

Bryozoans in polar latitudes: Arctic and Antarctic bryozoan communities and facies

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Abstract: Bryozoan community patterns and facies of high to sub-polar environments of both hemispheres were investigated. Despite the overall similarities between Arctic/Subarctic and Antarctic marine environments, they differ distinctly regarding their geological history and hydrography which cause differences in species characteristics and community structure. For the first time six benthic communities were distinguished and described for the Arctic realm where bryozoans play an important role in the community structure. Lag deposits resulting from isostatic uplift characterise the eastbound shelves of the Nordic Seas with bryozoan faunas dominated by species encrusting glacial boulders and excavated infaunal molluscs. Bryozoan-rich carbonates occur on shelf banks if terrigenous input is channelled by fjords and does not affect sedimentary processes on the banks. Due to strong terrigenous input on the East Greenland shelf, benthic filter feeding communities including a larger diversity and abundance of bryozoans are rare and restricted to open shelf banks separated from the continental shelf. Isolated obstacles like seamount Vesterisbanken, although under fully polar conditions, provide firm substrates and high and seasonal food supply, which favour bryozoans-rich benthic filter-feeder communities. In contrast, the Weddell Sea/Antarctic shelf is characterised by iceberg grounding that causes considerable damage to the benthic communities. Sessile organisms are eradicated and pioneer species begin to grow in high abundances on the devastated substrata. Whereas the Arctic bryozoan fauna displays a low degree of endemism due to genera with many species, Antarctic bryozoans show a high degree of endemism due to a high number of genera with only one or few species. However, the bryozoan growth forms of the Arctic seamount Vesterisbanken in the Central Greenland Sea show highest degree of correspondence with the Antarctic Weddell Sea shelf with a predominance of erect species.

Key words: Bryozoa, polar marine environments, benthic communities.

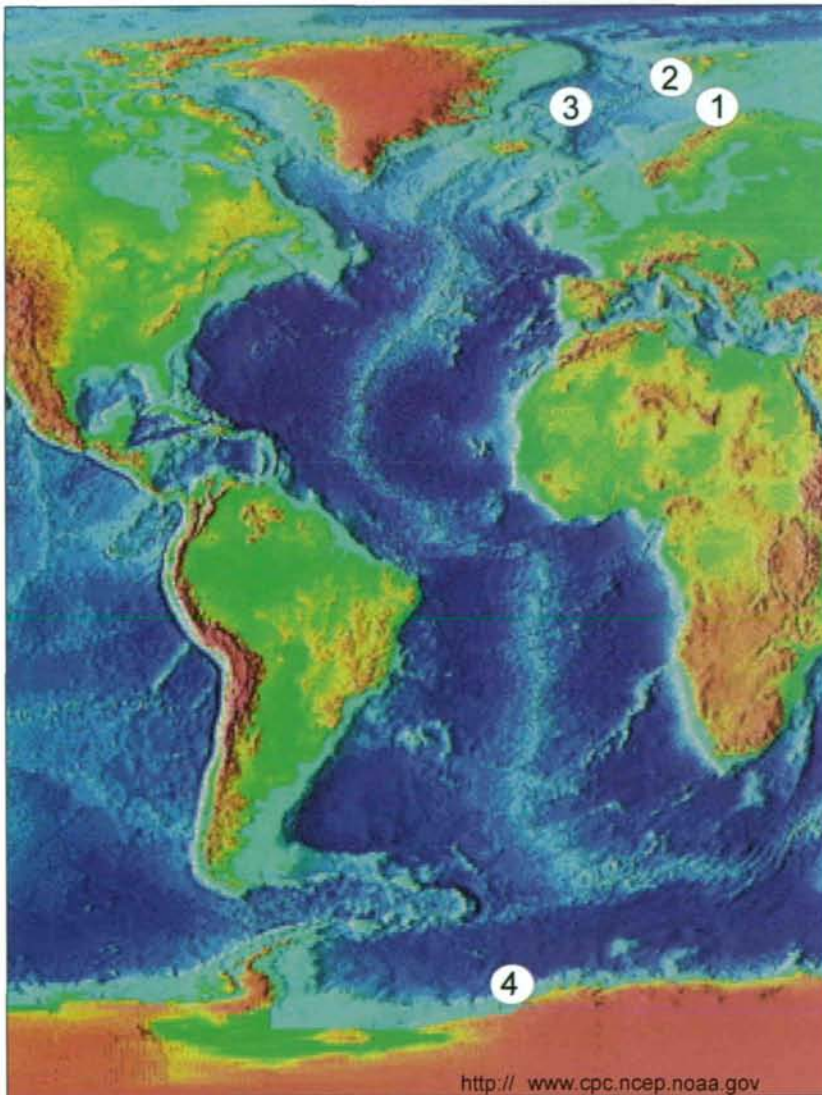
1 Introduction

Apart from their polar position, low temperatures and the seasonal trends in irradiance and ice cover, the north and south polar benthos are strikingly different from each other. The Arctic bottom fauna consists of a small number of species of all major taxa. These species are mostly eurythermal and may have successfully invaded the North Polar waters from the boreal Atlantic or Pacific. In the Antarctic benthos, only a few taxonomic groups have evolved into a large number of steno-thermal species, while the remainder of the higher taxa are poorly represented on the Antarctic shelf. Polar food webs show that annual primary production is poor and highly seasonal, the benthos is largely de-coupled from the pelagic zone and the majority of polar animals grow slowly and reproduce late.

In the Arctic realm bryozoans are very often the dominant component in benthic communities in boulder habitats and on epiphytes (BARNES et al. 1996; LIPPERT et al. 2001; BARNES & KUKLINSKI 2004). Although the systematic work is quiet advanced, the role of bryozoans in ecosystems is widely unknown. KUKLINSKI (2004) conducted the first study on the quantitative composition and distribution of bryozoan communities in Svalbard waters with a special focus on the Kongsfjorden ecosystem.

Bryozoa were found to be very species-rich in the Arctic; the diversity is estimated to be well above three hundred species (KLUGE 1975) and they are amongst the richest of the Arctic macrofauna (GULLIKSEN et al. 1999). West Spitsbergen is probably the best investigated of high Arctic sites,

Fig. 1: Research vessel Polarstern in the Weddell Sea in May 2000.



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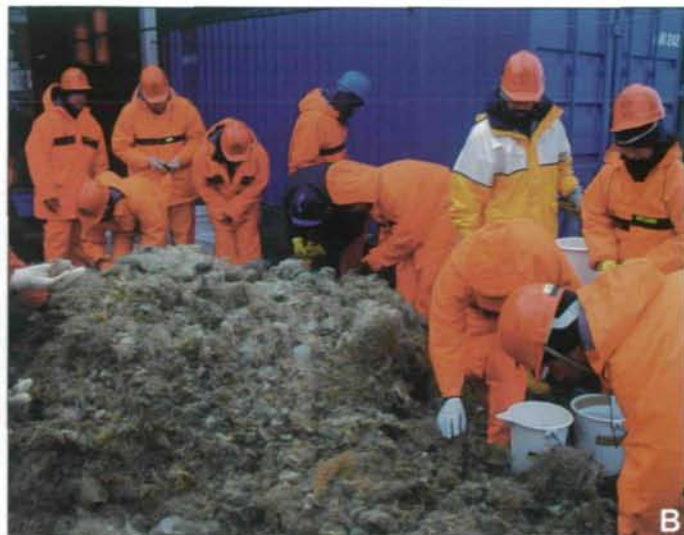
Fig. 2: Study areas with the shelves of North Norway (1), Barents shelf / SW Spitsbergen (2), Central Greenland Sea (3) and the Weddell Sea (4).

new species are still being added even in shallow water (KUKLINSKI & HAYWARD 2004).

Bryozoans are a major component of the Antarctic benthos in many of the areas that have been studied (BULLIVANT 1961, 1967; WINSTON 1983; VOB 1988; WINSTON & HEIMBERG 1988; GALERON et al. 1992; BARNES 1995a, b, BARNES & CLARKE 1998; MOYANO & RISTEDT 2000). The last few decades have seen a dramatic explosion of taxonomic and ecological work in southern polar waters. Many new Antarctic cheilostomatid bryozoan species and genera have been described, whilst the taxonomic status of many others has been elucidated (see HAYWARD 1995 and references therein). In contrast to other Antarctic shelf sites the bryozoan fauna of the Weddell Sea is not well known. RISTEDT (1995) presented a first description of the bryozoan fauna, ZABALA et al. (1997) a first taxonomic list of the Weddell Sea bryozoans.

2 Material and working areas

Living bryozoans and bryozoan carbonates were collected during several cruises in the years 1989, 1990, 1994 and 2000 with the German research vessels "Meteor", "Littorina", "Polarstern" (Fig. 1) and the Norwegian research vessels "Ottar" and "Johan Rud". The working areas are the Arctic domain with a main focus on the shelves of



North Norway, Northeast Greenland and the central Greenland Sea (Fig. 2, 4); and the Antarctic domain with the Weddell Sea as study area (Fig. 2, 13). The material was sampled by means of grab, giant box corer, and dredge (Fig. 3). The material was either dried or preserved in 70 % alcohol. Underwater video and camera was used to document distribution of the fauna and flora on the sea floor.

3 Bryozoan communities

3.1 Arctic and Subarctic communities

3.1.1 Hydrography

The temperate Atlantic waters in the East, the cold ice-covered Polar waters in the West and the seasonally ice-covered Arctic waters in between are the three major surface water masses in the Nordic Seas. They occur close together but are separated by steep oceanic gradients. The North Norwegian shelf is mainly affected by the Norwegian Coastal Current, which runs northward and parallel to the Norwegian Current (Fig. 4). Along the outer edge of the Barents Sea and the West Spitsbergen shelves, Atlantic waters of the Norwegian Current are separated from the polar water masses of the Spitsbergen Bank and the East Spitsbergen Currents by the Polar Front. In contrast, seamount Vesterisbanken in the central Greenland Sea and most of the Barents Shelf lie under polar water masses throughout the year.

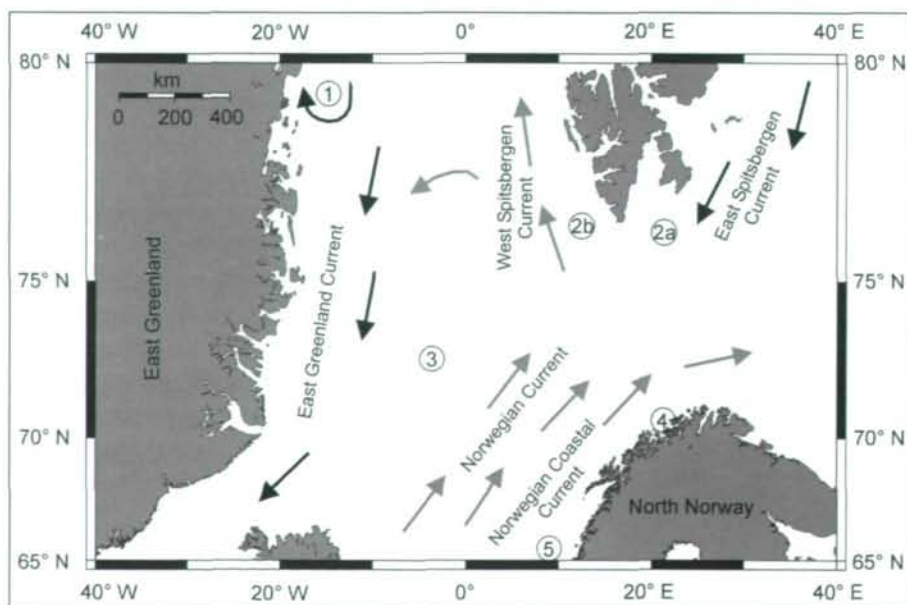
In contrast to the Norwegian continental shelf, the East Greenland shelf is fed by water masses of polar origin (East Greenland Current) with year-round lowest temperatures and salinities. Most of the year the shelf is covered by sea ice except of the northern section, where the seasonally developed coastal Northeast-Water polynya brings open-water conditions during summer months. This polynya affects Belgica Bank, an open shelf bank isolated from the East Greenland shelf and surrounded by an anti-cyclonic spin-off of the East Greenland Current (Fig. 4).

3.1.2 Holocene history

Due to Holocene eustatic sea level rise and isostatic uplift of the continental crust because of continental ice melting (Scandi-

Fig. 3: Preparation of an Aggassiz trawl (A) and catch of an Aggassiz trawl (B) on board of Polarstern in April 2000 in the Weddell Sea/Antarctica.

Fig. 4: Oceanographic current regime and location of study area with Belgica Bank/North-East Greenland (1), Spitsbergen Bank/Barents Shelf (2a) and Westspitsbergen Shelf (2b), Seamount Vesterisbanken/central Greenland Sea (3), Rakkfjord/North Norway shelf (4) and Trondheim Shelf/North Norway (5).



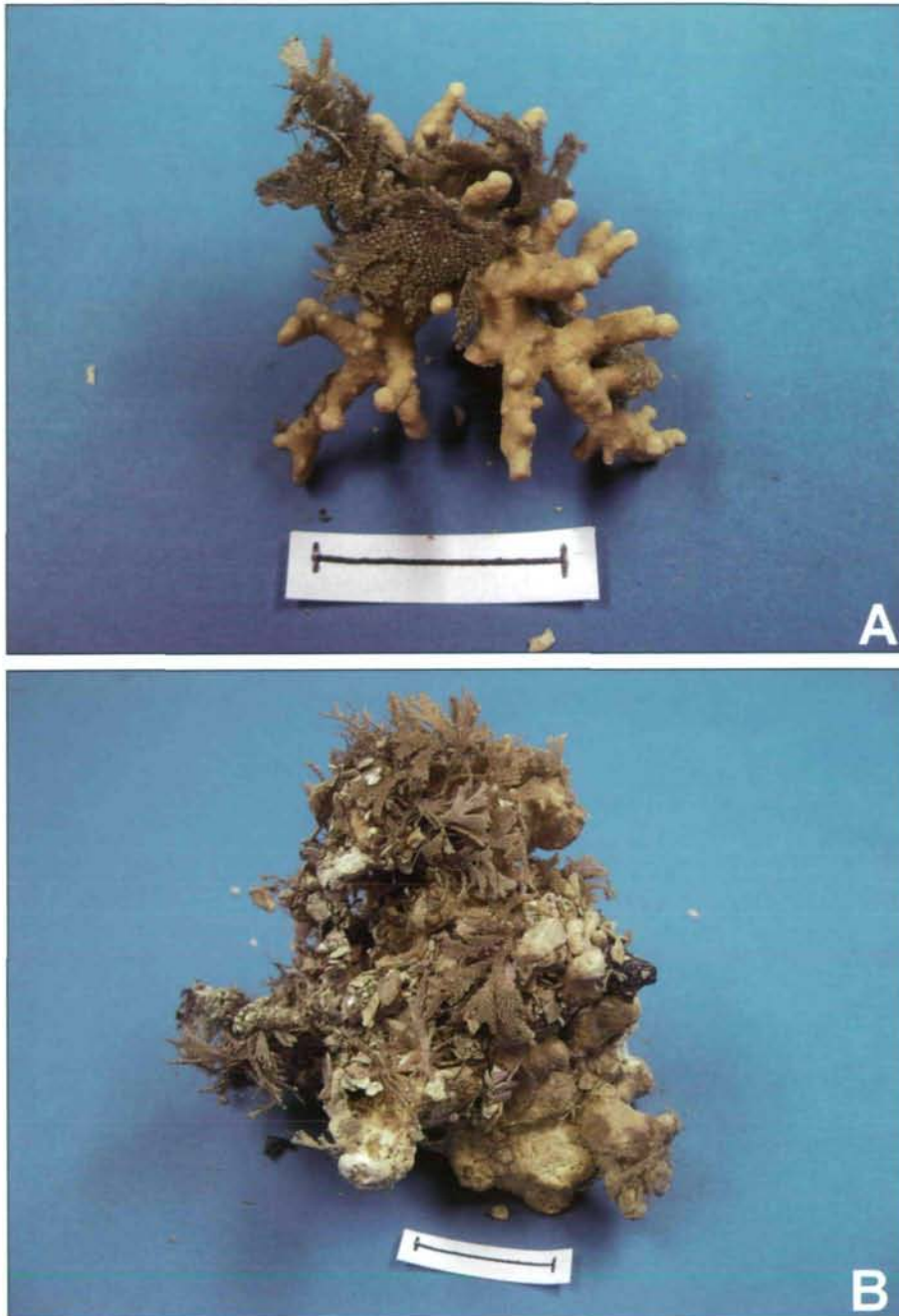


Fig. 5: Free living rhodolith of *Lithothamnium boreale* (A), *L. boreale* encrusted with weakly calcified bryozoan *Dendrobeania* spp. (B). Scale bar = 1 cm.

navia, Barents Sea, Greenland) the subpolar shelves surrounding the Nordic Seas encountered a very complex geologic history. The North Norwegian Shelf, the Barents Shelf and the West Spitsbergen shelf ran through several transgressions and regressions, the shelf break is in about 200 water depths, and the shelves are covered by carbonate-lag deposits. During Holocene history, shelves were affected by the interplay of eustatic sea-level rise and isostatic uplift resulting in erosion of an early Holocene bivalve endofauna forming a carbonate lag deposit. Colonisation of a late glacial di-

amic started around 12.6 ka on the North Norwegian shelf (SCHÄFER et al. 1996). Invasion by the marine benthos reached the Barents Shelf (Spitsbergen Bank) around 8.6 ka (HENRICH et al. 1997) and West-Spitsbergen shelf around 9.1 ka (ANDRULÉIT et al. 1996). Due to isostatic uplift after melting of the continental ice sheet, shelf banks uplifted, the endofauna was washed out and the lag deposit colonised by a diverse epifauna including bivalves, bryozoans and balanid cirripedians at around 2.0 ka (Northern Norway), at 2.8 ka (Spitsbergen Bank), and at 2.6 ka (West-Spitsbergen shelf).

In contrast, the Greenland shelf with its still prominent ice cover became less uplifted; therefore, the shelf break remains in a water depth of 500 to 600 m. Shelf banks are covered by silts and muds, prominent lag deposits are mostly lacking. Bank with lag deposits and coarse-grained sediments such as the Belgica Bank in the Northeast Water polynya are rare and completely separated from the continental hinterland.

3.1.3 Fjordic environments

Fjords in subpolar latitudes are characterised by nearly vertical walls and water depths from intertidal down to 200 m. Sea floor in deeper parts of the fjords is covered by fine mud. Shallow sites on trough shoulders and fjord sills, however, display a relatively large variety of communities in which bryozoans are important constituents. Two distinct bryozoan communities can be distinguished:

Red algae – bryozoan – polychaet communities

Dense consortia of coralline and non-coralline red algae and bryozoans fixed together by polychaete tubes occur in the Rakkfjord, Troms, North Norway, in about 10 m water depth. The red alga *Lithothamnium boreale* forms free living rhodoliths with an open branch structure; the bryozoans are mostly erect, often articulated and weakly calcified anascans such as *Dendrobeania murrayana*, *D. pseudomurrayana*, *D. fructicosa*, *Scrupocellaria sabra*, and *Notoplites normanni* (Fig. 5). The consortium forms a rich habitat housing a high diversity of delicate bryo-

zoans (*Callopora craticula*, *Tegella arctica* and others) and serpulids (*Spirorbis* sp.). The filter feeders benefit from the elevated position above the sea floor formed by the rhodoliths.

Chlamys islandica – banks

Fouling communities are well-defined ecosystems with narrow limitations in time and space. Larval recruitment and competition for space are considered to be the major factors that control the adaptive success of colonial and solitary organisms within this highly stressed environment.

The boreal-Arctic pectinid bivalve *Chlamys islandica* lives in great abundance in a water depth of 20 to 70 m in the outer fjords of Troms, North Norway. The living clams are heavily fouled by bryozoans associated with barnacles, serpulids, hydrozoans, sponges, small molluscs and brachiopods, crustose coralline algae, and foraminifers (SCHÄFER 1994, 1997).

Clams are attached by byssus (young individuals) or are free living (adults) on the sea bottom with their left valves turned upwardly and with their right valves facing the substrate. This specific orientation results in major environmental differences on left and right valve surfaces that in addition to the recruitment of pioneer taxa and competition for space strongly influence the ecological structure of the fouling communities.

Right valves roof a cryptic habitat and are mainly exposed to moderate, laminar water currents. Encrusting bryozoans and calcareous polychaets dominate the fouling communities. Diversity of higher taxa is low. Highest species diversity occurs on valves with moderate encrustation. Limited space and same requirements for food and space of the sessile-benthic organisms result in a distinct vertical succession of highly competitive but rather simple fouling communities finally dominated by a few species (*Porella minuta*, *Schizomavella linearis*) only. The latter species switch from zooidal to multi-zooidal budding pattern when encountering other colonies and, thus, have a competitive advantage against other species. The most competitive species, *Porella minuta*, as well as *Celleporella hyalina*, may even switch to frontal budding. Additionally, *Porella minuta*



Fig. 6: *Chlamys islandica* with *Dendrobeania* spp., encrusting bryozoans, hydrozoans and a balanid tube. Scale bar = 1 cm.

builds the largest colony and is considered to have higher growth rates than others.

Left valves, however, are exposed to a more complex physical environment where water turbulence prevails. A larger diversity of higher taxa occurs. It is indicated by a dominance of barnacles, flexible bryozoans (*Dendrobeania* spp., *Scrupocellaria* spp.) and hydrozoans, encrusting bryozoans (*Porella minuta*, *Microporella ciliata*, *Escharella immersa*, *Tegella arctica*, and *Oncousoecia diastoporoides*), and sponges (Fig. 6). "Unlimited spaces" is available due to upright-flexible growth of anascan bryozoans resulting in formation of a variety of ecological niches. The communities are, therefore, more complex, distinctly tiered, and interacting. A domination stage is rarely developed.

3.1.4 Open shelf banks eastern boundary shelves

Open shelf banks of the Norwegian shelf, the Barents shelf and West Spitsbergen shelf are exposed to waves, and to strong tidal and bottom current. Here, solid rock, moraine boulders and coquinas serve as an ideal ground for larval settlement (Fig. 7). Because of high water energies, multiserial-

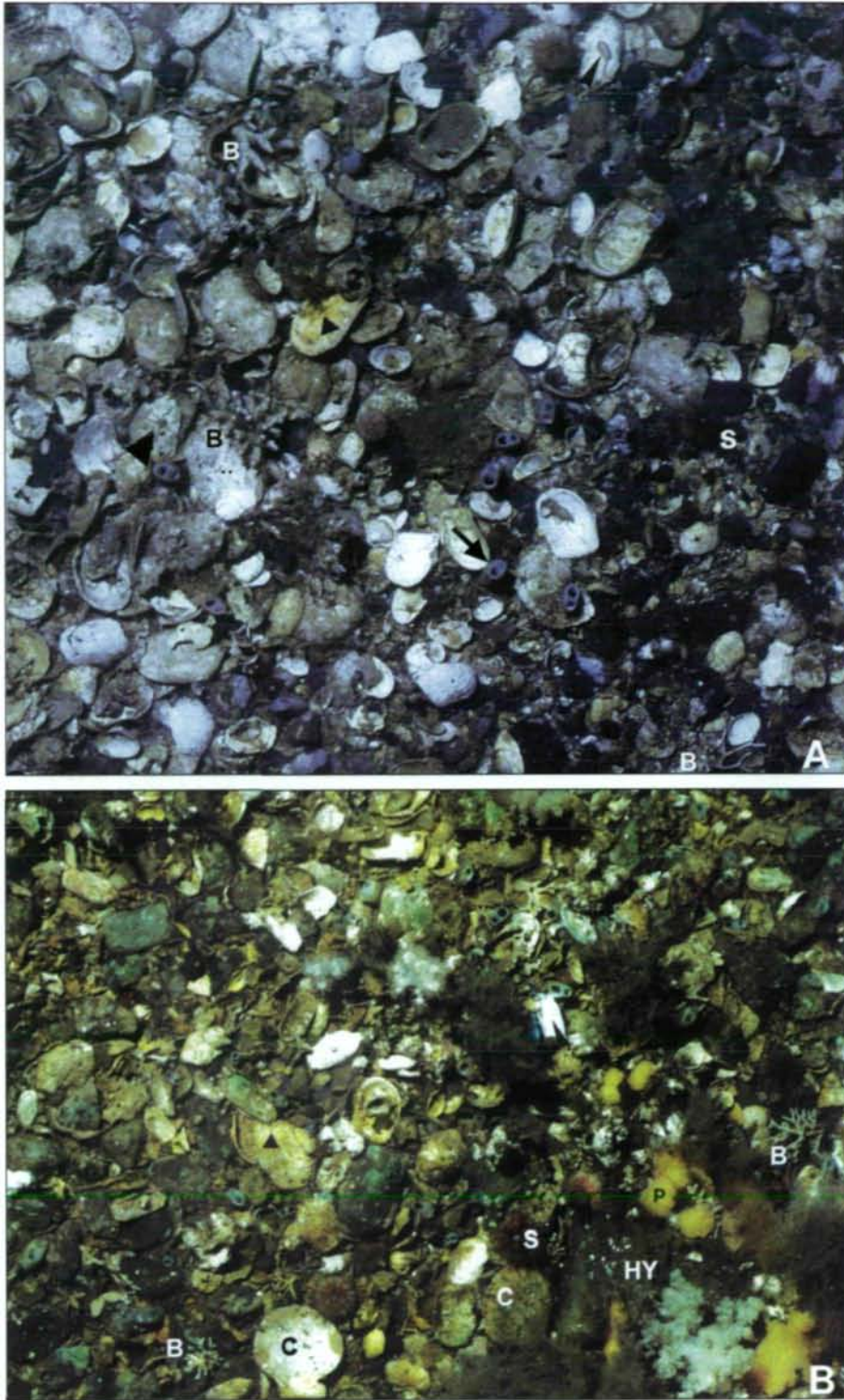


Fig. 7: Underwater photographs of Arctic epibenthic communities and carbonate deposits from Spitsbergen Bank, western Barents Sea taken during Meteor cruise M-21/4. **A:** *Mya truncata* lag-deposit with branched bryozoans (*Myriapora* sp., *Celleporella* sp.) (B) and numerous ophiuroids (black triangle), *Mya truncata* valves are grazed by stronglylocentroid echinoids (S). The siphones belong to *M. truncata* (black arrow). 74°34'N, 21°00'E, 101 m water depth, scale = 30 X 30 cm. **B:** *Mya truncata*-*Hiatella arctica* belt with boulders and pebbles, which are intensely encrusted by large bushy hydrozoans (HY) and sponges (P). Branched bryozoans (*Myriapora* sp.) (B) and stronglylocentroid echinoids (S) are quite abundant. 74°40'N, 20°47'E, 79 m water depth. The long axis of the *Chlamys islandica* (C) valve is 8 cm. Pictures from HENRICH et al. (1995).

encrusting species dominate today the bryozoan fauna on the shallow banks. Depending on the kind and abundance of suitable substrate to colonise, epibenthic organisms vary in diversity and abundance. In more soft-bottom habitats, uniserial runners such as *Hippothoa* spp. dominate on isolated rock pebbles, while large pebbles and boulders are colonised by a diverse multiserial-encrusting bryozoan community (Fig. 8A). They are associated with a few upright/branching (*Homera lichenoides*, *Myriapora* spp., *Idmidronea atlantica*), massive-domal (*Cellepora* spp.; Fig. 8B), fenestrate (*Sertella septendrionalis*) and upright-flexible (*Dendrobeatia* spp.) species. Competition for space among multiserial-encrusting species is distinctly higher than in uniserial colonies as well as in dendroid and fenestrate deeper-water bryozoan communities.

Western boundary shelves

Belgica Bank off the Northeastern Greenland shelf is characterised by grain size and seabed heterogeneity and a diverse invertebrate fauna of mostly vagile epifaunal and endofaunal organisms (see PIEPENBURG et al. 1997) (Fig. 9). Large ripple fields with dead valves of the infaunal *Mya truncata* accumulated in the ripple troughs indicate near-bottom currents. Larger fields of dead valves of *M. truncata* and living and dead *Astarte* sp. cover larger areas of the northern Ob Bank.

The bryozoan fauna revealed 68 cheilostomate, 12 cyclostomate and 2 ctenostome species indicating a typically high-Arctic circumpolar character with fewer boreal elements. Bryozoans display a patchy distribution. Suitable substrates are smaller and larger ice-rafted boulders and glaciogenic lag deposits (Fig. 9C, D). Species with upright branching colonies (*Myriapora subgracilis*, *Homera lichenoides*) and those with bifoliate fenestrate growth (*Diplosolen intricarius*) were found on UW-photographs (Fig. 9B, C, D) and in the sediment. Small and large boulders are encrusted by unilaminar, bi- and multiserial bryozoan colonies. Densest overgrowth occurs at sides of larger boulders, whereas upper sides of boulders are rarely colonised indicating a strong grazing pressure by vagile carnivorous organisms. Besides bryozoans, sessile foraminifers, poly-

chaet tubes, rare balanids and siliceous sponges cover the boulders. Hemisessile and vagile crinoids (*Heliometra glacialis*), pectinids (*Arctinula greenlandica*) as well as sea urchins, brittle and sea stars use boulders to rest and feed. The overall encrustation pattern indicates the intensity of colonisation increases with the boulder sizes.

The overall benthic colonisation pattern counts for a strong pelagobenthic coupling and its control over structuring of benthic communities (PIEPENBURG et al. 1997). It is presumed that also the bryozoans benefit from food-rich conditions along sea-ice margins of the NE Water polynya over Belgica Bank and Ob Bank. Organic fluff covering Ob Bank indicates a pulse-like export of green algae to the sea bottom as it is typical for mainly physically controlled particle flux in the Greenland Sea (PEINERT et al. 2001).

Small-scaled patchiness of bryozoan distribution on individual boulders/dropstones in an otherwise muddy environment follows the concept of "mini-islands". Tiering occurs in 4 levels: tier (1) is occupied by encrusting bryozoans (cyclostomids and cheilostomids). Tier (2) is structured by small, upright growing, mostly tubuliporid bryozoans (*Tubulipora* spp., *Entalophoroecia clavata*, *Idmidronea atlantica*). Encrusting species can benefit from irregularities of the boulder surfaces. The sessile, suspension feeding foraminifer *Rupertina stabilis* may reach into the second tier. The pectinid *Arctinula greenlandica* mediates between the second and third tier. Tier (3) is occupied by upright branching bryozoans (*Hornera lichenoides*, *Myriapora gracilis*, *Diplosolen intricarius*), small sponges, hydrozoans, and the cirriped *Balanus balanus*. Small epizoans (e.g. foraminifers) use older parts of bryozoan colonies for life within this tier. Tier (4), finally, is characterised by large crinoids (*Heliometra glacialis*) and large cylindrical sponges. Competition for spaces is rarely found in this environment due to the sparse benthic colonisation. In general, cheilostomids dominate over cyclostomes in monopolising colonisation of surfaces. The only exception is the small-sized cyclostome *Disporella hispida* successfully preventing overgrowth by other species. This is explained by the broad confluent budding zones and



the spinous zooidal apertures characterising the colonies (SCHÄFER et al. 1991).

Fig. 8: Massive-domal bryozoan *Celleporella* sp. (A); pebble encrusted with upright-flexible (*Dendrobeatia* sp.) and encrusting bryozoans, balanids and serpulids (B). Scale bar = 1 cm.

Bryozoans collected in August 2000 on Belgica Bank revealed a large number of small, non-fertile colonies; however, also mature colonies with embryos in ovicells (*Amphiblestrum trifolium* var. *quadrata*, *Hippodiplosia borealis*, *Smittina peristomata*) were found. The number of empty ovicells, however, exceeded the number of ovicells with embryos. Comparable substrates on Barents shelf and North Norwegian shelf collected in the same season (July 1990 and August 2000, resp.) showed a higher percentage of large colonies probably indicating a longer, several years life cycle.

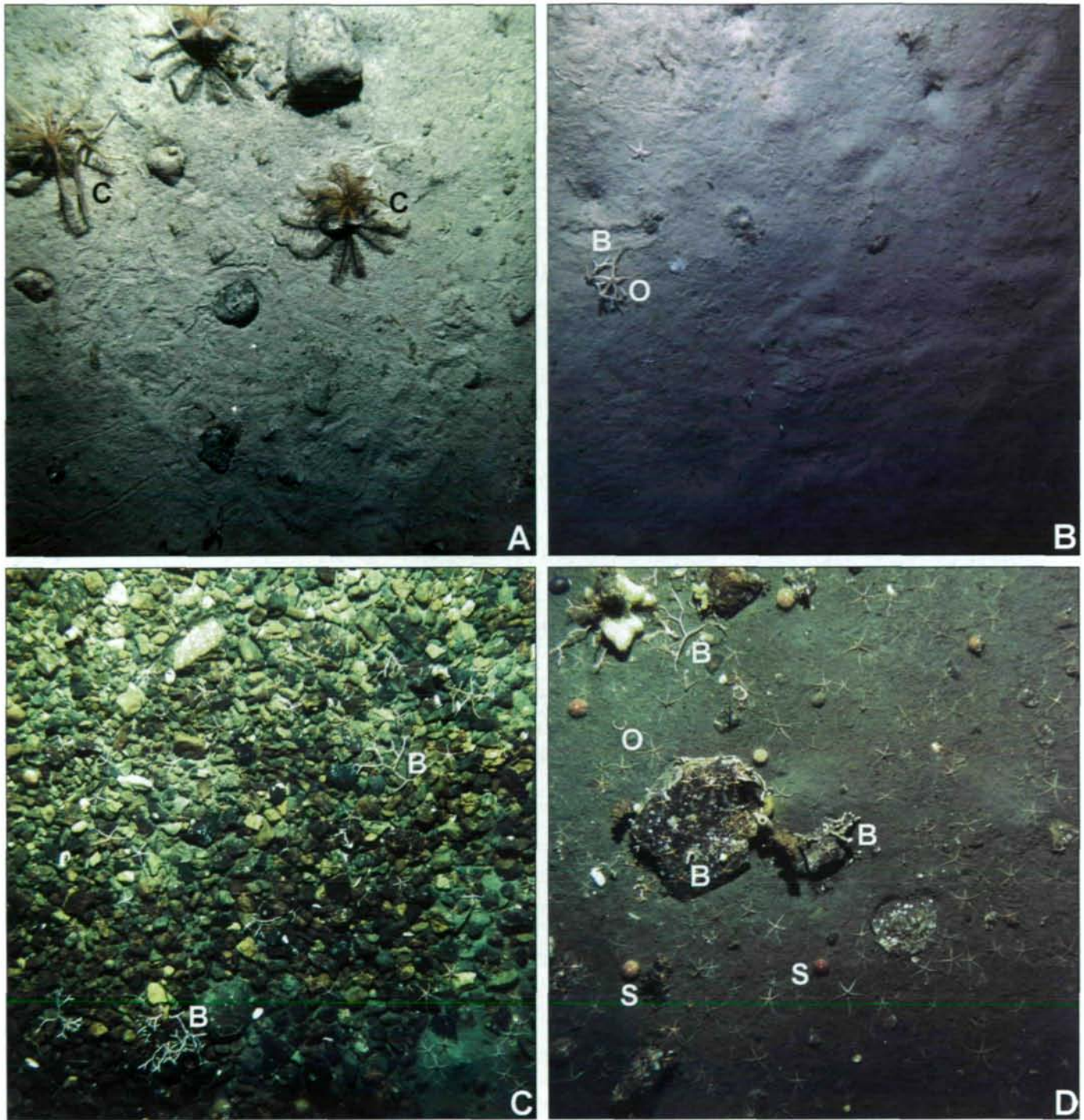


Fig. 9: Underwater photographs (scale = 1 m²) of Arctic epibenthic communities from Belgica Bank, North Greenland taken during Polarstern cruise ARK III. **A:** Muddy facies with some pebbles and crinoids (C). 78°46'N, 06°26'W, 270 m water depth. **B:** Muddy facies with ophiurids (O) and an upright branching bryozoans (*Myriapora* sp.) (B). 79°02'N, 07°44'E, 190 m water depth. **C:** Pebble field with ophiurids, upright branching bryozoans (*Myriapora* sp.) (B). 79°60'N, 14°01'W, 80 m water depth. **D:** Muddy field with pebbles and ophiurids (O), upright branching bryozoans (*Myriapora* sp.) (B) and echinoids (S). 79°59'N, 11°33'W, 80 m water depth. Pictures courtesy of D. Piepenburg (Institute of Polar Ecology, University Kiel).

3.1.5 Seamounts

The submarine, intra-plate volcano Vesterisbanken lies in the central Greenland Sea. A nearly year-round sea-ice cover, which retreats only during two months, very low temperatures (-1 to 0 °C), and salinity of 34.5 ‰ are recorded at nearly constant values over the entire water column (HENRICH et al. 1992).

Despite this polar environment, a rich and diverse benthic community dominated

by siliceous sponges and bryozoans have colonised the various habitats of the seamount down to more than 2000 m water depth (Fig. 10). The topography of the seamount, the limited terrigenous input, and the seasonal increase of nutrients by down-welling enables the predominance of filter feeders to occur with high diversity and population densities down to great water depths.

The top and flanks of the volcano display a pronounced depth zonation of benthic communities. An almost continuous biogenic mat composed of small demosponge-bryozoan-polychaet mounds and hedges covers the summit in 130 to 260 m water depth (Fig. 10A). In 260 to 400 m water depth, pectinid bivalves and polychaets dominate the substrate covered by volcanic ashes. Locally, demosponge-bryozoan-serpulid mounds are developed on volcanic elevations. The extremely steep slopes below 400 m reveal various kinds of sponge-bryozoan mounds, sponge mounds, and a typical hexactinellid sponge-crinoid assemblage on coarse volcanoclastics and firm lava ground (Fig. 10B, C).

Fig. 10: Underwater photographs (scale = 2 m²) of Seamount Vesterisbanken communities from Central Greenland Sea taken during Polarstern cruise ARK VII. **A:** A section of a bryozoan-sponge thicket in the crest facies. A dense bryozoan thicket covers the substrate completely. Bryozoans (BRY) are dominated by *Sertella elongata* which forms erect reticulate fans. Poecilosclerid *Clathria* (PCL), actinians (A), and serpulids live in this thicket. OFOS track 21880-7, 197 m water depth. **B:** A section of a sponge-bryozoan mound in the deep slope facies. The core of these deep slope mounds are *Thenea* (TH) and *Geodia* (G). The mound surface is colonised by large poecilosclerid *Clathria* (PCL), yellow poecilosclerid crusts (*Mycale?*) (PY), *Schaudinnia* (S), fan-type bryozoan colonies (BRY), and serpulids. OFOS track 21891-1A, 450 m water depth. **C:** A section of bryozoan thicket in the deep slope facies. The deep slope bryozoan thickets (BRY) are dominated by slender, dichotomously branching and reticulate growth forms, probably *Idmidronea atlantica* var. *gracillima* and *Sertella elongata*. The bryozoan thickets are associated with geodiid sponges (G), actinians (A), and large, blue ascidians (AS). OFOS track 21891-1C, 1008 m water depth. Pictures from HENRICH et al. (1992)

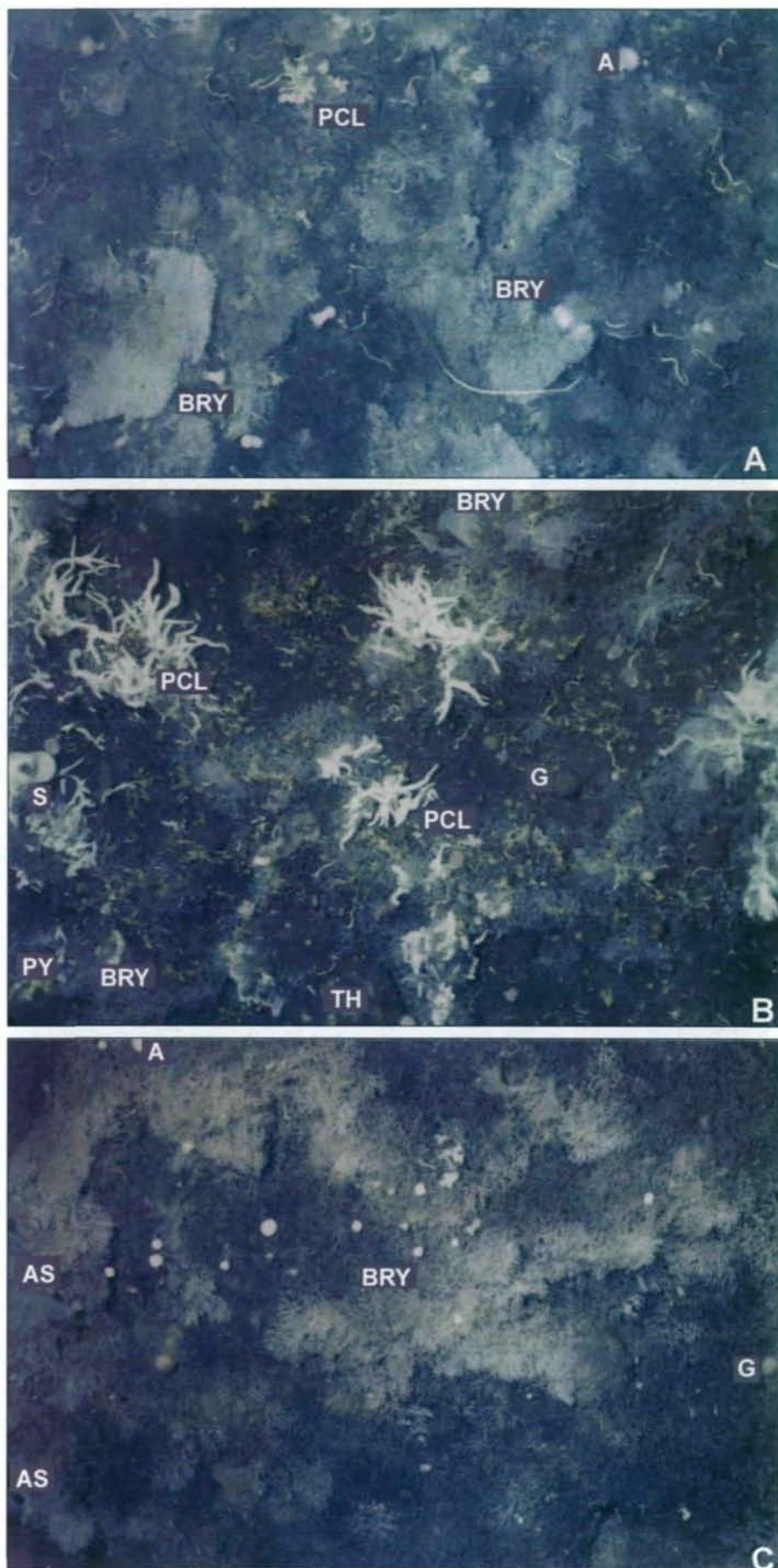




Fig. 11: Bryozoan taxa from Seamount Vesterisbanken. **A:** *Idmidronea atlantica* var. *gracillima* (BUSK), x 25. **B:** *Diplosolen intricarius* (SMITH), x 60. **C:** *Tubulipora* sp., x 35. **D:** *Hornera lichenoides* (LINNAEUS), x 25. **E:** Tubuliporid cyclostome, 25 x. **F:** *Crisia* sp., x 24. **G:** *Notoplites normanni* (NORDGAARD), x 50. **H:** *Palmicellaria skenei* (ELLIS & SOLANDER), x 80. **I:** *Tessaradoma gracile* (SARS), x 60. **J:** *Tricellaria gracilis* (VAN BEX NEDEN), x 95. **K:** *Sertella elongata* (SMITT), x 129. **L:** ?*Megapora rigens* (BUSK), x 129. **M:** *Cribrilina watersi* (ANDERSON), x 90. **N:** *Smittina glaciata* (WATERS), x 60. **O:** *Schizoporella porifera* (SMITT), x 120. 73°31'N, 09°11'W, 235 m water depth.

Bryozoans at Vesterisbanken show at least 21 taxa (Fig. 11) and display significant differences to those found on the eastern Arctic/subarctic shelves of the Nordic Seas. The lack of turbulence in the water and competition for food is supposed to be the major factor that causes the predominance of species with erect colony growth. In contrast, competition for space is distinctly reduced because of preferred upward growth of species that creates additional habitats and ecological niches.

Differences in faunal character depict influence of high-Arctic and a subordinate influence of Arctic water masses over the seamount (SCHÄFER 1994). In addition, some deep-water species occur. This results from the position of the submarine volcano within the Arctic water masses in an area in which Atlantic water impinges into the Arctic Current. Erect-growing species with upright-dendroid colony growth forms are *Idmidronea atlantica* (Fig. 11A), *Hornera lichenoides* (Fig. 11D), *Palmicellaria skenei* (Fig. 11H), *Porella plana*, *P. compressa*, *Myriapora subgracilis*, and *Tessaradoma gracile* (Fig. 11I). Species with reticulate growth are *Diplosolen intricarius* (Fig. 11B), *Sertella elongata* (Fig. 11K), and *S. beaniana*. In addition, *Notoplites normanni* (Fig. 11G), *Tricellaria gracilis* (Fig. 11J), and *Crisia* sp. (Fig. 11F), grow as weakly calcified, articulate colonies. Less frequent than erect-growing taxa are species with encrusting zoarial growth forms such as *Megapora rigens* (Fig. 11L), *Cribrilina watersi* (Fig. 11M), *Smittina glaciata* (Fig. 11N), *Schizoporella porifera* (Fig. 11O), *S. thomsoni*, and *Disporella* sp.

Preference of taxa with upright-dendroid often weakly calcified colonies is considered related mainly to the hydrographic position and topography. The seamount is characterised by hard substrates (lava rock and debris flows) down to considerable water depth and by extremely low sediment input in contrast to continental shelf conditions with partly strong terrigenous input. Bryozoan taxa with erect growth forms occur with striking diversity and abundance at Vesterisbanken in contrast to eastern shelves of the Nordic Seas with a dominance of encrusting species at all water depths. Judged from the volumetric dominance of species that either possess weakly calcified or articulate colonies, or erect rigid-articulate and fenestrate colonies, medium current velocity occurs at the seamount. *Palmicellaria skenei* is the most abundant species that contributes to the formation of skeletal carbonate at Vesterisbanken. Heavily corroded and iron-stained skeletal fragments indicate times of non-deposition and erosion on the sea floor.

3.1.6 Deep water coral reefs

In contrast to bryozoan-mollusc communities that grow within the well-mixed water masses above the summer thermocline on open, sub-Arctic shelves, deep-water coral reefs seem to be confined to open oceanic waters below the mixed water masses at the shelf slope. Along the Norwegian coast, such coral reefs occur in two different topographic settings: open shelf and fjords. One larger reef tract is positioned on the mid-shelf off Trondheim, Norway, in 250 to 320 m water depth and 80 km off-shore. Geometry of the reef is largely confined by the topography of a spur of Palaeocene sandstone underlying the reef (HENRICH et al. 1995; FREIWALD et al. 1997).

The reef framework is made by the deep-water scleractinian *Lophelia pertusa*, accompanied by *Madrepora oculata* and the octocoral *Primnoa resedaeformis* (Fig. 12A). The coral framework serves as a substrate for a moderately abundant and diverse bryozoan-sponge community (Fig. 12B, C). Encrusting cheilostomes such as *Escharella laqueata*, *E. octodentata*, *E. abyssicola*, *Hemicyclopora polita* and encrusting cyclostomes like small



colonies of *Disporella* sp. dominate; they are associated with upright-branching species like *Homera lichenoides*, *Idmidronea atlantica*, and the fenestrate *Sertella septentrionalis*. Despite the high northern latitude close to the Polar Circle the bryozoan fauna reveals a number of boreal Atlantic and Mediterranean elements indicating influence of Mediterranean water masses following the European continental slope and impinging in fjord troughs onto the Norwegian shelf.

3.2. Antarctic communities

3.2.1 Hydrography

The Southern Ocean is mostly a well-mixed, deep-water upwelling system. Its shelves are narrow and deep. One of the largest shelf areas around the Antarctic continent is found in the southern part of the Weddell Sea. The Weddell Sea is a well-defined, semi-enclosed system bordered by ice shelves on three sides and occupied by a large cyclonic gyre of the East Wind Drift in the centre and a coastal current along the shelf. The hydrography of the eastern shelf of the Weddell Sea is mainly influenced by the Weddell Sea gyre, a region of both permanent and seasonal ice cover fed by the Antarctic Coastal Current. Open water is present at most for about 3 months/year. In certain areas katabatic winds lead to seasonal formation of coastal polynyas, which vary in extent and position between the years. Along the eastern shelf, the Antarctic Coastal Current streams in a southwesterly direction but shows a considerably high short-term variability. Maxima in current speed along the eastern shelf can be assumed to be as high as 50 cm s^{-1} (BATHMANN et al. 1991).

Water temperatures on the eastern Weddell Sea shelf do not show pronounced seasonal variations. Measurements in 1989/1990 at -600 m depth off Kapp Norve-

Fig. 12: **A:** Underwater photograph (scale = 1 m^2) of deep-water coral *Lophelia pertusa* from North Norway. **B:** Colony of *Lophelia pertusa*. Scale bar = 2 cm. **C:** Encrusting bryozoans (*Escharella* spp.) on *Lophelia pertusa*. Scale bar = 2 cm. Picture A courtesy of A. Freiwald (Institute of Paleontology, University Erlangen).

gia, however, indicate short-term (days to weeks) temperature variations between +0.4 and -1.8 °C caused by "deep warm water" intrusions from the Weddell Sea on to the shelf (ARNTZ et al. 1992).

The eastern Weddell Sea, close to the shelf ice edge off Coats Land exhibits a rather high primary production with surprisingly high values for the Antarctic region (EL-SAYED 1971; BRÖCKEL 1985). Differences within primary production values in the Weddell Sea, as well as different phytoplankton populations are most probably due to differences in oceanographic situations such as the marginal zone, the closed pack-ice zone, and open polynyias.

3.2.2 Eastern shelf of the Weddell Sea

The southeastern Weddell Sea differs from other Antarctic areas as it has no shallow areas. The ice edge usually prevents work in areas shallower than 200 m, and even in the inlets the sea-floor is usually several hundred metres deep. The continental shelf in the southeastern Weddell Sea is relatively narrow and reaches depths of 300-500 m (CARMACK & FOSTER 1977). The surface sediments consist of silt and coarse sand, to gravel with isolated larger pebbles (ice rafted debris) and a thick layer of fragmented skeletal carbonate on the sediment surface. Faunistically, the parts of the benthos and fish fauna of the Weddell Sea are well known (VOB 1988; BARTHEL & GUTT 1992, 1994). A detailed community analysis has been published by VOB (1988), who separated three different communities (Fig. 13). The eastern shelf community is rich in suspension feeders, mainly sponges and bryozoans. Bryozoans are the principal component of the southern shelf community, whilst holothurians dominate the southern trench.

Bryozoans are almost ubiquitous in the Weddell Sea, they have been found to be extremely abundant on both hard and soft substrata (Fig. 14). In the last ten years a lot of taxonomic work was done on bryozoans in the Weddell Sea. Till now 156 species were identified, which is nearly half of the known Antarctic cheilostome bryozoans. This verifies the assumption of HAYWARD (1995) that all Antarctic bryozoans have a



Fig. 13: Major macrobenthic assemblages on the eastern and southern Weddell Sea shelf and slope. Orange: Eastern shelf community: mainly sponges and bryozoans, high number of species and high diversity, yellow: Southern shelf community: mainly bryozoans, high number of species and low diversity, brown: Southern trench community: mainly holothurians, lower number of species and diversity. After VOB (1988) and GALERON et al. (1992).

circum-Antarctic distribution. Four bryozoogeographical zones are recognised in Antarctic waters: East Antarctic seas, West Antarctic seas, the Antarctic Peninsula und Scotia Arc (BARNES & DE GRAVE 2000). Based on statistic analysis of all known cheilostome species for the southern polar region or the area south of 47° the species revealed two homogenous site groupings, corresponding to an Antarctic and a Magellanic group, and a third much more heterogeneous Subantarctic Island group. Ordination of just the Antarctic grouping shows that the Weddell Sea occupies an extremely isolated position (BARNES & DE GRAVE 2000).

Among bryozoans of the Weddell Sea diversity of skeletal morphology is large (Fig. 15). All growth forms are present: encrusting sheets (e.g. *Escharella watersi*), erect flexible (e.g. *Cellaria incula*), erect rigid (e.g. *Cellarinella nodulosa*), erect unilaminar (e.g. *Smittoidea malleata*), and erect bilaminar (e.g. *Isoschizoporella secunda*) colonies. Erect cheilostomate taxa predominate within the bryozoan fauna (Fig. 15). The same pattern was reported by WINSTON & HEIMBERG (1988) from Low Island (South Shetland Is-

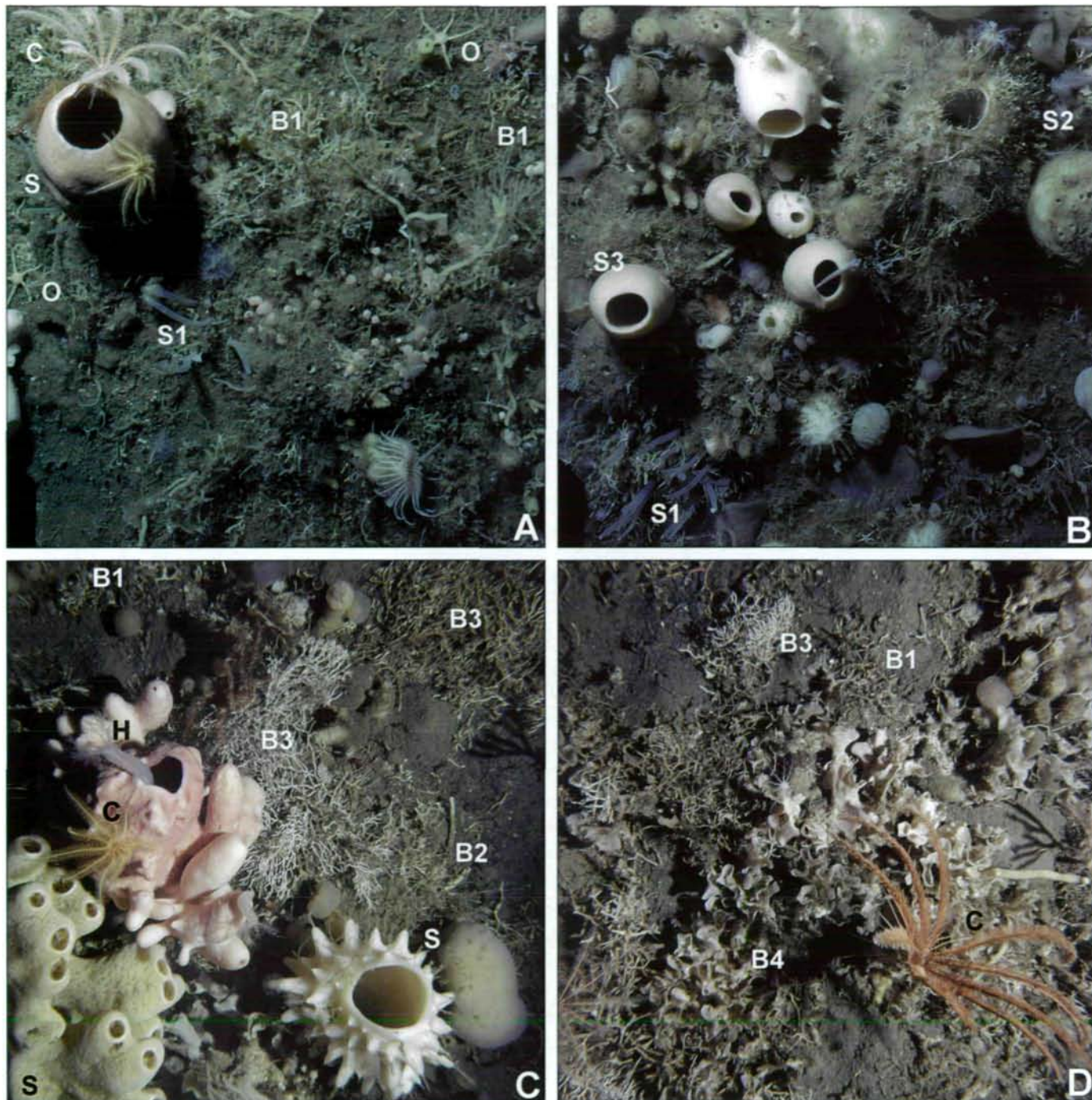


Fig. 14: Underwater photographs (scale = 1 m²) of Kapp Norvegia communities from the Weddell Sea, Antarctica taken during Polarstern cruise ANT XIII/3 and XV/3. Areas with a rich and diverse epibenthic assemblage **A:** Seafloor covered by sponges (S) (*Monosyringia longispina* (translucent siphons of the infaunal demosponge) (S1)), crinoids (C), ophiuroids (O) and erect, rigid bryozoans (*Cellerinella* sp.) (B1). 71°15'S, 13°08'W, 150 m water depth. **B:** Seafloor covered mainly by sponges (*Monosyringia longispina* (S1), *Rossella racovitzae* (S2), *Tetilla leptoderma* (S3)). 71°15'S, 13°08'W, 150 m water depth. **C:** Seafloor covered by sponges (S), crinoids (C), holothurians (H) and erect, rigid bryozoans (*Cellerinella* sp. (B1), *Melicerita obliqua* (B2)) and erect bryozoans (B3). 71°31'S, 13°30'W, 230 m water depth. **D:** Seafloor mainly covered by erect, rigid bryozoans (*Cellerinella* sp.) (B1), erect bryozoans (B3) and erect, unilaminar bryozoan (*Smittoidea malleata*) (B4). 71°31'S, 13°30'W, 230 m water depth. Pictures courtesy of J. Gutt (AWI, Bremerhaven).

lands) and by BARNES (1995a) from Signy Island (North Weddell Sea).

The surface sediments on the Weddell Sea shelf consist of soft bottom with varying proportions of mud, sand, gravel, and boulders; distribution patterns can be regarded as considerably heterogeneous (GERDES et al. 1992). Coarser sediment particles like sand grains allow larger, weakly calcified bryozoan species with roots to settle. Large colonies with rooted, rigid growth forms are dominant in areas with fine sediment and

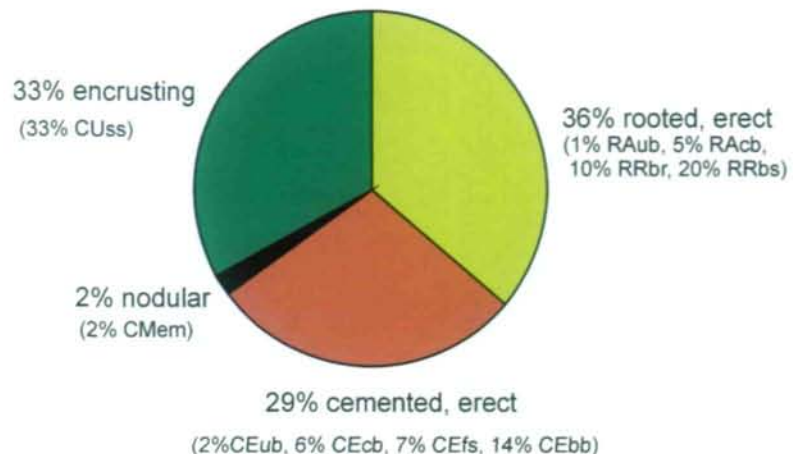
pebbles (Fig. 16A-D), which are almost completely covered by sediment. If stones are only partially covered by sediment, small, rigid colonies with a laminar growth form and small, encrusting species can settle. In pebbled areas large, rigid colonies with an encrusting base (Fig. 16E-H) dominate while rooted species are seldom.

3.2.3 Iceberg scours

Ice disturbance is regarded as a common event in the evolutionary history of Antarctic benthos (GROBE & MACKENSEN 1992; ZACHOS et al. 2001) and among the more important factors structuring these communities (ARNTZ et al. 1994; PECK et al. 1999; GUTT 2000). The major disturbance acting on the benthos of the deep continental shelves is the grounding and scouring of icebergs (GUTT et al. 1996, GUTT & STARMANS 2001; GERDES et al. 2003). They severely damage large areas of the seafloor, affecting the physical and biological environment by removing both hard and soft substrates and eradicating benthic life.

Apparent irregularities in the benthic structure West of Kapp Norvegia were identified as iceberg scour marks. They are indicated by an abrupt change in the epibenthic structure. Analysis of an underwater photo transect in 230 m water depth showed a changing gradient of colonisation: (1) areas with a poor benthic cover, and (2) areas with a high cover of epibenthic species (Fig. 17). In these communities either ascidians or bryozoans and sponges dominate. A first stage of recolonisation is defined by displaying a poor fauna composed of different taxa, or being dominated by one or two highly abundant pioneer species. In the poor covered areas, ascidians dominate the sessile benthos community with a high abundance. Among bryozoans only a few species occur; *Cellarinella* spp. and *Melicerita obliqua* being characteristic (Fig. 17B). Areas with high bryozoan cover represent a later stage of succession. At this later stage erect, flexible and erect, rigid colonies such as *Cellarinella* spp., *Melicerita obliqua* and *Cellaria* spp. are common; these are mostly species with roots (Fig. 17A). *Cellaria* sp. is a typical pioneer species in shelf areas disturbed by iceberg grounding (GUTT et al. 1996). However, ar-

Growth forms of bryozoans off Kapp Norvegia



eas with a high cover of bryozoans do not portray a mature and diverse community, which consists mostly of sessile suspension feeders such as gorgonarians, ascidians and ophiuriids (STARMANS 1997).

3.3 Bioprovinces and endemism of polar bryozoans

On Nordic Sea shelves, Arctic (48.2 %) and boreal species (41.9 %) dominate largest parts of the bryozoan fauna. In contrast Atlantic species (19.3 %), Pacific species (3.9 %), species of the Bering Sea (0.6 %) and endemic species (4.3 %) contribute with minor species richness. Distinct differences in species composition exist between the different regions of the Nordic Seas. Thus, shelves influenced by Atlantic waters display more species of Atlantic-boreal distribution, whereas faunas of polar water masses in the Greenland Sea, the East Greenland Shelf, the Vesterisbanken Seamount, as well as northern and eastern regions of the Spitsbergen- and Barents Shelf are dominated by Arctic and circumpolar species.

Compared to Nordic Sea cheilostome bryozoans, those of Antarctica reveal a distinct pattern of endemism (Fig. 18). While only 4 % of bryozoan species are endemic in Arctic waters, 90 % of bryozoan species in Antarctic waters are endemic. Comparison of genera revealed a very small correspondence of genera occurring simultaneously in Arctic and Antarctic waters. Whereas 21 % of Arctic cheilostome genera also occur in

Fig. 15: Growth forms of bryozoan species in the Weddell Sea after HAGEMAN et al. (1997). Rooted, articulated, unilaminar branches (RAub), Rooted, rigid, bilaminar sheet (RRbs), Rooted, articulated, cylindrical branches (RAcb), Rooted, rigid, bilaminar branches (RRbr), Cemented, erect, bilaminar branches (CEbb), Cemented, unilaminar, solid substrate (CUss), Cemented, erect, cylindrical branches (CEcb), Cemented, erect, unilaminar sheet (CEub), Cemented, multilaminar, encrusting massive (CMem), Cemented, erect, fenestrate sheet (CEfs).

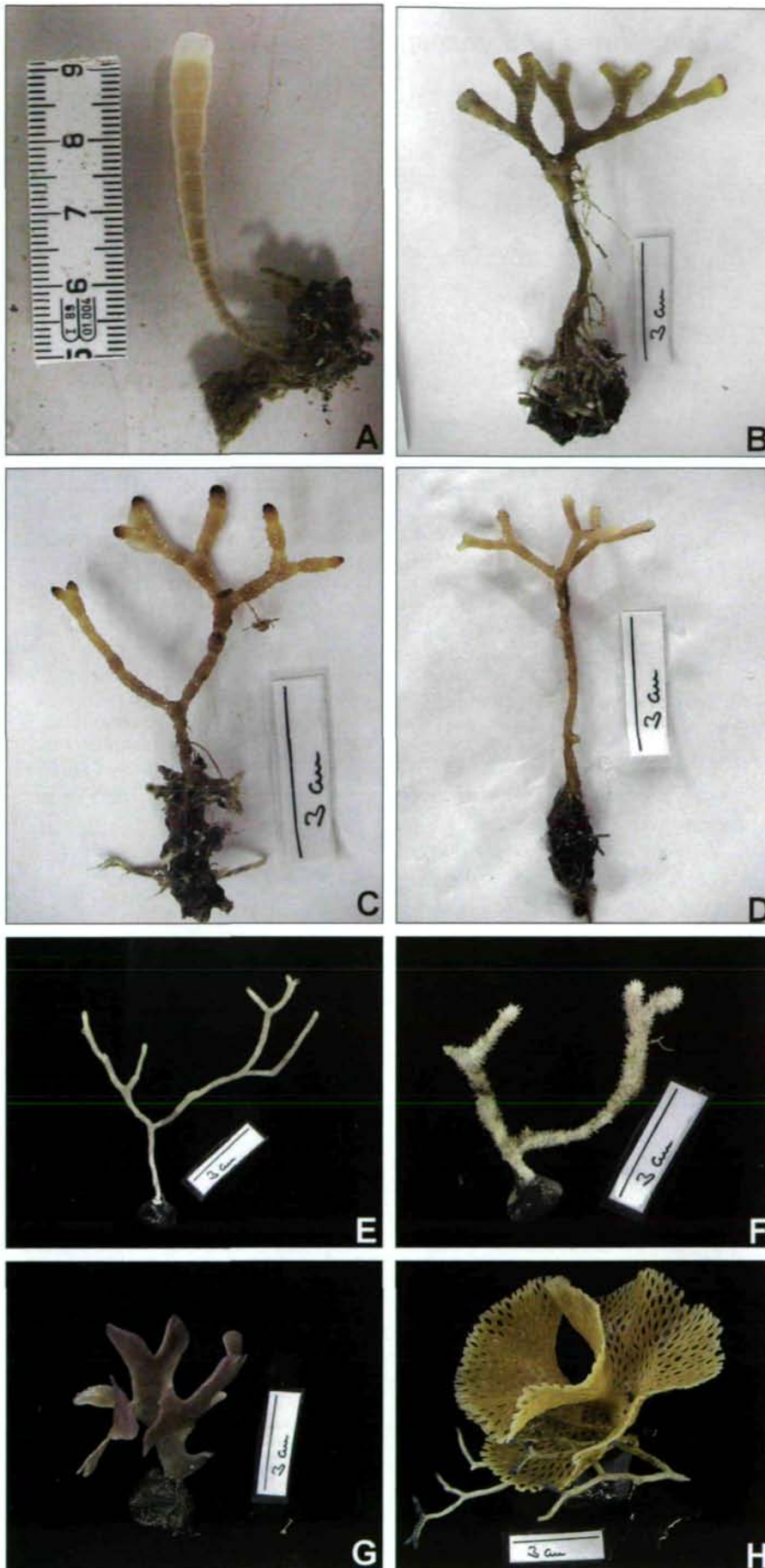


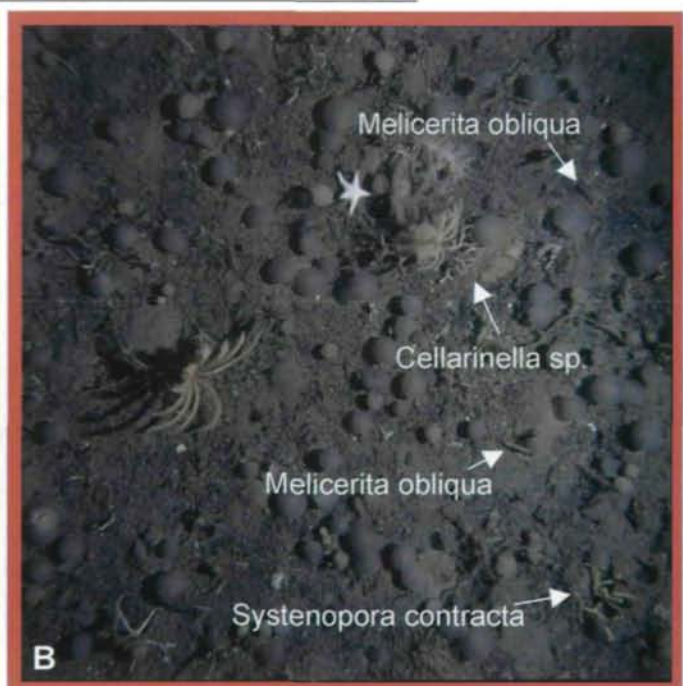
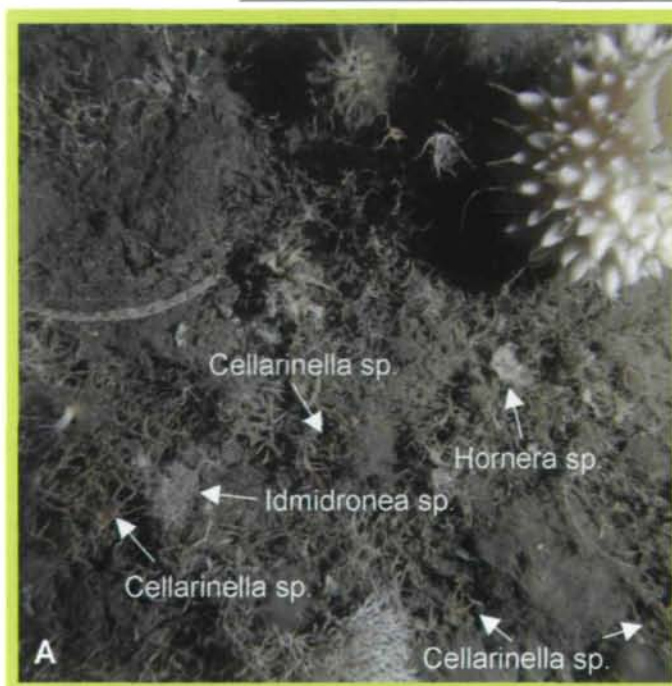
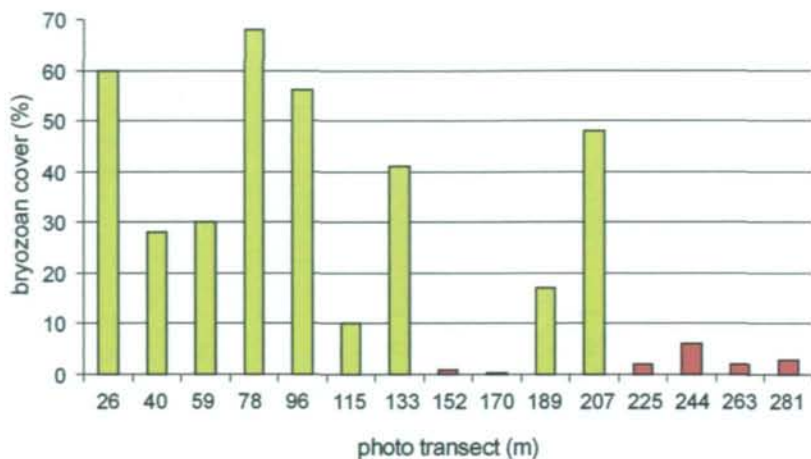
Fig. 16: Bryozoan taxa from the Weddell Sea. **A:** *Melicerita obliqua* (THORNELY). **B:** *Systemopora contracta* (WATERS). **C:** *Cellarinella laytoni* (ROGICK). **D:** *Swanomia membranacea* (THORNELY). **E:** *Cellarinella faveolata* (WATERS). **F:** *Orthoporida stenorhyncha* (MOYANO). **G:** *Smittina antarctica* (WATERS). **H:** *Reteporella* sp.

Antarctic waters, only 12 % of Antarctic genera were also reported from Arctic waters. Bipolar species do not exist.

Bipolar genera occur at least in one of the two regions with larger species numbers (>4 species), rarely also in both regions. Cheilostome genera with many species in both regions are *Amphiblestrum*, *Notoplites*, and *Smittina*. The Nordic Seas region is characterised by 27 species-rich genera in contrast to Antarctic waters with only 19 species-rich genera. The high degree of endemism in Antarctic waters results especially from the high number of genera represented by only one or a few species.

Among the 27 species-rich cheilostome genera (>4 species) in Nordic waters only *Amphiblestrum*, *Notoplites*, and *Smittina* do also occur in Antarctic waters. Genera with more than 10 species are *Cellepora*, *Dendrobeatia*, *Escharella*, *Porella*, *Rhamphostomella*, *Schizoporella*, *Smittina*, and *Tegella*. Only *Escharella* and *Smittina* are also present in Antarctic waters. Among species-rich genera in Antarctic waters, only *Camptoplites*, *Cellarinella*, and *Smittina* occur with > 10 species.

The higher percentage of cheilostome genera with higher species numbers but low number of genera in total and less endemism of Arctic bryozoan faunas compared to those of Antarctic waters correlates with a wider distribution of that genera. Arctic genera display a wider catchment area from the North Atlantic and North Pacific and sometimes are reported even from southern parts of those oceans. Species display a closer relationship to taxa from Tertiary epicontinental deposits of Europe and eastern North America.



In contrast, species-rich Antarctic genera are mostly restricted to the Southern Hemisphere and limited to the North to Patagonia, South Africa, Australia/New Zealand (*Cellarinella* spp., *Klugeflustra* spp., *Isochizoporella* spp.). Very often such species are only reported from the Recent and display a high degree of endemism (e.g. *Amastigia* spp., *Camptoplites* spp., *Cellarinella* spp.). Connections exist to taxa from Tertiary outcrops of South Australia (*Arachnopusia* spp.) or are reported from Cretaceous sediments in Europe and eastern North America (*Arachnopusia* spp., *Celleporella* spp., *Melicerita* spp., *Exochella* spp., *Fenestrulina* spp.). Some of the latter display a distribution of individual species as far as to

the North Atlantic and North Pacific. The hypothesis of bipolar distribution of bryozoan taxa can only be confirmed for the generic level but does not hold true for the species level.

3.4 Colony growth forms of polar bryozoans

Bryozoans with different colony growth forms are unequally distributed in the different Polar regions. Distinct differences in the abundance of species with different growth forms were found between the East Greenland shelf including the Belgica Bank, the Seamount Vesterisbanken, the Barents shelf and North Norwegian shelf. The East

Fig. 17: Underwater photograph transect (Antarctic, Weddell Sea, 71°31'S, 13°30'W, 230 m water depth, scale 1 m²). Abundance of bryozoans along the transect, each bar represents a photograph. Yellow bars indicate sections with diverse bryozoan assemblage. Red bars show a scour mark partly recolonised by bryozoans. **A:** Area adjacent to the iceberg scour showing a rich and diverse epibenthic assemblage which totally covered the sediment. **B:** Iceberg scour partly recolonised by bryozoans and ascidians, whereas ascidians dominate the epifauna. Picture courtesy of J. Gutt (AWI, Bremerhaven).

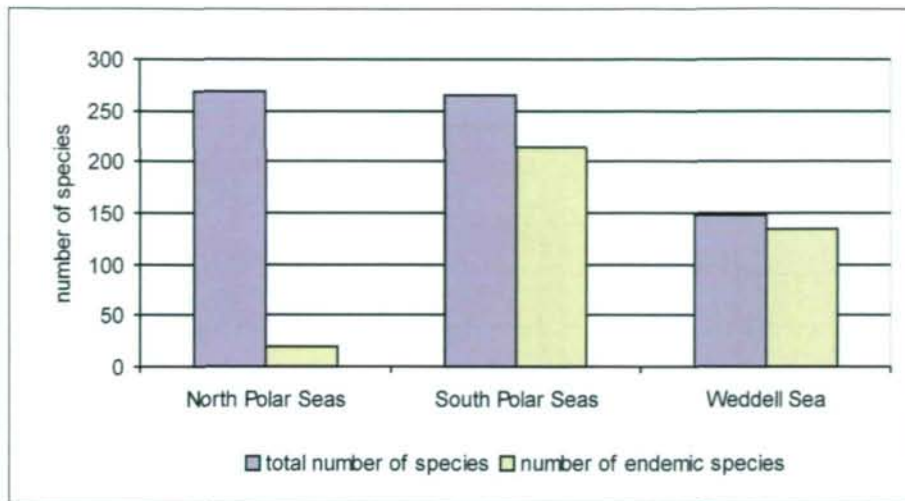


Fig. 18: Endemic distribution of polar cheilostome bryozoans.

Greenland shelf is dominated by unilaminar encrusting species followed in abundance by upright articulate, upright dendroid, robust branching and, less common, delicate branching species. In general, the same pattern is found on the Barents shelf, whereas the North Norwegian shelf shows an absolute dominance of unilaminar encrusting species. Largest differences display the Seamount Vesterisbanken being characterised by nearly the same abundance of the different growth forms except of a clear reduction of species with unilaminar encrusting growth. In this respect, the sea mount shows the highest degree of correspondence with the Antarctic Weddell Sea shelf the latter displaying >60 % taxa with erect colonies. Additional correspondence between the two regions is the presence of sponge needle mats being an ideal habitat for filigree branching colonies.

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