reasons to categorize the Antarctic benthos as a relatively homogenous biological unit: in general, many species share the same evolutionary constraints (Clarke 1990, Clarke & Crame 1992, Crame 1994, Clarke *et al.* 2004, Arntz *et al.* 2005) and some large-scale ecological conditions are similar around most parts of the continent, e.g. low and relatively stable temperature, a short phase of primary production, as well as low terrigenous input (Bullivant 1959, Clarke 1996). In addition, there is the presence of a circumpolar coastal current that transports food particles and supports the dispersal of juveniles (Underwood & Fairweather 1989, Raguá-Gil *et al.* 2004). As a consequence, some authors analysing the occurrence of single species or systematic groups at a coarse spatial resolution have come to the conclusion that there is a generally circumpolar distribution (Dell 1968, Arnaud 1977, Barthel 1992, Sarà *et al.* 1992). Dayton (1990) provided two examples of communities that were found to occur at different sites around the continent, one characterized by sponges and the other by the scallop *Adamussium colbecki*, which led to the conclusion that identical conditions support similar faunistic assemblages, a phenomenon identified to be "unique in marine biogeography". A similar conclusion is based on three colonization experiments at Signy Island (South Orkney Islands), Adelaide Islands (west of the Antarctic Peninsula) and at Casey Station (East Antarctica, 110°E) cited by Barnes & Conlan (2007). Another study is based on a faunistic survey showing a surprisingly rich megabenthic fauna at Bouvetøya, despite its extremely remote position (Gutt *et al.* 2006). These are good reasons to compile

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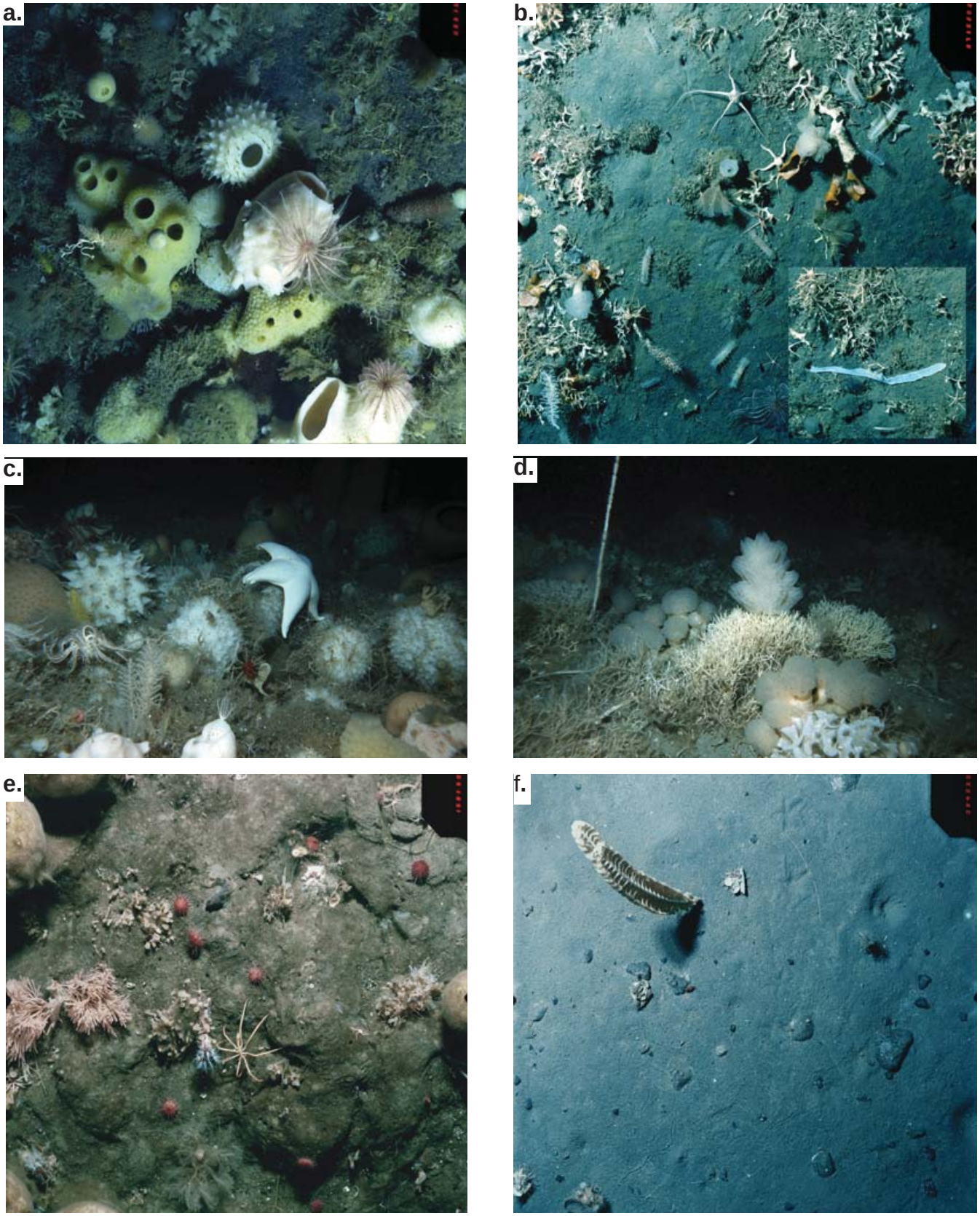


Fig. 1. Antarctic sea bed images. Photographs are from the south-eastern Weddell Sea if not otherwise mentioned. Vertical photographs were taken by Photosea 70 camera and represent 1 m^2; oblique photographs taken by ROV, sprint 103, width in foreground *c.* 50 cm. Positions refer to start of photographic transects. Depths refer to best guess of exact position of the photographs along transects.

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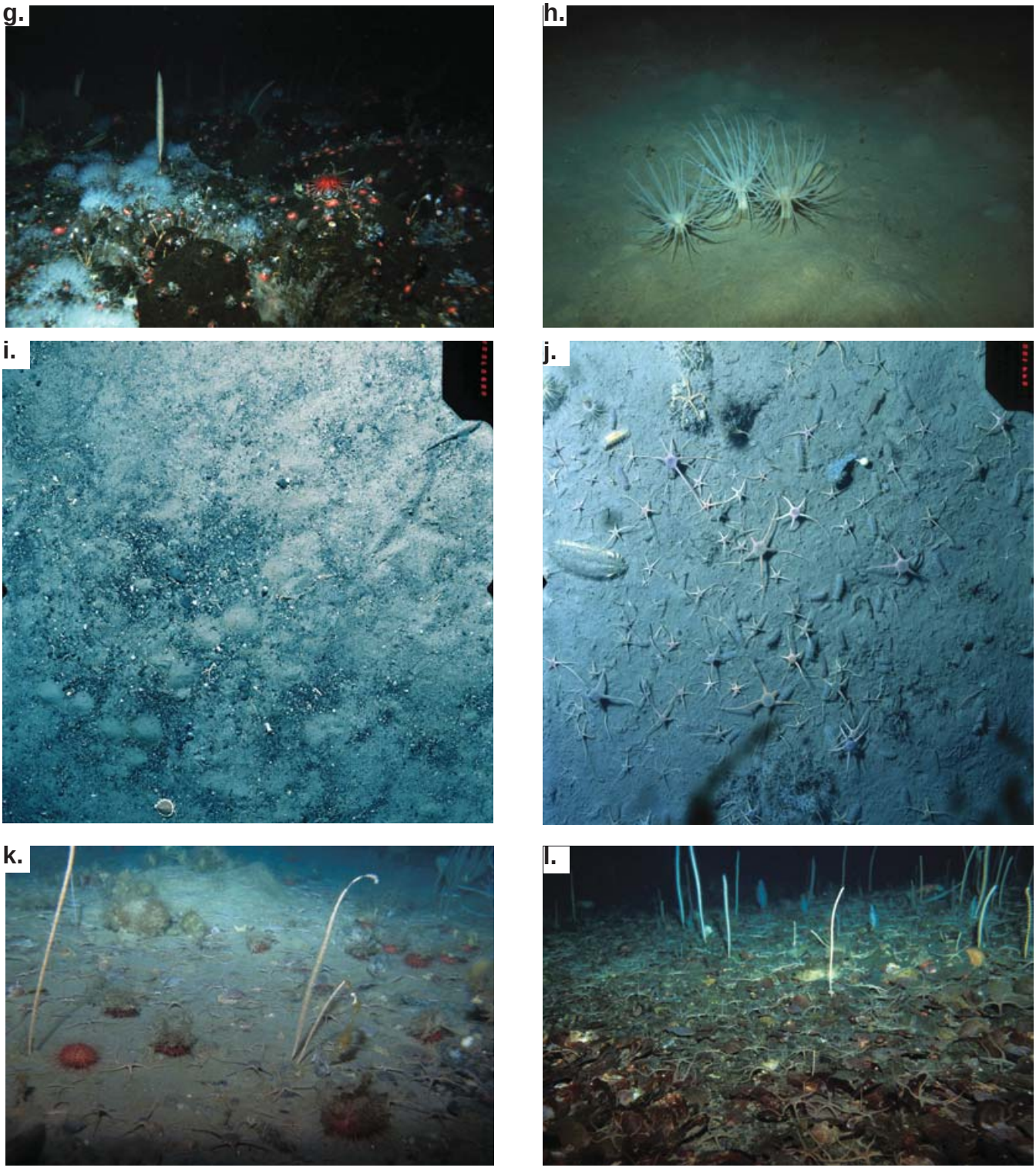


Fig. 1 (cont.) Photograph numbers according to the database PANGAEA. **a.** SFC: Suspension feeder community with dominance of demosponges *(Cinachyra barbata, Stylocordyla borealis, Mycale acerata*) and hexactinellid sponges *(Rossella racovitzae, Scolymastra joubini*) and, in addition, with hemicordates, bryozoans, cnidarians, compound ascidians; associated mobile fauna is represented by epizoic crinoids and ophiuroids. 70°49.27'S, 10°28.95'W; 272 m; PS48_232_083. **b.** MXC: Mixed community with suspension feeders such as bryozoans, compound ascidians, hemichordates, sponges, cnidarians, mobile fauna, e.g. ophiuroids, elasipode holothurians, crinoids and infauna such as the prostomium of an echiuroid inserted from a different photograph of the same station. 71°14.73'S, 12°29.91'W; 313 m; PS56_083-1_071. **c.** PDC: Predator driven community. The presence of the sea star *Acodontaster conspicuus*, here on the hexactinellid sponge *Rossella racovitzae* can serve as an indicator for this variant of the SFC. 70°52.22'S, 10°31.27'W; 245 m;

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Fig 1. (cont.) PS56_127-1_133. **d.** FAO: Filter feeder assemblage dominated by others than sponges. Here bryozoans and different compound ascidians are most abundant. 71°31.72'S, 13°31.36'W; 242 m; PS39_006-22_002. **e.** ELA: Assemblage with extremely low abundances. This specimen of the gorgonian *Ainigmaptilon antarcticus* was the only sessile suspension feeder of this size observed in a total of 22 photographs at this station. 70°29.65'S, 08°58.73'W, 437 m; PS65_042-1_004. **f.** SSM: Sponge spicule mat habitat. A massive spicule mat obviously originated from demosponges (e.g. *Cinachyra barbata*, left margin) and hexactinellid sponges (*Rossella* sp., right margin). It provides a microhabitat for these sponges and other sessile and mobile animals e.g. cnidarians, bryozoans, holothurians (*Ekmocucumis spatha*), echinoids (*Sterechinus neumayeri*), pycnogonids and fish. 71°07.28'S, 11°28.37'W; 230 m; PS65_247-1_168. **g.** PCA: Physically controlled assemblage with dominance of only two species: the sessile hydrozoan *Tubularia ralphii* and mobile echionoid *Sterechinus neumayeri* on boulders. 71°07.33'S, 11°26.79'W; 85 m; PS39_24-3_121. **h.** INC: Infaunal community. Cerantharia belonging at least partly to the infauna are a typical faunistic element of soft sediments; monds indicate additional true infauna. Marguerite Bay, Antarctic Peninsula; 67°44.39'S, 68°16.77'W, 200 m; PS29_079_101. **i.** ZAG: Zero abundances within trophic guilds as shown here for a relatively small area can be expected under ice shelves. This photograph has been taken close to the ice shelf edge. 70°25.88'S, 09°15.11'W; 320 m; PS65_053-1_009. **j.** MIC: Mobile deposit feeder community. c. 50 elasipode holothurians, 90 ophiuroids (cf. Ophionotus victoriae), 1 polynoid polychaete and sparse sessile epifauna. Off King George Island, South Shetland Islands; 62°15.58'S, 58°44.13'W; 305 m; PS56_197-1_044. k & l. The same most abundant taxa prefer gravel and predominantly soft sediments: cf *Ophionotus victoriae*, *Sterechinus neumayeri*, *Primnoella* sp. Marguerite Bay, Antarctic Peninsula. **k.** JR37_010_018; 68°10.17'S, 67°21.04'W, 70 m. l. JR_005_139; 67°48.657'S, 67°20.792'W, 63 m.

species lists for the entire Antarctic shelf fauna and to develop general conceptual models on predominantly evolutionary but also key ecological processes. A number of review articles have such a scope: Hedgpeth (1977), Arntz *et al.* (1994, 1997), Clarke & Crame (1997), Gutt (2000), Arntz & Gili (2001), Gray (2001), Clarke (2003), Clarke & Johnston (2003), and Thrush *et al.* (2006). At the other end of the gradient ranging from large to small spatial scales, Gutt (2006) focussed on processes that help explain the local coexistence of Antarctic benthic species. Gallardo (1987) and Clarke (1996) emphasized such heterogeneity, especially in sediment characteristics of the Antarctic sublittoral environment and related dynamics. The latter topic was reviewed by Barnes (1999) and considerably updated by Barnes & Conlan (2007) who concentrated on the benthic response to different kinds of disturbance. Examples of some of these mechanisms can be found all around the continent, such as wave action, iceberg scouring, and impact of sea ice in shallow water, and other more specific and rare disturbances e.g. volcanic activities or anchor ice; for review of ice impact see Gutt (2001). The last comprehensive compilation and comparison focussing at the community level was that of Dell (1972), which consequently concentrated on the intermediate spatial scale between the zoogeographic and local approaches, nowadays considered as a concept of species turnover or beta-diversity. In the meantime, many studies have been carried out that provide additional information on the faunistic composition, key species or abundant higher taxa in new investigation areas, especially those contributing to the SCAR programme EASIZ (Ecology of the Antarctic Sea Ice Zone; Arntz & Clarke 2002).

Unfortunately, such investigations almost never alow true comparison of results for a number of different reasons. One important aspect in this context might be that beta-diversity concepts are complex, since they include information ranging from small (local), over intermediate (regional), to large (global) scales (Levin *et al.* 2001). Consequently, dealing with beta-diversity requires, in most cases, a not yet widely applied standardization. Instead, many of the studies that could contribute to such an approach had different scopes, used different methods, applied different analyses and provided different kinds of results. Interestingly, the enormous improvement in marine research infrastructure over the past few decades has not solved the difficulties of comparative quantitative community ecology, which were already recognized by Dell (1972). One major problem (which is critical in this context) is that in many studies the absence of species from the samples is not recorded and the most relevant environmental conditions, such as near bottom current, are only described and not quantified. Nevertheless, there is enough information based on the presence, dominance, and life history of some species, as well as enough general knowledge of the environment, to answer the first overall question of this article: Does "the Antarctic macrobenthos" really exist if the community level is considered? The approach to answer this question includes an updated brief review on macrobenthic communities using examples, and a proposal for a partially new classification that is based on the general macrobenthic structure and includes key ecological processes. The latter is also the reason why in the following text, the term *community* is used assuming that species assemblages are shaped by ecological processes and do not simply reflect the co-occurrence of species. The term *assemblage* is used if subsystems deviate significantly in their structure from the core community, or when interactions are not obvious.

Even a brief check of the relevant literature, as well as unpublished results from ongoing projects, make a short and preliminary answer easy: The Antarctic macrobenthos does not exist, as determined by species compositions. Instead the classification proposed here comprises two core communities. The first can be relatively easily defined as having a dominance of sessile and sedentary suspension

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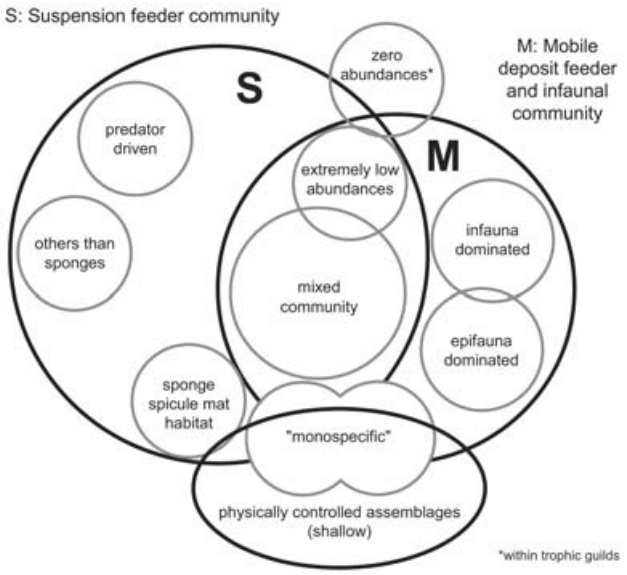


Fig. 2. Scheme of two core communities, partly overlapping mixed communities, sub-communities and assemblages, respectively, of the Antarctic shelf-inhabiting macrobenthos.

feeders in terms of abundance, biomass and maybe diversity, with an associated mobile fauna (Figs 1 & 2). *Suspension feeding* is defined here as active or passive capturing of dead organic particles or living organisms from the water column that are dispersed predominantly or exclusively by currents and not by their own locomotion. The main reason to propose the second core community is the existence of a faunistic gradient characterized by decreasing numbers of sessile animals and, as a consequence, a higher proportion of vagrant deposit feeders and infauna. This trend can continue towards a species composition in which the deposit feeders and infauna become clearly dominant. In both communities, this pattern can be overlaid by a second gradient ranging from very high to extremely low abundances. In addition, within both main communities a third gradient ranges from areas with a high diversity to those with almost monospecific assemblages. In this context, it has to be considered that a separation between local assemblages and communities at a regional scale is an artificial classification that, in most cases, is based on natural gradients.

Community types

Suspension feeder community (*SFC*)

Dell (1972) recognized that an inshore zone, below areas affected by anchor ice, is characterized by the high density and biomass of sponges and other sessile taxa (Dayton *et al.* 1970). This extends to greater depths and includes the "McMurdo Sound Glass Sponge Assemblages" shown and described by Bullivant (1961, 1967) as a variant of the "Deep Shelf Mixed Assemblage". As a consequence he assumed that such a community "deserves somewhat more importance than that of the minor assemblage status Bullivant gives it". If this core community is defined by a dominance - simply in terms of biomass or sea floor coverage - of sessile and sedentary suspension feeders it can be stated that this community exists in patches with its variants all around the Antarctic continent in water depths between 30 m and (with restrictions) the shelf break at *c.* 600 m (Fig. 1a). It includes, in addition to sponges, mainly bryozoans, cnidarians, and ascidians. Additional early but not very detailed descriptions of this core community are those of Gruzov *et al.* (1968) and Propp (1970) for the Davis Sea (Haswell Island, Mirny Station) and maybe also at Enderby Land (Molodezhnaya Station), of Hamada *et al.* (1986) for the area at the adjacent Syowa Station and of Belyaev & Ushakov (1957) for a region at 120°E. All these refer to water depths below 40–50 m. Since these early studies, generally similar findings based on intensive sampling have been recorded for the shelf of the south-eastern Weddell and easterly adjacent Lazarev seas (Voß 1988, Gutt 1991, Galéron *et al.* 1992, Gerdes *et al.* 1992, Gutt & Starmans 1998, Starmans *et al.* 1999) and confirmed for the Ross Sea, including mixed and deposit feeder assemblages (Barry *et al.* 2003, Cummings *et al.* 2006). West of the Antarctic Peninsula this community seems to be less obvious (for examples see below) compared to East Antarctica, including the Weddell and Ross seas, especially on the shallower shelf (see also Mühlenhardt-Siegel 1988, Gerdes & Montiel 1999, Piepenburg *et al.* 2002). All the above mentioned studies also show clearly that within the larger study areas, especially on the deeper shelf, a Mixed Community (MXC) exists. This community occurs for the megabenthos e.g. in Marguerite Bay (Raguá-Gil *et al.* 2004) and the Bellingshausen and Amundsen seas (Starmans *et al.* 1999), although with a lower diversity than the Weddell Sea (Starmans & Gutt 2002). The relatively constant and spatially homogenous coastal current is most probably the main driving force that supports erected suspension feeders and suspension feeding epibionts by producing an advective food supply in the nepheloid layer (Gutt & Schickan 1998), and these organisms are also assisted by the very low terrigenous sediment input. For a conceptual model approach and the general relevance of advective food supply see Grebmeier & Barry (1991) and Dayton (1990), respectively. Recent Antarctic publications referring to the importance of advection include, e.g. Gili *et al.* (2001), Orejas *et al.* (2003) and Isla *et al.* (2006). The resulting benthic "three-dimensional" or "multi-storied" structure provides a microhabitat for a broad variety of associated fauna, mainly consisting of highly specialized species, although also including a few opportunists. In the south-eastern Weddell Sea, these associated fauna are predominantly members of a comparably diverse asterozoan fauna (Piepenburg *et al.* 1997), crustaceans

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(Dauby *et al.* 2001, De Broyer *et al.* 2001), and others (Kunzmann 1996, Gutt & Schickan 1998). This habitat diversification provides the best explanation for the development of possibly the highest diversity in the Suspension Feeder Community (Gutt & Starmans 1998). A general or local decline in abundance of suspension feeders can be interpreted as the result of less favourable food conditions and consequently as a result of trophic limitation. This effect has been documented by Cummings *et al.* (2006) at the western side of McMurdo Sound for the benthic epi- and macrofauna at water depths ≤ 24 m. Reductions in the abundance of suspension feeders may result from a lower near-bottom current velocity at any water depth, or may be associated with the distance that food particles have to sink from the euphotic zone to the sea floor as this can affect the time available for them to be biochemically modified (see also Fabiano *et al.* 1997, Povero *et al.* 2003). Regardless of whether or not the decrease in abundance of suspension feeders along a vertical or horizontal gradient is also correlated with an increase in deposit feeders and infauna (Fig. 1b), this change must be considered as a shift towards the Mixed Community. Owing to its prevalence on the deeper shelf (> 350 m) it might dominate the entire Antarctic shelf. Apart from the very interesting but open question on how to explain extremely low abundances, one potential indicator of limited food conditions might be the size of hexactinellid sponges. For instance, the species *Scolymastra joubini* reaches a height of 1.3 to 2.0 m living in the euphotic zone in McMurdo Sound and at Mirny and Molodezhnaya, whereas in the Weddell Sea intensive sampling below 100 m depth has never revealed species of more than 1.3 m (Gutt 2006). The possibility that this example is related to *in situ* sources of primary production is discussed in general by Dayton (1990). Nevertheless, in the Weddell Sea, smaller hexactinellid sponges including *S. joubini*, as well as demosponges, can be very successful numerically. An alternative explanation is that recolonization since the past ice age may be incomplete, and in addition there may be a long-term effect of trophic amensalism or permanent iceberg disturbance (see Gutt & Starmans 2001, Gutt & Piepenburg 2003).

Although clear evidence for a correlation between this core community of sessile suspension feeders and an advective food supply is still missing, there are several hints and some detailed results. Gusev & Pasternak (1958, cited after Arnaud 1977) developed a similar hypothesis for Antarctic and sub-Antarctic ecosystems, in which they also cited the relevance of the sediment. Other authors that came to the same conclusion, based on their faunistic results, include Arnaud (1977), Voß (1988) and Gutt (2000). Comparisons with other benthic systems, e.g. at sea mounts (Genin *et al.* 1986) and mid-oceanic ridges (Piepenburg & Juterzenka 1994) support this theory. Ravaioli *et al.* (1999) investigated three sites between 500 and 810 m in the Ross Sea where in two cases they related high biogenic sedimentation with a community dominated by infauna, surface and subsurface feeders. In contrast, in an area characterized by residual glacial-marine sediment and the winnowing effect of currents, they found high abundances of epibenthic filter feeders. In this case physical processes and their consequences for the benthos at the shelf break can differ in detail from those on the shelf, but the general principle of currents shaping the community structure remains the same. In the Weddell Sea, a higher current velocity was measured above a relatively rich suspension feeding community compared to an area with roughly half the average current speed where the species composition consisted of a mixture of a few suspension with more deposit feeders (Lavaleye *et al.* 2005, Gutt unpublished results). For a larger area in the south-eastern Weddell and Lazarev seas, Gutt *et al.* (1998) found an indication, but not a significant correlation, between a low current velocity, as indicated by a high amount of phytodetritus deposited on the sediment surface, and sparse sea floor cover by the mega-epifauna. The only studies that provides evidence for the effect of reduced food supply rather than for current velocity on the benthos are those of Dayton & Oliver (1977) and Barry & Dayton (1988) in McMurdo Sound. They compared two communities at the ice shelf edge, one with a current from under the ice shelf and the other with a current from the open ocean. The current from under the ice shelf reduced *in situ* primary productivity and was associated with low benthic faunal abundances. Based on coarse taxonomic identification with quantitative data they also described a clear shift in community composition from an arthropod to a worm dominated system. In regions "with vehement current" in Maxwell Bay, King George Island, Bannasch *et al.* (1984) reported a poverty of species and individuals in contrast to "areas with quiet water" with a rich benthic life, predominantly consisting of sessile species. Such an assemblage with a variety of sessile ascidians, bryozoans, sponges, polychaetes and brachiopods is also described at only 20 m depth at Adelaide Island (Bowden 2005).

A certain spatial heterogeneity within this core community (including its variants described below) seems to be mainly caused by continuous variations in environmental characteristics, the potentially broad-scale patchiness of the most abundant species, species interactions and locally restricted physical impact (Clarke 1996, Gutt & Starmans 2003, Raguá-Gil 2004, Stark *et al.* 2005, Cummings *et al.* 2006). In general, however, this community must be considered to be more homogenous in terms of species composition than the deposit feeder and infauna dominated core community, as well as the physically controlled assemblages. In addition, the suspension feeder community is, at least in the Weddell Sea, significantly more diverse in mega-epibenthic species compared to the core community of deposit feeders and

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infauna. However, it remains unclear whether this pattern is applicable to all benthic species and life forms since comparative studies are missing. Picken (1985a) mentioned, in general, that the (sessile) epifauna is more spectacular but the infauna is at least as important.

A predator driven community (*PDC*)

A predator driven community (PDC) has been most intensively investigated in McMurdo Sound (Dayton 1972, 1979, 1989, Dayton *et al.* 1994). The idea for this as a separate sub-unit of the suspension feeder core community was stimulated by a discussion with P.K. Dayton based on the experience of his own studies. The generally low number of predators elsewhere has been noted, and it has also been shown that most suspension feeders as well as echinoderms are nutritionally only poorly utilisable (Dearborn *et al.* 1978, Barthel 1995). In this sub-community, echinoderms and nudibranchs seem to be the most effective predators that directly or indirectly control sponge population growth. Less detailed descriptive studies provide the impression that such an assemblage also exists in other areas, e.g. in the Weddell Sea (Fig. 1c; Voß 1988, Raguá-Gil 2004). It remains uncertain whether this assemblage in McMurdo Sound is unique in the Antarctic or whether its recognition is biased by the intensity of this process-orientated study. However, it seems to be clear that, assuming such a sub-community is restricted to a relatively shallow water depth of 30–130 m, it provides the most complex predator-prey relationships in combination with a high diversity of trophic levels and species within different trophic levels; for a graphic scheme see Gutt (2006). The ecological key species in this depth range, the asteroid *Odontaster validus*, a deposit feeder and facultative predator, indicates that the availability of fresh phytoplankton and favourable conditions for the sponges and other sessile suspension feeders might play the key role for this sub-community (Dayton *et al.* 1974). The comprehensive reduction of the fast-growing demosponge *Mycale acerata* biomass due to feeding by the asteroid *Acodontaster conspicuus* might also be a mechanism that allows a co-existence of a variety of suspension feeding species that otherwise would be outcompeted. Another study from the adjacent Tethys Bay confirms the role of *O. validus* as a facultative sponge eater (Cerrano *et al.* 2000). Unfortunately this ecological key species is not at all a useful indicator for this predator-driven (sponge) sub-community due to its omnivority and its common occurrence in many shallow water areas. Dearborn (1977) listed *Acodontaster conspicuus* and *A. hodgsoni* as exclusive sponge eaters in his comprehensive classification of asteroids according to feeding guilds, which could serve in the future as appropriate, key species. Both these species have been recorded by Voß (1988) in the relatively shallow Atka Bay and in a very few other places in the south-eastern Weddell Sea, but he did not find any specimen of *O. validus*. At only one station in this area, at Kapp Norvegia, Gutt *et al.* (2000) later listed the co-occurrence of all three species, which could serve in general as a fast and preliminary check for the existence of this predator-shaped sub-community. Both *Acodontaster* species are not in the list of Dearborn & Fell (1974) for an area west of the Antarctic Peninsula "around Anvers Island and south along the coast to Adelaide Island". *Acodontaster conspicuous* has been found only twice at the Melchior Islands (Palmer Archipelago) by Bellisio *et al.* (1972) and not at all at the Esperanza Base and Peterman Island. Both species are also not listed by Arnaud (1964) for a relatively intensively investigated area ≥ 50 m deep along the coast of Terre Adélie between 136° and 141°E.

There is also one study that shows that relatively high species richness is maintained within a polychaete assemblage owing to predation by the tanaidacean crustacean *Nototanais dimorphus* and the amphipod *Heterophoxus videns* (Oliver & Slattery 1985).

Filter feeder assemblage dominated by others apart from sponges (*FAO*)

Interestingly, in McMurdo Sound the largest sponges appear between 30 and 80 m water depth, directly below a zone of moderate to intensive physical disturbance due mainly to sea ice. In the Weddell Sea, however, in the unusually shallow Atka Bay (60–130 m) and surrounding area, bryozoans, gorgonians and ascidians dominate this depth zone (Fig. 1d). Here also iceberg scouring has been observed, but it is not more intensive than in areas where long-living hexactinellid sponges exist. In this area sponges become abundant only below *c.* 130 m depth. At Syowa Station bryozoans are reported to be the most dominant group at 200 m depth (Hamada *et al.* 1986). For the Ross Sea, Bullivant (1967) classified areas without or with only few sponges as the "McMurdo Sound Mixed Assemblage" which is a variant of the larger "Deep Shelf Mixed Assemblage". Similar results are found in the south-eastern Weddell Sea indicating that, despite their obviousness, sponges are not good indicators for the sessile suspension feeder community (Gutt & Koltun 1995, Barthel & Gutt 1992). As a consequence, there seem to be more unknown effects, apart from physical disturbance and predation that control the population growth and presence of sponges in particular. The fact that the quantitative food supply and the sediment characteristics do not satisfactorily explain extremely low abundances of suspension feeders (Fig. 1e) is discussed below. In a recent investigation Gutt *et al.* (in press) confirmed earlier suggestions by Arnaud (1972) for the dominance of this assemblage off Terre Adélie.

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Sponge spicule mat habitat, (*SSM*)

It is well known that sponge spicules can exist in dense layers up to 2 m thick (Koltun 1968). These originate from either modern or glacial aggregation by currents, *in situ* mortality caused by unknown nature processes, or ice disturbance (for examples see Seiler & Gutt in press). These spicule mats provide a suitable microhabitat for a highly diverse macrofauna (Dayton *et al.* 1970, Arnaud 1974) including hexactinellid sponges and also demosponges e.g. *Cinachyra barbata* (Barthel 1992, Barthel & Gutt 1992) from which the spicules originate (Fig. 1f). Mats are also known to have a rich infauna (Dearborn 1967) with the most conspicuous species being *Limatula hodgsoni*, and they also provide a habitat for the lesser known meiofauna (Lee *et al.* 2001). It seems, however, as if the composition of macrobenthic species on spicule mats is not unique, but a modification of that on the predominant poorly sorted sediments with a rich epifauna. There are also sites where especially thick mats have very low abundances of epifauna. The question remains open whether the conditions on the thick mats are too extreme and therefore provide a significantly different microhabitat, or whether the poor life on spicule mats results from an insufficient time interval since an impact to re-establish a mature community of sponges and other sessile suspension feeders. The sponge spicule mats are especially abundant below zones of intensive ice impact where conditions for sponge growth are favourable but where the physical impact is intense enough to cause a certain level of mortality. It is assumed that mortality of sponges due to disease does not play a major role in creating spicule mats, but local exceptions cannot be excluded. Cattaneo-Vietti *et al.* (2000b) describe a community in Terra Nova Bay, where "a peculiar community characterized by crustaceans, polychaetes and the bivalve *Limatula hodgsoni*" lives in a sediment composed of ≤ 500 000 spicules g^{-1} dry weight sediment (≤ 50%). This quantified measure of the sediment is consistent with a sponge spicule mat habitat. However, it is generally possible that such samples may contain spicules from living hexactinellid (glass) sponges or demosponges, which could lead to the false conclusion that the sediment is characterized by spicule mats. This uncertainty requires a more precise and definition-based use of the term 'spicule mat'. The question of how unique the species composition in and on spicule mats really is can only be answered by detailed quantitative biodiversity surveys in combination with sediment analyses.

Physically controlled and monospecific assemblages (*PCA*)

It seems as if an upper limit of the core community of sessile suspension feeders is defined more strongly by physical impacts, especially by ice disturbance, wave action, and light penetration, than by water depth. These physical effects can cause relatively sharp zonations (Andriashev 1968, Dayton *et al.* 1970, Gruzov & Pushkin 1970, Zamorano 1982, Hamada *et al.* 1986, Di Geronimo *et al.* 1990, Lenihan & Oliver 1995, Cattaneo-Vietti *et al.* 2000a, Barnes 2005) or gradients in the faunistic composition (Rauschert 1984, Gambi *et al.* 1994, Sahade *et al.* 1998, Echeveria & Paiva 2006). Within these zones the species composition can vary considerably, even at a local scale (DeLaca & Lipps 1976), depending on food supply, the current regime, physical and terrigenous impact, and the structure of the coastline in addition to the sea floor topography. As a consequence, the classical separation in species composition between muddy and true hard substrata is clearer in this predominantly shallow zone than in other assemblages or in deeper areas (Fig. 1g & h). A comprehensive review of disturbance effects on the Antarctic benthos, which is most intensive above 100 m water depth, is provided by Barnes & Conlan (2007); see also Teixidó *et al.* (2004). Intensive sea ice impact in the shallowest depths results in a community generally inhabited by mobile animals, often with only a few dominant species (see below). Clear seasonal changes in composition and abundance occur to depths ≥ 20 m, as recorded for polynoid polychaetes, interestingly including one epibiont in the Davis Sea (Averincev 1977), as well as for amphipods and gastropods (Jazdzewski *et al.* 2001). A similar example of interannual variation within a hard-bottom assemblage is provided by Gambi *et al.* (2000). A rich sessile life has been described for very shallow depths in sheltered rocky microhabitats between 3.5 and 26 m at Signy Island (White & Robins 1972, Barnes 1995a, 1995b). In contrast, large boulders and sandy areas at an unusually shallow site (60 m) in the Weddell Sea are almost devoid of any epifauna, with the main structuring elements sponges and gorgonians, becoming abundant below 130 m (Raguá-Gil 2004). Arnaud (1964) also observed a very poor fauna at Terre Adélie due to ice scouring down to 80–100 m and due to the close proximity of a glacier (Gutt *et al.* in press). In areas with a clear gradient in disturbance intensity, there is a transition from the littoral areas, with almost exclusively mobile life, and the deeper sessile suspension feeder communities characterized by fast-growing and fast-recruiting species and mobile species. The sessile epifauna of the upper sublittoral zone consists mainly of ascidians, hydroids, and alcyonarians (see also Andriashev 1968, Dayton *et al.* 1970). In relatively sheltered depressions with high sedimentation rates and soft sediments, typical elements of the infauna include bivalves in addition to the above mentioned polychaetes. Areas more exposed to physical forces are the habitat for mobile animals such as echinoderms, the isopod *Glyptonotus antarcticus*, also found in the sponge community, and *Serolis* spp., which seems to prefer areas without a rich sessile epifauna. In shallow waters ≤ 30 m Sahade *et al.* (1998) described communities dominated by one or more of the taxa

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Laternula elliptica (Bivalvia), *Molgula pedunculata* (Ascidiacea) and pennatularians. These communities are not typical of either soft bottom or hard bottom communities, and are similar to the assemblage described by White & Robins (1972) at Signy Island between 5 and 26 m, although with additional echinoderms, sponges and nemerteans, which occur predominantly on hard substrata. In McMurdo Sound, bivalves and mobile polychaetes can be dominant, with the latter especially abundant in the anchor ice affected areas (Lenihan & Oliver 1995).

A clear local dominance -monospecific assemblages or "oligomixity" *sensu* George (1977) - of a variety of species can be observed in areas with frequent disturbance. Such species are either almost the only ones that are well adapted to the specific conditions, in other words this simple assemblage has a high resilience to disturbance (Dunbar 1977), or are competitively superior in the highly dynamic environment. The corresponding faunistic heterogeneity described below (see also Barnes 1999) might reflect environmental differences, different stages of succession or factors purely of chance during recruitment. At one site at the coast of Terre Adélie hundreds to thousands of the asteroid *Odontaster validus*, the echinoid *Sterechinus neumayeri* and the amphipod *Waldeckia obesa* have been recorded (Arnaud 1972), and similar results are known for Syowa (Hamada *et al.* 1986) and Adelaide Island (Bowden 2005). At Signy Island the brachiopod *Liothyrella uva* and the limpet *Nacella concinna* (Barnes & Clarke 1995) are extremely abundant in cryptic habitats, and *Laternula elliptica* as well as other clams can be dominant in soft sediments (Hardy 1977). In Maxwell Bay, King George Island, the limpet *Patinigera* sp. is able to dominate littoral environments in areas affected by anchor ice due to its mobility (Bannasch *et al.* 1984). Tubeworm reefs formed by *Serpula narconensis* are known from the Ellis Fjord (Kirkwood & Burton 1988), where they are explained by a high level of organic input and from South Georgia (Ramos & San Martín 1999). Around Syowa Station at 40°E, the scallop *Adamussium colbecki* can live in several layers and reach wet weight biomass of up to 2 kg m^{-2} (Nakajima *et al.* 1982), and corresponding densities are known from the Victoria Land coast in the Ross Sea (Chiantore *et al.* 2001) and shown for Marguerite Bay (Bellingshausen Sea) by Raguá-Gil *et al.* (2004). A variety of animals are very abundant in shallow depths in the Davis Sea: the sea cucumber *Cucumaria spatha* (= *Heterocucumis grandis*), the hydroids *Tubularia ralphii* and *Oswaldella antarctica*, the alcyonarian *Eunephthya* sp. as well as *Laternula elliptica* and *Odontaster validus* (Gruzov 1977; see also Gruzov & Pushkin 1970). A very similar pattern is also known from the unusually shallow site in the south-eastern Weddell Sea (Norsel Bank) mentioned above (for example see Fig. 1g). Even under the ice shelf an aggregation of a small actiniarian with hundreds per m^2, have been found (Littlepage & Pearse 1962). In more stable and deeper areas, some if not most of the above mentioned species with local dominance seem to be inferior in competition and/or not well adapted to the environmental conditions.

In first stages of recolonization after iceberg disturbance there is also a clear dominance by one or only a very few species, e.g. the bryozoan *Cellaria incula*, the gorgonians *Primnoisis* spp. and *Ainigmaptilon antarcticus* and the hydroids *Oswaldella antarctica* and *Corymorpha* spp. are not unusual on the deeper shelf (Brey *et al.* 1999, Raguá-Gil *et al.* 2004). The unusually fast growing sponges *Homaxinella* sp. and *H. balfourensis*, are known from areas of iceberg disturbance in the Weddell Sea as well as in sediments devastated by anchor ice (Dayton 1989) and glaciers (Powell *et al.* 1996, Dawber & Powell 1997) in McMurdo Sound. High abundance of only one species due to superiority in direct competition is rare, but is assumed for the sponge *Cinachyra barbata* at some sites in the Weddell Sea (Gutt 2006). However, this pattern reflects local effects of within-community processes rather than general between-community differences.

Most mechanisms supporting species-specific patchiness discussed so far lead to variants of the Suspension Feeder Community. Another mechanism, which may cause local aggregation of mobile animals, may be related to food conditions (Fig. 1g) rather than to physical impacts. Among typical deposit feeders, different species of elasipod sea-cucumbers are occasionally observed to aggregate, in contrast to their generally scattered occurrence in mixed and deposit feeder (sub-) communities. Aggregations of > 40 m^{-2} of two species, *Elpidia glacialis* and *Achlyonice violaecuspidata*, in the southernmost Weddell Sea (Gutt & Piepenburg 1991) associated with a short period of open water, might be typical of limited food conditions, as is also known from the deep sea. In a nutrient-saturated situation, as assumed for eastern Weddell Sea shelf and the deeper shelf west of the Antarctic Peninsula, there might be no need for such a behaviour. However, aggregation due to a patchy occurrence of especially favourable conditions can also not be excluded.

The highly patchy nature of the processes, which cause a locally high dominance of a species, contributes considerably to a high beta-diversity in shallow waters as well as slightly deeper waters affected by disturbance and patchy food conditions. Species dominance due to competitive displacement (Gutt 2006) is generally not frequent enough to have a general relevance.

Assemblages with extremely low abundances (ELA) and zero abundances within trophic guilds (ZAG)

Very few results on life below ice shelves and in areas affected by the nearby ice shelf edge are available. Some are reviewed by Dayton (1990) including a very specific "local biological oasis" below a proglacial lake in the George VI Sound west of the Antarctic Peninsula. In the most extreme

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case, under the Ross Ice Shelf *c.* 450 km from the open sea and almost 600 m below sea level, Lipps *et al.* (1979) and Bruchhausen *et al.* (1979) found a very much impoverished but "normal" Antarctic fauna consisting of fish, crustaceans, shells of foraminiferans, bivalves, gastropods and polychaetes, but no infauna. At this site "the sediment was essentially devoid of chlorophyll, or its degradation products" but benthic bacterial biomass was comparably high compared to that in the water column (Holm-Hansen *et al.* 1979) and "similar to that reported for deep-sea samples". Heterotrophic activity had "probably the slowest rate of turnover" (Azam *et al.* 1979). Photographs and videos from under the Amery Ice Shelf show that 100 km from the ice shelf edge sponges, and other sessile animals including polychaetes and gorgonians and bryozoans exist. The occurrence of planktonic foraminiferans, radiolarians and pteropods indicate that a strong advective transport of organic material supports benthic life under ice shelves (Riddle *et al.* 2007). Consequently, it is not surprising that the benthos only 22 to 30 km from the open sea beneath the Ross Ice Shelf is interpreted as an impoverished or sediment modified shallow water community (Littlepage & Pearse 1962), which includes the aggregation of small actinarians mentioned above. Fifty kilometres from the Ross Ice Shelf edge, Davis *et al.* (1983) and Dayton *et al.* (1984) reported a diverse invertebrate community with "most components of the McMurdo sponge community" (Dayton 1990) described for the adjacent ice edge. In this area, Barry & Dayton (1988) measured an inflow with high velocity in the water column. However, in all these studies the incomplete taxonomic identification and the difficulty of representative sampling does not allow a final conclusion about the possible uniqueness of species compositions under ice shelves. Domack *et al.* (2005a) found cold seep clams beneath the former Larsen B Ice Shelf, east of the Antarctic Peninsula in an innershelf depression, which is an additional biological element so far not known from the Antarctic shelf. The mechanism behind this supposed chemotrophic benthic system, however, is not yet understood. In the same area, diatom concentrations in the sediment were "several orders of magnitude lower" than in the adjacent Larsen A area, indicating significant differences in historical food supply in these formerly shelf ice covered areas (Domack *et al.* 2005b).

A simple question based on faunistic results from habitats affected by the ice shelf in combination with current direction is: If some extremely rare individuals, let us assume one per ecological guild per > 100 m^2, are obviously successful in terms of recruitment and growth (Fig. 1i) why does the system not support a higher density? On the Antarctic shelf extremely low abundances of sessile suspension feeders in particular, compared to the much higher abundance in the core community described above are known from areas below the ice shelf and innershelf depressions close to the ice shelf edge (Jones 2005). The answer to this question should not only help explain extremely low abundances on Antarctic shelves but have also implications for "normal" benthic structures with rare species but overall higher abundances. Trophic limitation, as well as other unfavourable conditions, can explain the complete absence of adult specimens (Fig. 1i) for areas far behind the ice shelf edge, as well as the rareness of individuals above a certain threshold where competition exists. But in a kind of ecological range in-between, with extremely low abundances, competition for resources (primarily food) and a corresponding limitation is of no value as an explanation. Dispersal seems to be an unlikely limiting factor (Potthoff *et al.* 2006), since the entire time span since the end of the last glaciation of ≥ 8000 years has to be considered to allow species to invade into a relatively undisturbed area. Besides the general circumpolar occurrence of many species, sources of evidence to support this assumption include a study focussing on a single species, the barnacle *Bathylasma corolliforme* (Dayton *et al.* 1982), studies at the community level (Raguá-Gil *et al.* 2004, Gutt *et al.* 2006) and another based on the planktotrophic reproduction mode of most shallow water invertebrates (Pearse *et al.* 1991). Even minimum dispersal capacities, in combination with low current velocity, would allow most species to invade any large region on the Antarctic shelf since true barriers, such as those resulting from separated water masses, cannot be expected in areas affected by the coastal current. Locally, such a mechanism cannot be excluded in especially heterogeneous seascapes such as that described for the St. Lawrence Gulf Estuary (Ardisson & Bourget 1992). Mortality of juveniles due to predation e.g. by bottom dwellers (trophic amensalism), in combination with historical changes may shape the habitat of mobile invertebrates (Goodsell & Connell 2005). However, such negative effects must be selective and constant over a long period but not so intense as to remove the majority of specimens before they become too large to serve as prey. From the perspective of a tiny recruit for example of deposit feeders, predators can occur in high densities, such as *Odontaster validus* in McMurdo Sound, and shape the entire benthic system. However, for the areas discussed here, such predators have low abundances. Trophic limitation for adults is the main driver in this system, more juveniles must exist at least locally since they have much lower food demands, but there are no hints of such a demographic structure.

A more realistic answer is probably that ecological requirements shift significantly during ontogeny, or are simply more specific during early life compared to the more general requirements of adults. In this case, a mismatch between ecological demands and environmental conditions leads to an unpredictable survival of only extremely few individuals, those that simply had good luck. This becomes a match when the animals grow since they widen or change their ecological requirements, and may in the end perform

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especially well since they do not experience competition. The availability of a favourable substratum for the recruits can be regarded as such a critical condition, in addition to food availability in terms of quality and predictability. The latter was identified by White (1984) as a major problem with which Antarctic benthic suspension feeders have to cope. McClintock *et al.* (2005) speculated about a high level of complexity in nutrient exploitation among sponges. According to Alldredge & Gotschalk (1988) it is the variability in quality of marine snow aggregates or fresh phytodetritus and not the current speed alone that can shape benthic patterns. Bathmann *et al.* (1992) and Isla *et al.* (2006) provided examples for the variability in the quantity and quality of organic matter flux to the sea floor from the high latitude Antarctic shelf. Beaulieu (2002) reviewed this topic including the problems of resuspension and ice edge effects as well as a link to the benthic fauna. Berkman *et al.* (1986) studied resuspension in McMurdo Sound, indicating that in shallow water systems not only is the seasonal predictability relevant but the short-term variation might also play an important role. This conceptual model of a shift from a mismatch to a match during ontogeny can also be applied to communities with higher total abundances to explain the extreme rareness of specific species, but only to subsystems/areas without intra- and interspecific competition within ecological guilds, or in other words, without trophic limitation. Within the same constraints, explanation can be sought for extremely low abundances for species at the margin of their distribution and for the macrofauna at continental slopes and in the deep-sea, especially rare sessile suspension feeders. However, detailed answers might differ from those proposed above for the Antarctic shelf benthos (Isla *et al.* 2005, Rex *et al.* 2005). Gage (1996) reviewed competition and disturbance as the main drivers for the deep-sea fauna. Beaulieu (2001a, 2001b) analysed and showed a few representative examples of rare suspension feeding deep sea sponges, including some trophic problems.

Mobile deposit feeder community (MDC) and infaunal community (INC); the sediment problem

A number of cases where the infauna (Fig. 1h) and/or the mobile epifauna (Fig. 1j) dominate muddy sediments or where, by contrast, sessile species colonize true hard substrata, demonstrate that discrete differences between assemblages exist based on sediment characteristics. Examples are predominantly described for shallow waters with a heterogeneously structured coastline and bottom topography. In the following, a few studies are summarized which document a relatively strong correlation between sediment properties and macrobenthic communities. Barnes (1995a) described substratum as "…the most important factor influencing community composition…" in the shallow sublittoral zone at Signy Island (see also Platt 1980). A correlation between sediment and the benthic fauna has also been found by Kirkwood & Burton (1988) at ≤ 32 m depth in Ellis Fjord, East Antarctica, whilst Picken (1985b) emphasized the general importance of sediment for the Antarctic benthos. Maybe the best example of a soft bottom community is that studied by Richardson & Hedgepth (1977) at Arthur Harbour, Anvers Island. They described different assemblages between 5 and 700 m, which did not contain any obvious suspension feeders, while many polychaete and crustacean species were found and locally molluscs seemed to be abundant. In the same area, also on soft substrata, Lowry (1975) reported that the most abundant species in the mixed assemblage were the mobile amphipod *Ampelisca bouvieri*, which is suspected to be a suspension feeder, the infaunal nuculanid bivalve *Yoldia eightsi* which is a deposit feeder and the polychaete *Apistobranchus* sp. which has an unknown food preference. Around the South Shetland Islands, including Elephant Island, infaunal polychaetes were most abundant followed by bivalves and gastropods (Mühlenhardt-Siegel 1988), whilst hydrozoans, sponges and bryozoans "rarely occur". Another typical soft bottom assemblage in the same area was that studied by Gallardo *et al.* (1977) in Chile Bay, Greenwich Island. Below 100 m depth the macrobenthos was dominated by the sessile polychaete *Maldane sarsi* and the pelecypod mollusc *Genaxius bongrainii* and in shallower waters by the mobile cumacean *Eudorella gracilior* and the bivalve *Yoldia eightsi*. A high number of bryozoans were also noted without further quantification. Sessile suspension feeders, consisting of only a few sponges, as well as the infauna are poorly represented at Bahia Esperanza, Peterman Island and in the Dallmann Bay surrounded by the Melchior Islands, in the area where Bellisio *et al.* (1972) described an assemblage almost exclusively dominated by mobile species. In depths < 60 m this mobile fauna consisted of gastropods *Eatoniela caliginosa*, *Laevilittorina antarctica*, *Margarella antarctica* and *Patigera polaris*, the amphipods *Paradexamine fissicauda* and *Pontogeneia antarctica*, the echinoderms *Granaster nutrix* and *Sterechinus neumayeri*, the polynoid polychaete *Antinoe hastulifera* and chitons. These species could also be attributed partly to the monospecific and physically-controlled assemblages. At water depths down to 400 m at these three sites along the Antarctic Peninsula, the assemblage was dominated by mobile animals such as ophiuroids, e.g. *Ophioparte gigas* which was identified by Arnaud (1964) as an indicator for sublittoral soft sediments, a variety of asteroids, nemerteans and the amphipod *Waldeckia obesa*. In Paradise Bay at depths ≥ 60 m a typical mobile fauna with some infaunal elements was also described by Castellanos (1973); sessile species such as hydrozoans, bryozoans and sponges seemed to have only locally intermediate abundances, especially at depths below 30 m for hydrozoans and 40 m for sponges. An assemblage investigated at Casey Station (110°E) by grab sampling

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(Stark 2000) showed a soft-bottom assemblage clearly dominated by (mobile) crustaceans (90–97% of specimens), gammarids, ostracods, and tanaids with very low abundances of echinoderms, polychaetes, and molluscs. A similar fauna was described by Everitt *et al.* (1980) at Davis (78°E) on sandy and silty sediments. In McMurdo Sound at depths ≥ 60 m typical elements of such an assemblage of mobile animals are the isopod *Glyptonotus antarcticus*, the nemertean *Lineus corrugatus*, the ophiuroids *Ophiurolepis gelida*, *Ophiacantha antarctica*, and the asteroids *Odontaster validus* and *Diplasterias brucei*. At various localities sedentary infaunal polychaetes are very abundant or dominant (Oliver & Slattery 1985), even in soft-bottom areas with an obvious epifauna (Dayton & Oliver 1977, Oliver 1978). Such areas can also be considerably affected by ice disturbance and are not only shaped by sediment characteristics (Bullivant 1967). In the adjacent Terra Nova Bay at water depths ≤ 200 m Cattaneo-Vietti *et al.* (2000a) distinguished between hard-bottom communities characterized by sedentary cnidarians as well as sponges, the sessile polychaete *Serpula narconensis*, the mobile amphipod *Paramoera walkeri*, and soft-bottom communities with important key species including the infaunal bivalves *Yoldia eightsi* and *Laternula elliptica*. Lovell & Trego (2003) and Cranmer *et al.* (2003) documented a dominance of mobile echinoderms (*Sterechinus neumayeri* and *Ophionotus victoriae*) and crustaceans, as well as infaunal bivalves in the caldera of Deception Island. These organisms were also abundant at two adjacent reference sites at Livingston and King George islands (South Shetland Islands), but in these more exposed habitats sessile suspension feeders, such as sponges and cnidarians, were relatively more abundant.

The great difficulty of making a general correlation between Antarctic macrobenthic composition and sediment characteristics is especially obvious in these last studies (see also Fig. 1k & l). Schiaparelli *et al.* (2003) reported a hard-bottom community in which soft sediment preferring species were abundant, such as *Odontaster validus*, *Sterechinus neumayeri* and *Adamussium colbecki*, as well as a variety of demosponges with associated fauna such as *Haliclona dancoi*, ascidians and polychaetes. Hexactinellid sponges, known to prefer hard or mixed substrata (Cattaneo-Vietti *et al.* 2000b) have also been found associated with soft-bottom communities. A weak relationship between sediment and community structure was confirmed by the comprehensive community analysis also in the Ross Sea at water depths ≤ 24 m by Cummings *et al.* (2006). Dayton & Oliver (1977) classified all the rich epifaunal and more poor assemblages in the adjacent McMurdo Sound at < 100 m as a soft-bottom benthos. Interestingly, *S. neumayeri* was also found with high abundances on the deeper shelf on poorly-sorted sediments (Gutt & Starmans 1998), in the "suspension feeders, rich" community in the Weddell Sea and on boulders and gravel fields in Marguerite Bay, Bellingshausen Sea (Raguá-Gil 2004). Similarly, Arnaud (1974) found mobile as well as sessile assemblages on muddy sand to sandy mud sediments and a "very opportunistic choice of substrates by invertebrates" with a "rarity of endofauna" in these predominantly soft sediments (Arnaud 1977). Gutt (2000) could not find a true correlation between megafauna and coarse sediment characteristics in deeper shelf areas in the south-eastern Weddell Sea. Bullivant (1967) provided much information on generally poorly sorted sediments on the shelf and the benthic composition, but general conclusions cannot be drawn from this descriptive comparison. For example, Bullivant (1967) described sandy bottoms "with sparse fauna" and in a different area the same sediment class was covered by the densest epifauna.

There are three reasons, which may contribute to these partly confusing and contrasting results, which makes the general application of a classification according to sediment characteristics difficult, if not impossible.

1) A generally accepted, and for ecologists useful, definition and classification of the poorly sorted Antarctic sediments is missing,

2) Statistical analyses of the relationship between sediment - among other environmental characteristics - and the macrobenthos are almost missing,

3) The "opportunistic choice of substrates" by many invertebrates in most parts of the Antarctic shelves provides evidence that a clear correlation between sediment and benthic fauna does not exist since other environmental characteristics are more relevant, and consequently more able to explain differences in community structures.

These ideas are the main reason to propose a separation that distinguishes between the first core community in which sessile suspension feeders are abundant and profit from an advective food supply independently of sediment characteristics, and the second core community consisting predominantly of infauna and the mobile epifauna. This second core community may be supported by three main conditions:

a) primarily vertical food supply and immediate sedimentation of phytodetritus providing food for vagrant deposit feeders,

b) trophic amensalisms in which bottom dwellers cause physical micro-scale disturbance in the sediment, leading to reduced recruitment of sessile species or increased mortality of juveniles, (where a considerable proportion of the sessile fauna survives, coexisting with the mobile and infaunal species, we observe the mixed assemblages between both core communities),

c) apart from mechanisms which may give the infauna

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and mobile epifauna competitive superiority, suitable conditions for the infauna must at least include the availability of soft sediments, independently of the presence of additional hard substrata.

If the soft sediments can be explained predominantly by low current velocities, then these conditions will also support the mobile deposit feeders which benefit from the vertical flux of food, as mentioned above. In contrast to the suspension feeder community, these conditions can be locally more restricted, e.g. in fjords and bays, and consequently more spatially heterogeneous, which makes it difficult in some cases to call the corresponding species composition a true community (see also Barnes & Conlan 2007). However, the assumed mechanisms that support this core community and its two sub-communities seem to be independent of their spatial extent. Partly due to this, the proper core community of mobile deposit feeders and infauna seems to be less abundant, and spatially as well as faunistically more heterogeneous than the sessile suspension feeder community, especially due to the inclusion of the two completely different ecological guilds.

Conclusions

A very brief answer to the question raised in the introduction "Does the Antarctic macrobenthos really exists if the community level is considered?" is simple: It does not, since extremely obvious differences in the faunistic composition, infauna versus epifauna, and in ecological processes, dynamic versus static, are known! The difficulty, however, in coming to a better generally applicable classification, results from the way in which several ecological gradients are superimposed on each other, and clear differences occur only at the extreme ends of these gradients. The proposed classification based on the dominance of either sessile suspension feeders or infauna and mobile deposit feeders might be more applicable than the sediment-community concept, since it is based on the community structure and this can be relatively easily investigated in a quantitative way, or simply observed and described. This classification is based on mainly assumed or observed, and rarely directly measured general ecological processes and life history traits. This classification does not depend on a strict split between soft and hard bottoms that are impossible to separate in large areas, and difficult to correlate consistently with the benthic fauna. In the same way, water depth and geographical location have no predictive power for species assemblages since there are other environmental variables that are more relevant. The concept proposed here includes a broad gradient in the mixture between both core communities. Nevertheless, this classification can be considered a step forward but only additional quantitative results can improve its general applicability. The urgent need for prediction of ecosystem response to large-scale environmental changes makes a continuation of surveys at the community level particularly necessary. Only these kinds of studies can provide information on regional species richness, abundance, biomass, dominance, as well as spatial patterns, and can cover the full range of all larger ecological guilds and/or systematic groups and their dynamics. This information provides the basis for further physiological, genetic, flux, or life history studies on representative components of the ecosystem. Ongoing and nearly finished projects will reveal valuable additional results, e.g. BENTART (Spain), FOODBANKS (USA), IBMANT (Arntz *et al.* 2005), BIOROSS (New Zealand), LGP (Berkman *et al.* 2005), EBA (SCAR), CAML (Sloan Foundation), further studies under the Amery Ice Shelf, and other IPY approved projects. A considerable step forward, however, is only possible if such approaches are coordinated, sampling and measurement strategies are standardized, if more attempts to correlate biological and physical results are included, and if long-term ecological processes and developments are considered. The use of faunistic and ecological data banks such as SCAR MarBIN (http://www.scarmarbin.be/) or PANGAEA (http://www.pangaea.de/) can also help improve our understanding of ecological and evolutionary processes if the presence-absence problem is solved and if data from the past can be included.

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