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Diversity Patterns of Modern Arctic and Antarctic Bryozoans

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ABSTRACT

A comparison of Arctic Sea and Antarctic Sea bryozoan faunas (cheilostomes) was conducted by compiling comprehensive data sets from both realms [1, 2] and own additional collections from the European Sector of the Arctic Realm. The analysis documents the high endemism in Antarctic faunas also indicated by the high species/genera relationship compared to the extremely reduced endemism in the Arctic Realm. These different patterns are explained by the long-lasting geographic isolation of the Antarctic continent due to tectonic break-up of the Gondwana continent in contrast to the Arctic Ocean, which since the Neogene became a transit system to promote migration of bryozoan species between the North Atlantic and North Pacific oceans. Cluster analysis was applied to identify the biogeographic regions within the two polar realms.

Keywords: Bryozoa, Arctic Realm, Antarctic Realm, Biodiversity, Biogeography

INTRODUCTION

Bryozoans are abundant constituents in modern Arctic and Antarctic marine communities. They occur on shallow and deep shelves, seamounts, mid-ocean ridges as well as along coastlines and in fjords. They occur in year-round ice-free or seasonally ice-covered habitats as well in polynyas. Arctic and Antarctic settings show similar trends in year-round low temperatures, irradiation and ice cover [3]. Nevertheless, 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 larger number of stenothermal species, while the remainder of the higher taxa are poorly represented on the Antarctic shelf [3].

The different geological histories of the Arctic and Antarctic Oceans help to explain the differences in evolutionary history of the benthos. While the Artic Ocean repeatedly held open connections to the North Pacific and the North Atlantic (16–12 Ma, opening of Fram Strait [4]; 5.5–4.8 opening of Bering Strait [5, 6]), Antarctica encountered a stepwise separation from the other Gondwana continents since 37 Ma (Eocene/Oligocene boundary) and a complete isolation from the mid Oligocene onward (30 Ma) [7]. Faunal exchange between North Atlantic and North Pacific faunas through the Arctic Ocean and its shelf seas on the one hand and long-time isolation of Antarctic shelf seas shaped the benthic faunas in the two polar realms.

The present study is a re-examination of published data from various sources with the focus on taxonomic and biogeographic aspects of polar bryozoan species. Some new data on European Nordic Sea faunas are included into the survey.

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RESEARCH METHODOLOGY

The present study was based mainly on a compilation of primary data obtained from monographs for the Arctic Realm [1] and the Antarctic Realm [2]. The compilation was concentrated on the Cheilostomata because of the same high quality of the compared data sets. Own fresh bryozoan material from the North Norwegian inner and outer shelf, the Barents shelf (Spitsbergen Bank), West Spitsbergen shelf and the Seamount Vesterisbanken (Central Greenland Sea) was included into the analysis.

Generic and species *alpha diversities* (= species richness) were used to describe the number of taxa in Arctic and Antarctic Realms, respectively. Sörensen similarity index [8] was calculated as a means of species diversity between ecosystems (realms) involving comparison of the number of taxa unique to each of the regions.

Cluster analysis was applied on the data sets compiled from [6] (Arctic Realm) and [7] (Antarctic Realm) using PAST from Microsoft with Ward's method as linkage and Euclidian distances to determine faunal patterns and biogeographic provinces. The Arctic Realm includes 285 species (vertical axis) and nine regions (horizontal axis) with the North Atlantic region (A), Barents Sea (B), White Sea (C), Kara Sea (D), Laptev Sea (E), East Siberian Sea (F), Chukotsk Sea (G), American Sector (H) and North Pacific Region (I). For the Antarctic Realm, a data set with 265 species at 40 stations around the continent including shelves, Antarctic Peninsula and islands/islands groups was clustered. A second cluster analysis was performed for the Antarctic Realm (same species) on a selected set of 4 stations including Weddell Sea (A), Ross Sea (B), Bellinghausen Sea (C) and South Shetland Islands (D) because of the extremely biased data sets with respect of species numbers per station.

RESULTS

Diversity

Arctic Realm

Two hundred and eighty five cheilostome species belonging to 75 genera were compiled for Arctic waters. Composition and diversity of taxa vary between different environments within the European Sector and depend on the type of environment (shelf, deep sea, submarine rises such as mid-ocean ridges or volcanic seamounts; polynyas, seasonally ice covered or year-round ice-free). In the Greenland Sea, cheilostomes occur with 64 species distributed among 31 genera, whereas 52 species are found on the West Spitsbergen shelf distributed among 26 genera [9]. Number of species shared between the two regions is 24, number of genera is 17. The volcanic seamount Vesterisbanken, forming an isolated obstacle within the Central Greenland Sea provides firm substrate for 23 cheilostome species distributed among 16 genera [10]. In contrast to other sites, however, the cyclostomes show a considerable species richness (10). The North Norwegian Shelf, on the opposite, gives substrate for 60 species belonging to 35 genera. In addition to the open shelf, 35 cheilostome species (24 genera) were found on living valves of *Chlamys islandica* [11] collected from the inner shelf of northern Norway. The fauna displayed 12 species in common with the open shelf fauna (Sørensen similarity index = 0.29).

Antarctic Realm

The Antarctic Realm is equally diverse as is the Arctic Realm (265 species), however, generic diversity (99 genera) is nearly twice as high as in the Arctic region. Major problems involved in faunistic analysis result from the fact that the Antarctic shelves are, with a few exceptions, far less studied than the Arctic Realm. Well documented are the Weddell Sea and the Ross Sea as well as the Antarctic Peninsula; all other shelf regions and isolated island groups are far less investigated. Therefore, compilation of data and comparison is concentrated on the Weddell Sea, the Ross Sea and the Antarctic Peninsula (Palmer Land, South Shetland Islands). 158 species (66 genera) were counted in the Weddell Sea, 138 species (65 genera) in the Ross Sea with 101 species found in both. 61 species (40 genera) were documented from Palmer Land, 73 species (42 genera) with a Sørensen similarity index of 0.7 (Weddell Sea/Ross Sea), 0.38 (Weddell Sea/South Shetland Islands) and 0.34 (Ross Sea/South Shetland Islands).

Comparison of Arctic Realm and Antarctic Realm

Similarity between Arctic and Antarctic bryozoans was 0.11 (generic level) and 0.00 (species level) indicating very low similarity on generic level, whereas no similarity exists on species level. Number of species within Arctic genera ranged from 1–21 with a mean = 4.32 species/genus (median = 3; stand. dev. = 4.48; var. = 20.11). Number of species within Antarctic genera ranges from 1–15 with a mean = 2.626 (median = 1; stand. dev. = 2.855) (Table 1).

Table 1 Richness of species and genera and number of species per genus including statistic indices (mean, median, standard deviation, curtosis and skewness).

	Number of species	Number of genera	Species per genus	mean	median	stand dev.	curtosis	skewness
Arctic Realm	285	75	1 to 21	4.32	3	4.48	3.47	1.84
Antarctic Realm	265	99	1 to 15	2.62	1	2.85	5.28	2.31

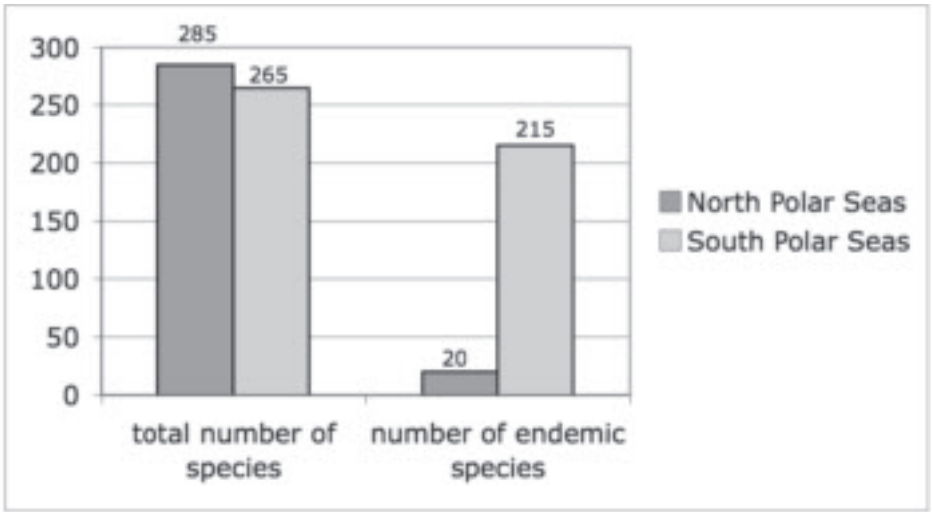

Fig. 1 Total number of cheilostome species versus number of endemic species for the North Polar Seas and South Polar Seas.

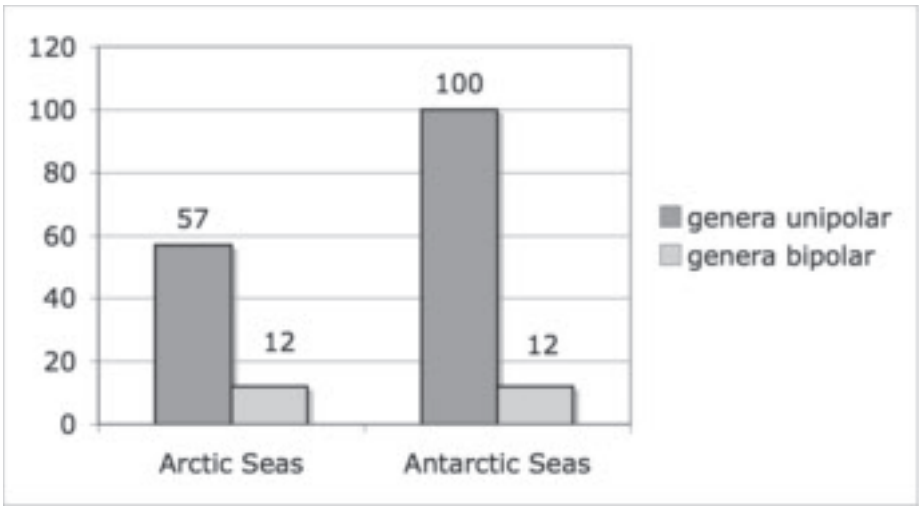

Fig. 2 Comparison of unipolar and bipolar genera in Arctic and Antarctic Seas.

Endemism

Antarctic cheilostome bryozoans reveal a pronounced pattern of endemism compared to cheilostome bryozoans of the Nordic Seas (Fig. 1). 90% of Antarctic cheilostome species are endemic compared to only 4% species in Arctic waters.

Comparison of genera revealed a very small percentage of genera, which occur both in Arctic and Antarctic waters. Whereas 21% of Arctic cheilostome genera also occur in Antarctic waters, only 12% were also reported from Arctic waters. Bipolar species occurring both in Arctic and Antarctic wa-

ters do not exist (Fig. 2).

Bipolar genera occur at least in one of the regions, either Arctic or Antarctic waters, with more than four species, rarely also in both regions. Cheilostome genera with many species in both regions are *Amphiblestrum*, *Notoplites*, and *Smittina*. Arctic waters house 27 species-rich genera (> 4 species), whereas Antarctic waters are known with only 19 species-rich genera.

Amphiblestrum, *Notoplites* and *Smittina* are the only species-rich genera in Arctic waters, which also occur in the Antarctic realm. Arctic genera with > 10 species are *Cellepora*, *Dendrobeania*, *Escharella*, *Porella*, *Rhamphostomella*, *Schizoporella*, *Smittina*, and *Tegella*. Of those only *Escharella* (2 species) and *Smittina* (13 species) are also present in Antarctic waters. Antarctic genera with > 10 species are *Camptoplites*, *Cellarinella* and *Smittina*.

Zoogeography

The higher percentage of Arctic cheilostome genera with higher species numbers but low number of genera in total and less endemism corresponds with a wider distribution of those genera. Many of the Arctic genera are distributed into the North Atlantic and/or North Pacific and sometimes occur even into the southern parts of those oceans.

Species-rich (> 4 species) Antarctic genera are mostly restricted to the Southern Hemisphere and limited to the North to Patagonia, South Africa and Australia/New Zealand (*Cellarinella* spp., *Klugeflustra* spp., *Isoschizoporella* spp.). Very often such species display a high degree of endemism (*Amastigia* spp., *Camptoplites* spp., *Cellarinella* spp.).

Arctic Realm

Cluster analysis based on the distribution of 284 species and nine regions displays 9 individual clusters of which clusters ARK-1 to ARK-5 form one cluster group (ARK-I), whereas clusters ARK-6 to ARK-9 from a second cluster group (ARK-II) (Fig. 3).

Within ARK-I, cluster ARK-1 (10 species) holds closest connections to the North Pacific Ocean. ARK-1 is dominated by Chukotsk species (100%) found also in the North Pacific (90%), the Laptev Sea (80%) and East Siberian Sea (70). ARK-2 to ARK-5 represents clusters with a much wider distribution of species included. ARK-2 and ARK-3 are species-rich clusters, whereas both ARK-4 and ARK-5 include a distinctly smaller number of species. All clusters show a dominance of Barents Sea species (100%). ARK-2 (45 species) is further characterized by species described from the White Sea, North Pacific and American Sector (all 97.7%). ARK-3 (47 species) shows an equal percentage of Barents Sea and North Atlantic species (both 100%), followed by the Kara Sea and American Sector (97.8%), North Pacific (93.6%) and American Sec-

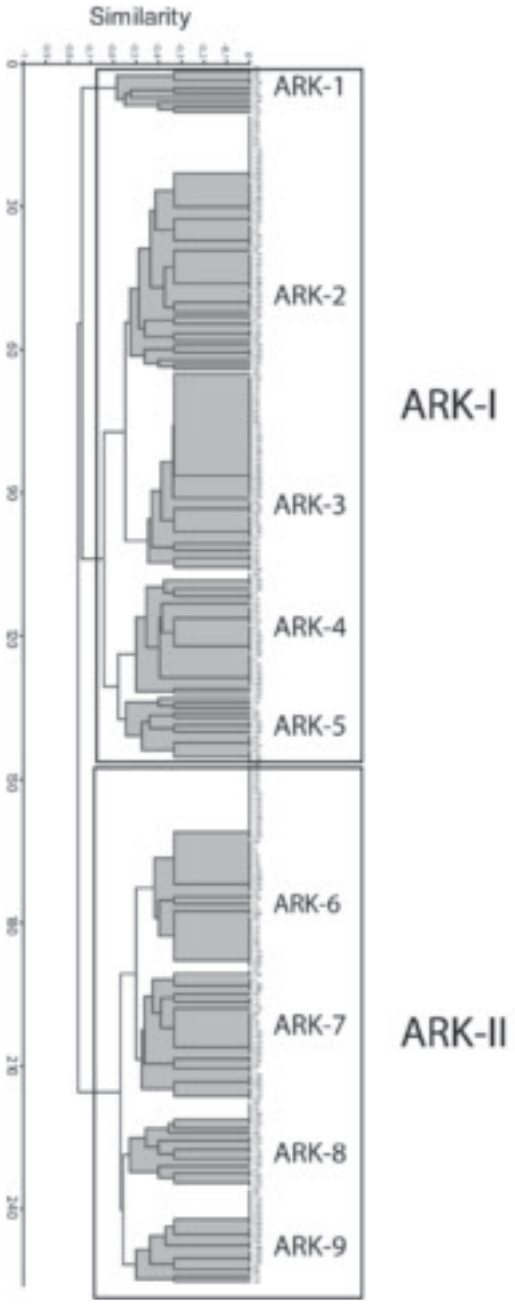

Fig. 3 Cluster dendrogram (Ward's method, Euclidian distance) for bryozoan occurrences in North Polar Seas (284 species, 9 regions). The dendrogram distinguishes two cluster groups (ARK-I and ARK-II) each with 5 and 4 individual clusters, respectively.

tor (91.4%). Barents Sea and Kara Sea contribute with 100% species (24 species) to ARK-4, followed by the American Sector (75%) and East Siberian Sea (58%). In ARK-5 (16 species), the fauna is characterized by species found in the Barents Sea (100%), Kara Sea (93.7%), American Sector (81.2%) and North Atlantic (68.7%).

ARK-II includes 4 clusters (ARK-6 to ARK 9), of which ARK-6 (42 species) and ARK-7 (31 species) are characterized by a larger number of species reported from the Atlantic (64.2% and 74.1%, respectively). While ARK-6 is dominated by species found in the Barents Sea (73.8%), ARK-7 reveals a dominance of species (100%) in the American Sector. ARK-8 (15 species) includes species found all along the Siberian shelf (East Siberian Sea: 46.6%; Laptev Sea and Barents Shelf: both 26.6%). The two species described from the North Atlantic do also occur in the East Siberian Sea. ARK-9 (19) displays 100% North Pacific species of which 26.3% are reported also from the Chukotsk Sea. Interestingly, 36.8% of the North Pacific species do also occur in the American Sector and 26.3% in the North Atlantic.

Compilation of fauna of bryozoan species of the Nordic Realm given in Ref. 10 revealed that the deep Greenland Sea contains 100% Arctic-circumpolar species, whereas the Norwegian Sea contains equal number (50%) of Arctic-circumpolar and Arctic-Eurasian species (based on few literature data; Gontar, pers. com.). The East Greenland shelf shows a dominance of Arctic-circumpolar species (41%), while the remaining 59% are distributed among Arctic-circumpolar (22.9%), boreal-Arctic, Pacific-circumpolar species (11.9%) and boreal-Arctic, Atlantic, circumpolar species (9.4%). The Norwegian shelf shows 43.7% boreal-Arctic species comparable to the East Greenland shelf, however, relatively high are the percentages of boreal-Arctic, Pacific-circumpolar (17.9%) and Arctic-circumpolar species (12.3%) species. Data for the East Greenland and West Spitsbergen shelves provided by Kuklinski and Bader (2007) fit into the picture of Polar and Atlantic water masses, respectively, affecting the two sides of the European Sector of the Nordic Seas.

Adding the author's own data from the North Norwegian outer and inner shelves [12], the Seamount Vesterisbanken [13] and Spitsbergen Bank (Barents shelf) [14] (Fig. 4), one finds all regions to have a dominance of Arctic species with the exception of the outer Norwegian shelf, which is impinged by the Atlantic water masses of the Norwegian current. Second in abundance are Arctic-boreal species, whereas Arctic-Pacific and endemic species occur with low abundances. Comparing own data with those of [9], the Norwegian shelf is domi-

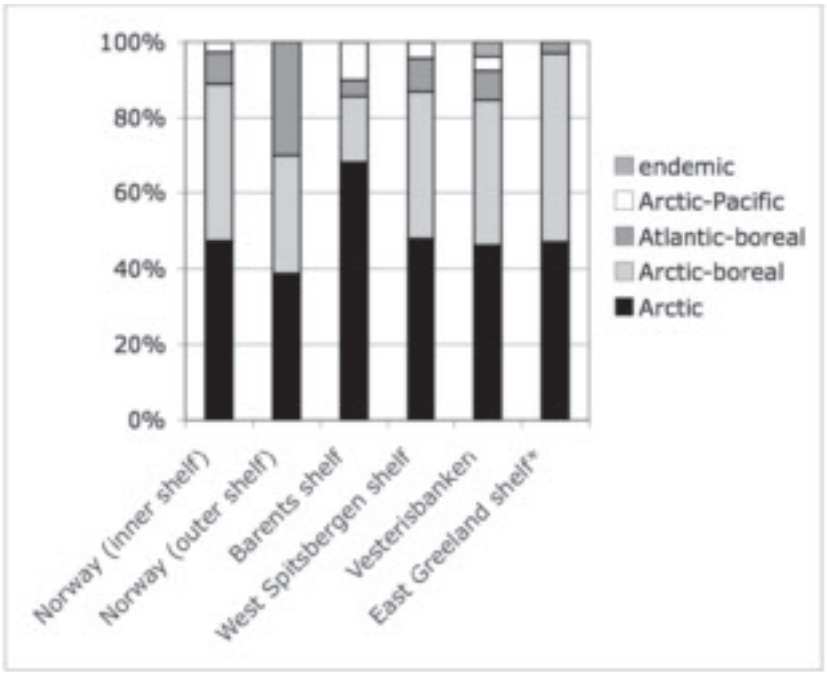

Fig. 4 Percentage of cheilostome species with biogeographic affiliation. The main regions of the European sector of the Arctic Realm are distinguished. Data for the East Greenland shelf were taken from [9].

nantly Atlantic whereas the Barents shelf is dominantly Arctic with a stronger influence of Arctic-Pacific elements. This is in contrast to the East Greenland shelf, from where no Pacific species are cited by Kluge [1]. Vesterisbanken Seamount is the only site with clearly endemic species.

Faunistic characterization and cluster analysis confirm that both the North Atlantic and North Pacific oceans have been refuges from where colonization of bryozoan species during the Holocene took place. A debate exists whether or not bryozoan species on Arctic shelves survived the severe mass extinction during the last glaciation event (Weichselian Glaciation). Distribution patterns suggest, however, that bryozoan species used several routes for migration along continental coasts after the shelf ice had finally retreated. One major route, certainly, is along the eastern European coast. It follows the Norwegian Current (high percentage of Atlantic-boreal species on the outer Norwegian shelf). Clusters ARK-2 to ARK-5, which are all characterized by a high percentage of Atlantic species (68.7-100%), hint at migration of Atlantic species even further eastward (Kara Sea, Laptev Sea and East Siberian Sea). This is in accordance with [15], in which the authors state a second important migration route for bivalve species along the eastern and western coasts of Greenland with one branch of dispersal further East into the Kara Sea, the second branch following westward along the North American shelf.

On the other hand, Pacific elements in the fauna of Vesterisbanken Seamount (own data) and the East Greenland shelf [9] support the hypothesis of migration of Pacific elements not only entering the Arctic realm and migrating along the North Siberian shelf. A second branch probably followed along the shelf of the American Sector (clusters ARK-3 and ARK-9) with some species migrating into the North Atlantic.

Antarctic Realm

Cluster analysis based on 265 species and 40 regions revealed a large number of clusters (ANT-1 to ANT-16) (Fig. 5) of which some clusters seem to contain a large number of sub-clusters (i.e. ANT-7 to ANT-11) whereas others include only a few species (as few as 2 species). This indicates the overall high degree of endemism, which results especially from the patchy distribution of individual species on isolated island groups.

A second cluster analysis based on 216 species and 4 regions (Weddell Sea, Ross Sea, Bellinghausen Sea and South Shetland Islands) revealed three main cluster groups, of which ANT-I and ANT-II

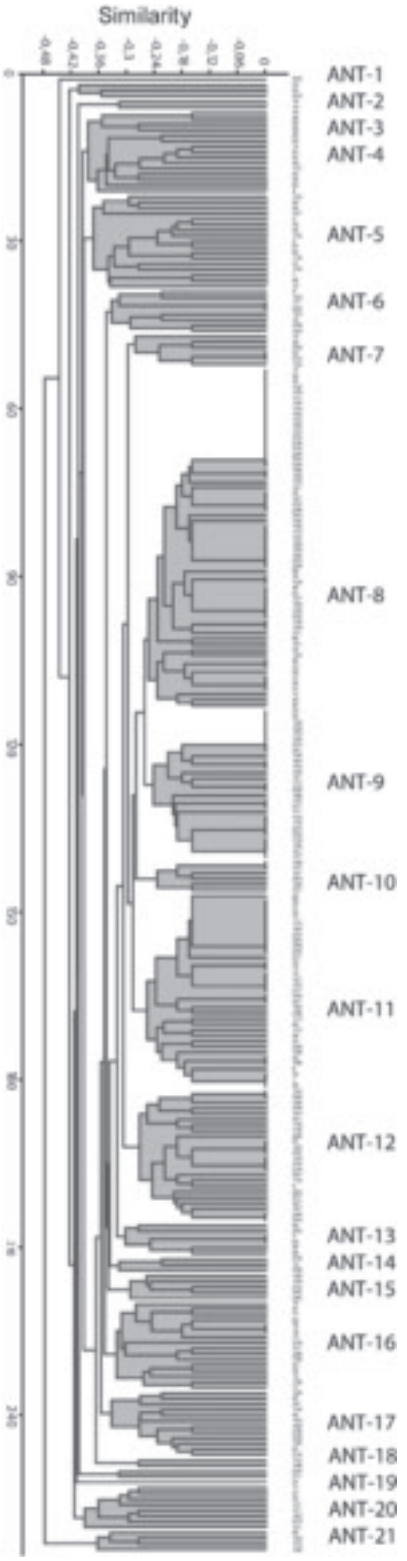

Fig. 5 Cluster dendrogram (Ward's method, Euclidian distance) for bryozoan occurrences in Antarctic waters (256 species, 40 regions). The large number of very small clusters correspond with the high degree of endemism among Antarctic species.

are grouped together whereas ANT-III is distinctly separated (Fig. 6). All clusters except ANT-4 are dominated by species reported from the Weddell Sea. ANT-1 shows a dominance of Weddell Sea species (61% and 62%) over the Ross Sea (55%), South Shetland Islands (31%) and Bellinghausen Sea (20%). ANT-1a and ANT-1b are distinguished by a distinctly higher percentage of species (12.5% versus 53%) found at South Shetland Islands in the latter cluster. ANT-2 (115 species) displays by far the highest percentage of species found in the Weddell Sea (71.6% to 85%). Ross Sea species are represented with 60% to 65% in the individual subcluster. Species from South Shetland Islands outnumber the species reported from Bellinghausen Sea (92.13 versus 19.1, mean values). ANT-III includes clusters ANT-4, ANT-5 and ANT-6 all characterized by a higher percentage of species recorded from the Ross Sea (53% to 80%) and from South Shetland Islands (62%).

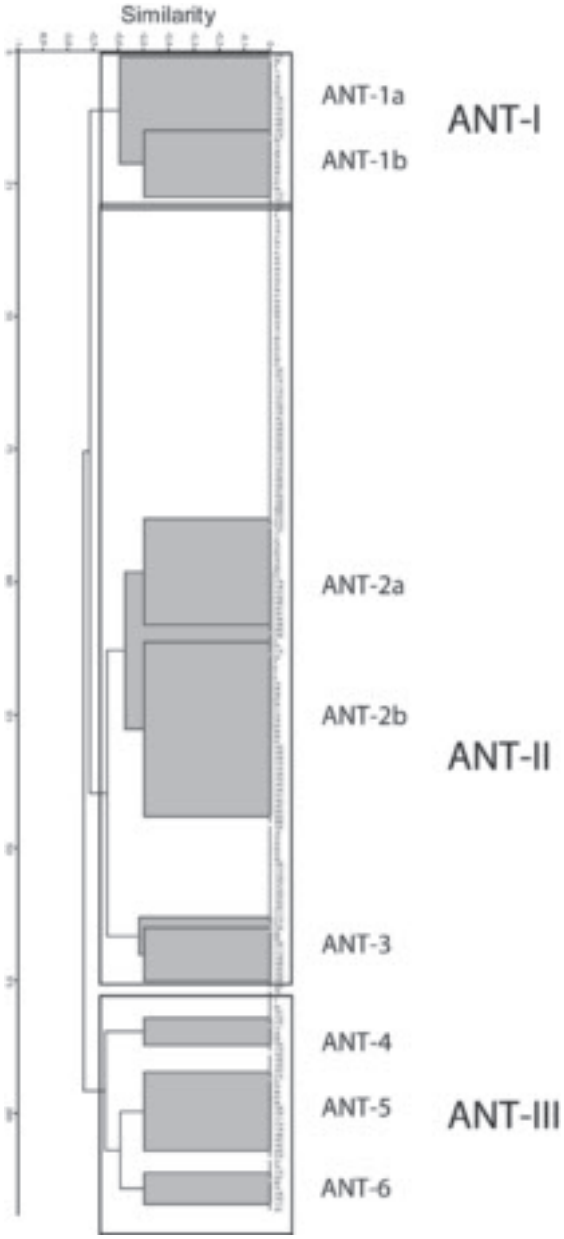

Fig. 6 Cluster dendrogram (Ward's method, Euclidian distance) for cheilostome bryozoan occurrences in selected Antarctic regions (Weddell Sea, Ross Sea, Bellinghausen Sea, South Shetland Islands) (216 species). The dendrogram includes 3 cluster groups (ANT-I, ANT-II and ANT-III).

Comparing similarity indices between the 4 regions (Table 2) highest similarity occurs between Weddell Sea and Ross Sea (0.68) followed by Weddell Sea/South Shetland Islands (0.38) and Ross Sea/South Shetland Islands (0.37). Lowest similarities occur between Ross Sea and Bellinghausen Sea (0.35) and Weddell Sea and Bellinghausen Sea (0.33). One possible explanation to the lower similarity between the Ross Sea and Bellinghausen Sea than the Ross Sea/South Shetland Islands would be the lower number of species reported from Bellinghausen Sea.

The dominance of Weddell Sea species in nearly all clusters corresponds with the findings of [2] that all Antarctic bryozoans are distributed around Antarctica. Statistical analysis of all known bryozoans for the southern polar ocean (South of 47°S) revealed two homogenous site groupings, corresponding to an Antarctic and a Magellanic group, and a third much more heterogenous Subantarctic Islands group [16]. As part of the Antarctic group, the Weddell Sea group is described to hold a very isolated position. Cluster analysis (Fig. 6) of the Antarctic group using four sites including Weddell Sea and South Shetland Islands (the latter holding closest connections to the Magellan group), however, does not seem to approve the findings by Barnes and De Grave (2000) [16] of an extremely isolated position of the Weddell Sea fauna. Comparing the number of species unique to one of the four regions, 17% were restricted to the Weddell, 9.4% to the Ross Sea, 9.3% to the Bellinghausen Sea, and 19% to the South Shetland Islands. Slightly increased endemism among Weddell Sea species combined with a higher similarity index (0.68) may be therefore explained also by higher total number of Weddell Sea species (158) compared to species richness in the Ross Sea (137 species). The higher percentage of species restricted to South Shetland Islands, however, may well be a hint towards a more separate grouping around Antarctic Peninsula as stated by [16].

Table 2 Similarity indices for co-occurring species in regions of the Arctic Realm and Antarctic Realm.

Arctic Realm	North Atlantic / North Pacific	Barents Sea / North Pacific	American Sector / North Pacific	American Sector / North Atlantic	North Atlantic / Barents Sea
Similarity Index	0.6	0.68	0.7	0.76	0.82

Antarctic Realm	Weddell Sea / Ross Sea	Weddell Sea/ Bellinghausen Sea	Weddell Sea / South Shetland Islands	Ross Sea / Bellinghausen Sea	Ross Sea/ South Shetland Islands
Similarity Index	0.68	0.33	0.38	0.35	0.37

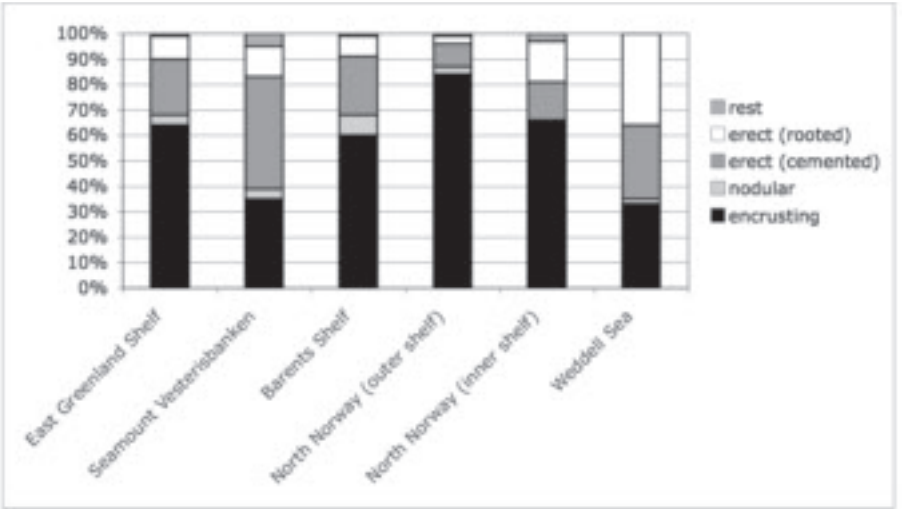

Fig. 7 Percentage of species with distinct colony growth forms in the different regions of the European Nordic Sea and the Weddell Sea. Data for Weddell Sea from [17].

Comparison of growth forms

Comparison of growth forms displays a clear dominance of encrusting species on all Nordic shelves (East Greenland, Barents Sea and North Norway), followed by species with erect cemented growth (Fig. 7). Erect rooted colony types are of minor importance on exposed shelves, however, they become more abundant in more protected regions of the inner shelf. The firm substrate of volcanic seamount Vesterisbanken in the central Greenland Sea holds a larger percentage of erect cemented than of encrusting species. The pattern found on Nordic shelves is distinctly different from Kapp Norvegia (Weddell Sea shelf), where erect rooted species become more abundant [17].

Reasons for the difference between the Nordic shelves and the Weddell Sea may be seen in the depth of sea floor. This is due to pronounced isostatic uplift of Nordic shelves in the Holocene resulting in the formation of gravel lag deposits [14, 18–19], in contrast to the Weddell Sea shelf mostly covered with fine-grained sediments but lacking hard bottom and post-glacial gravel deposits [17].

CONCLUSIONS

Compilation of Arctic Sea and Antarctic Sea cheilostome bryozoan faunas based on monographs [1–2] and my own additional collections from the European Sector of the Arctic Realm revealed that:

1. Species and genera are equally diverse (species richness) in the Arctic Realm. Most genera occur with high species numbers and are found widespread in a larger number of Arctic regions. Endemism is extremely low.

2. Species are equally diverse (species richness) in the Antarctic Realm, however, the number of genera is relatively low. This in one measure documents the high degree of endemism in the South Polar Region.

3. Low endemism and many genera with a large number of species in Arctic and adjacent waters mirror the role of the Arctic Ocean in connecting the North Pacific and North Atlantic Oceans since

the Miocene.

4. High endemism and the large number of genera with only one species in Antarctic waters refer to complete isolation of the Antarctic shelf seas since the mid Oligocene.

5. Arctic bryozoans depict a distribution pattern indicating a North Pacific/East Siberian, an Atlantic/Barents Sea/West Siberian and a North American/Atlantic/Pacific zoogeographic province. Highest species richness obtained in the Barents shelf indicates that this region receives species both from Siberia and the North Atlantic. The North American/Siberian (Laptev Sea) cluster refers to a possible migration route between the two regions as stated for bivalves [15].

6. In the Antarctic Realm, the high number of small clusters refers to the high degree of endemism. Endemism is highest around the large number of islands/island groups surrounding the Antarctic continent. The few larger clusters with a large number of small sub-clusters refer to a continuous Antarctic shelf province as stated in [16], however, with a considerable number of sub-provinces. Among all regions, the Weddell Sea holds the highest number of species. Clustering three selected sites of the West-Antarctic region (Weddell Sea, Ross Sea and Bellinghausen Sea) and the Antarctic Peninsula, one finds one cluster-group (ANT-III) dominated by Ross Sea species, while all other cluster are dominated by Weddel Sea species.

7. Whereas all Arctic regions show high species similarity indices, those of the West Antarctic region only half as high as in the Arctic. The only exception is the Weddell Sea/Ross Sea showing a higher similarity index.

In contrast to the comprehensive and well weight data set for Arctic waters, the Antarctic Realm data set is far from being unbiased. Thus, the different Antarctic regions (East Antarctic shelf, West Antarctic shelf, Antarctic Peninsula and the many Subantarctic islands/island groups), which are considered into cluster analysis, are characterized by very variable numbers of species. Therefore, more data, especially from the isolated Subantarctic islands/island groups are needed to draw an improved picture of Antarctic bryozoan zoogeography.

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Appendix 1 Cheilostome genera of Arctic and Antarctic Realms including number of species.

Genus	Arctic Seas	Antarctic Seas
Adelascopora	†	2
Aetea	†	2
Aimulosia	†	1
Amastigia	†	8
Amphiblestrum	4	4
Andreella	†	1
Antarcticaetos	†	1
Apiophragma	†	1
Arachnophragma	†	1
Arachnopusia	†	9
Aspericreata	†	3
Aspidostoma	†	2
Astochoporella	†	1
Austroflustra	†	1
Beania	†	7
Bicellaria	1	†
Bicellariella	1	†
Bostychopora	†	1
Brettiopsis	†	1
Buffonellaria	†	1
Buffonellodes	†	1
Bugula	7	2
Bugulopsis	1	†
Cabarea	1	1
Callopora	9	†
Camptoplites	†	10
Carbasea	†	2
Cauloramphus	3	†
Cellaria	1	8
Cellarinella	†	15
Cellarinellopsis	†	1
Cellepora	10	†
Celleporella	†	5
Chaperiopsis	†	8
Cheilopora	3	†
Chondivelum	†	1
Cornucopia	†	4
Corynoporella	1	†
Crassimarginatella	†	2
Cribrilina	6	†
Cylindroporella	1	†
Dekariella	†	2
Dendrobeania	11	†
Dendroperistomata	†	1
Doryporella	1	†
Electra	7	1
Ellisina	†	2
Eminooecia	†	1
Escharella	12	2
Escharelloides	4	†
Escharoides	5	3
Escharopsis	2	†
Eucratea	4	†
Exallozoon	†	1
Exochella	†	5
Fenestrulina	†	8
Figularia	†	2
Flustra	7	†
Flustrapora	†	1
Gephyrotes	1	†
Galeopsis	†	1
Harmeria	1	†
Harpecia	†	1
Hemicyclopora	2	†
Himatozoum	†	2
Hippadenella	†	1
Hippodiplosia	9	†
Hippomanavella	†	1
Hippoponella	2	†
Hippothoa	4	1
Icelozoon	†	2
Inversiula	†	1
Isoschizoporella	†	4
Isosecuriflustra	†	3
Kinetoskias	4	†
Klugeflustra	†	4
Klugella	†	2
Klugerella	†	1
Kymella	†	1
Lacerna	†	3
Lageneschara	†	1
Larnacicus	1	†
Larvapora	†	1
Leiosalpinx	†	1
Lepraliella	1	†
Lepraloides	1	†
Megapora	1	†
Melicerita	†	5
Membranipora	1	1
Membraniporella	1	†
Menipea	†	3
Micropora	†	2
Microporella	4	1
Microporina	1	†
Myriapora	3	†
Nematoflustra	†	1
Notoplites	4	9
Obivalia	†	1
Orthoporidra	†	3
Osthimosia	†	11
Palmicellaria	3	†
Paracellaria	†	3
Pemmatoporella	†	1
Phylactella	2	†
Plesiothoa	†	1
Polirhabdotos	†	1
Porella	15	†
Pseudoflustra	5	†
Pyriporoides	†	1
Ralepria	†	1
Retepora	4	†
Reteporella	†	9
Reussina	1	†
Rhamphonotus	2	†
Rhamphosmittina	†	1
Rhamphostomella	10	†
Romancheima	†	2
Sarsiflustra	1	†
Schizoporella	21	†
Scruparia	†	1
Scrupocellaria	6	†
Semibugula	1	†
Smittina	18	13
Smittinella	†	1
Smittipora	1	†
Smittoidea	†	6
Spigaleos	†	1
Stomachetosella	4	†
Stomlypselosaria	†	1
Swanomia	†	3
Systeneopora	†	1
Talvittaticella	†	1
Tegella	12	†
Tessaradoma	1	†
Thrypticocirrus	†	3
Thynchozoon	†	1
Toretocheilum	†	2
Tracheoptyx	†	1
Tricellaria	†	1
Trilaminopora	†	1
Trilochites	†	1
Turritigera	†	1
Umbonula	4	†
Uschakivia	1	†
Valdemunitella	†	1
Xylochotripens	†	1