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Fútalág 40, FO-100 Tórshavn, Faroe Islands
Tlf (*Telephone*): + 298 79 05 78
Email: doreteb@savn.fo
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Bókamiðsølan
Óðinshædd 2
P.O. Box 3222
FO-110 Tórshavn
Faroe Islands
Tlf (*Telephone*): + 298 31 37 56
Fax: + 298 31 99 06
E-mail: bms@bms.fo

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Bryozoan epifauna on brachiopods from the Faroe Islands (NE Atlantic)

**Nina V. Denisenko¹, Elsebeth Thomsen²,
Ole S. Tendal³**

¹Zoological Institute of the Russian Academy of Sciences, Department of Marine Research, 199034, Saint Petersburg, Russia, E-mail: ndenisenko@zin.ru

²Tromsø University Museum, Department of Natural Sciences (Geology), NO-9037 Tromsø, Norway, E-mail: elsebeth.thomsen@uit.no

³The Natural History Museum of Denmark, The Invertebrate Department, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark, E-mail: ostendal@snm.ku.dk

Abstract

Fifteen bryozoan species were found on three species of brachiopods in the Faroe area, but only two of the brachiopod species can be regarded as common biogenic substrates for bryozoans. Incrusting bryozoan species were the most diverse compared to other growth-forms. A maximum of five species were found on one valve, but usually from one to three species. Most species were found in restricted depth zones and they can be regarded as accidental epibionts due to the absence of any relationship between the bryozoan species richness and brachiopod abundance in total. *Diplosolen obelia* and *Disporella hispida* are the most common species, their frequency of occurrence exceeding 50% and their abundance correlating significantly with the brachiopod abundance. The preference

of some brachiopod species as substrate for bryozoans is related to the morphology of the brachiopod valves. Boreal and boreo-arctic species predominate in the study area. Occurrence of arctic forms of bryozoans corresponds to the waters with low temperature, where significant relationship is found between them and brachiopod abundance, although the last one is low in the cold water area.

Introduction

Bivalve, gastropod and cephalopod (*Nautilus*) shells, worm tubes, corals and sponges as well as biogenic debris of different origin are often reported as substrates for incrusting and sessile organisms (Seben, 1991; Tyrrel, 2005). Such biogenic substrates, sediments and habitats are well known and widespread around the Faroe Islands (Jensen and Frederiksen, 1992; Tendal and Dinesen, 2005; Thomsen, 2005).

Bryozoans use a variety of substrates for larval attachment (Hageman *et al.*, 2000; McKinney and Jackson, 1989; McKinney, 1996; Taylor, 1994,). Several patterns of this colonization have been described, especially with regard to diversity, autecology of different species, relation between the percent of covering and the substrate form, and the importance of size and textural characteristics of the

substrate (Thomsen, 1977; d'Hondt 1984; Denisenko and Savinov, 1984; Cadée and McKinney, 1994; Taylor, 1994). Bryozoans are often the most abundant group among incrusting taxa on living substrates, both in frequency of occurrence and with regard to percentage of covering (Denisenko, 1990; Denisenko and Denisenko, 1991). On bivalves, incrusting bryozoan assemblages are quite diverse: 42 bryozoan species were found on *Chlamys islandica* in the Barents Sea (Denisenko and Denisenko, 1991) and 44 species on shells of *Modiolus modiolus* from the Faroe Islands shelf (Dinesen, 1999; K. Bille Hansen, personal communication, 2007). While bivalves dominate as biogenic substrates in shelf areas, brachiopods dominate in outer shelf areas and on continental slopes (Zezina, 1976), where they can be found in high densities and one species can be dominant in the local benthic fauna (Zezina, 2001).

Six brachiopod species have been found in Faroese waters and three (*Macandrevia cranium*, *Dallina septigera* and *Terebratulina retusa*) are common in depths from 200 to 500 m (Thomsen, 2001). The epifauna on the brachiopods has been found to comprise Foraminifera, Porifera, Hydrozoa, Polychaeta, Cirripedia, Bivalvia, Brachiopoda and Bryozoa with poriferans and bryozoans as the dominant groups (Tendal and Thomsen, 2005). Compared to other groups, bryozoans were not only the most frequent in occurrence, but also the most diverse group in the Mediterranean Sea and on the Brazilian shelf brachiopods (d'Hondt, 1984; Rodland *et al.*, 2004).

With knowledge of variations in bryo-

zoan species composition, and comparing our results to other published data, we can analyse patterns of changes in a fauna under environmental fluctuations, not only on local, but also in wider spatial scale.

The aims of the present study are: 1) to describe the species composition of the bryozoan epifauna on brachiopods from the Faroe Islands area; 2) to identify the most important environmental factors influencing the diversity of the bryozoans; 3) to point out bryozoan species that can be considered indicators of environmental conditions in the area; and 4) to find possible interrelationships between the brachiopod species and the incrusting bryozoans, especially whether bryozoan species exhibit selectivity in relation to brachiopod morphology and valve microstructure.

Study area and background

The small island group of the Faroes and its shallow banks are situated at approximately 62° N and 7° W, in the middle of the area where Atlantic and Arctic water masses meet in a complicated pattern over the varied topography of the Iceland-Scotland Ridge. During the international BIOFAR project (1988-1990) more than 800 stations were sampled in Faroese waters with different kinds of gear, mostly at depths between 100 and 1000 m. Toward the northwest and the southwest, the Faroese plateau gradually falls off to 400 depth, whereas a sharp fall to 1000 m is found northeast and southeast of the islands (Nørrevang *et al.*, 1994; Tendal *et al.*, 2005).

Bottom types have not been mapped in detail around the Faroe Islands. Scattered

information in a number of publications indicates the domination of soft sediments at greater depths (Bruntse and Tendal, 2001; Thomsen, 2005), although underwater photographs show mixed gravelly bottoms with many fragments of shells, sand and sometimes rocky outcrops (Tendal *et al.*, 2005).

Hydrographical investigations in Faroese waters began in 1868 and 1869 during the British expeditions with the H.M.S. *Lightning* and H.M.S. *Porcupine*, where the marked differences in bottom temperatures north and south of the subsequently discovered Wyville-Thomson Ridge were recorded (Thomson, 1874). Since then observations have been made by a large number of Danish and foreign expeditions, as well as by the Fisheries Laboratory of the Faroe Islands, resulting in the discovery of a very complicated pattern of waters masses and currents in this part of the Iceland-Scotland Ridge (Kiilerich, 1928; Westerberg, 1990; Hansen and Østerhus, 2000; Tendal and Bruntse 2001). The basic dynamic is the exchange of warm Atlantic water and cold water from the Norwegian and Icelandic seas over the Iceland-Faroe Ridge and through the deep channel east of the Faroe Islands. In a simplified scheme, the Faroese shelf and upper slope are dominated by warm Atlantic water down to depths of 400-500 m, with an admixture of cold East Icelandic Water on the northern and eastern side of the islands at depths of 400-600 m. At depths larger than 500-600 m, most of the area is dominated by cold water from the Nordic seas flowing through the Faroe-Shetland Channel, which turns west south of the Faroe Islands and spreads over the southern flank of the Iceland-Faroe Ridge.

Because of steep topography, there are in many places strong gradients of temperature within short distances, from 10°C in shallow areas to 0° (or even -1°) at depths below 550 m. For most BIOFAR stations general characteristics, such as position, depth, gear, estimated bottom temperature, water mass, near bottom water velocity and seabed sediment, are available (Nørrevang *et al.*, 1994).

Material and methods

The material was collected during the BIOFAR programme on the Faroese R/V „*Magnus Heinason*“ and the Norwegian R/V „*Håkon Mosby*“ using different benthic sampling gear (Tendal *et al.*, 2005). Brachiopods were collected from 187 stations out of a total of about 600 stations (37%) with five qualitative types of gear: 97 (ca. 52 %) triangle dredgings, 13 (ca. 7 %) scallop dredgings, 10 (ca. 5 %) trawlings, 60 (ca. 32 %) detritus sledge deployments and 7 (ca. 4 %) hyperbenthos sledge deployments. They were identified by the second author, who also inspected about 5000 specimens for epibionts (Thomsen 2001, 2005; Tendal and Thomsen 2005). Recently, the first author identified the epizoic bryozoans found in this collection.

The biogeography of the bryozoans was analysed. The biogeographic terminology used here combines the geographical origin of the species (Atlantic) with the biogeographic zonation of the ocean (Subtropic (Lusitanian)-Boreal, Boreal, Arctic, Boreo-Arctic) and the latitudinal zones of occurrence (widespread, circum-polar, etc.) (e.g. Golikov, 1982). For the present work, the biogeographic

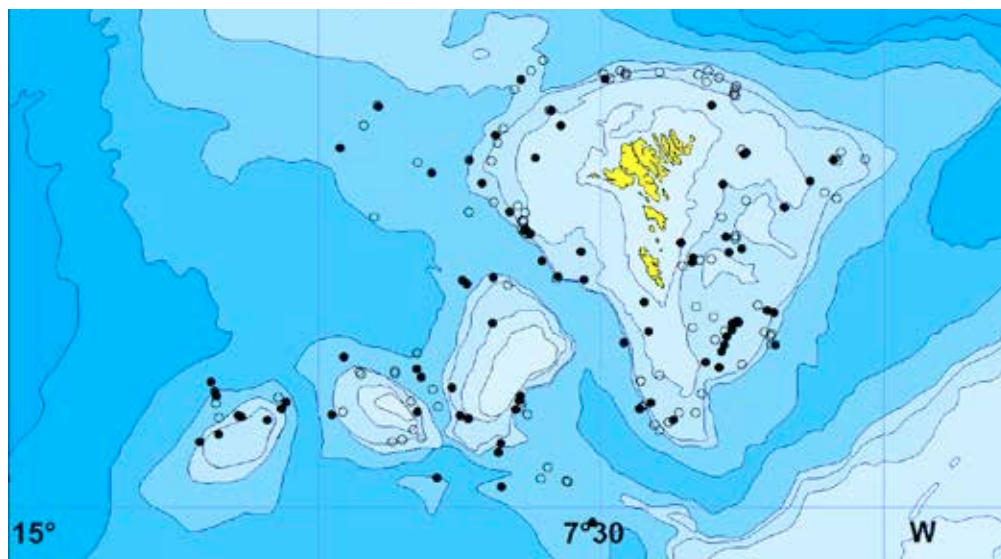


Fig. 1. Distribution of *Dallina septigera* and *Macandrevia cranium* in the Faroe Islands area (all circles) and occurrence of epibiont bryozoans on their shells (full circles).

characteristics of the Faroese bryozoans were obtained from Denisenko (1990).

Pearson correlation coefficients were calculated in order to analyse relationships between species composition and environmental factors. The similarity of species composition at the stations and determination of faunal bryozoan complexes on the brachiopods was estimated by a clustering procedure on data obtained from each station calculated by the Czekanowski-Sørensen index (Cz) (Czekanowski, 1909; Sørensen, 1948) using a standard hierarchical clustering procedure on data obtained from each sample using the Average Linkage Method (e.g. Pesenko, 1982; Pielou, 1984; Gray and Elliott, 2009) using Primer 4 software (www.primer-e.com).

Results

A total of 15 species of bryozoans (Table 1) was found on 1379 brachiopods at 114 stations (59% of the total number of stations where brachiopods were collected). These species were mainly registered on shells of *Macandrevia cranium* and *Dallina septigera* (83 and 47 stations, respectively). *Terebratulina retusa* was very rarely incrustated by bryozoans (less than 5 % of all shells), and only one species was found on its valves at 12 stations. The total number of bryozoan colonies was 1998 at 112 stations (Figure 1). The bryozoan species in question belong to 15 genera, 11 families and two classes. Incrusting species were the most diverse (Table 1). A maximum of five species was found only once (Station 290) and usually there were one to three species per station. The number of species co-existing on a single

Species	Biogeo- graphic characteris-tic	Frequency of occurrence on brachiopods, %	Growth form
<i>Bicellarina alderi</i> (Busk, 1859)	B, at	4.6	Erect
<i>Chartella bareleei</i> (Busk, 1860)	BA, at	1.8	Erect
<i>Crisia</i> sp (juv.)	-	0.9	Erect
<i>Diplosolen obelia</i> (Johnston, 1838)	SBA, at	86.2	Incrusting
<i>Disporella hispida</i> (Fleming, 1828)	BA, ws	52.3	Incrusting
<i>Entalophoroecia deflexa</i> (Couch, 1844)	BA	0.9	Incrusting
<i>Escharella octodentata</i> (Hincks, 1880)	B, at	3.7	Incrusting
<i>Escharoides bidenkapi</i> (Kluge, 1946)	A, cp	5.5	Incrusting
<i>Palmiskenia skenei</i> (Ellis et Solander, 1786)	BA, at	0.9	Massive, erect
<i>Pyripora catenularia</i> (Fleming, 1828)	B, at	2.8	Incrusting
<i>Plagioecia patina</i> (Lamarck, 1816)	B	0.9	Incrusting
<i>Ramphonotus minax</i> (Busk, 1860)	BA, at	28.5	Incrusting
<i>Reteporella beaniana</i> (King, 1846)	BA, at	6.4	Massive, erect
<i>Smittina landsborovii</i> (Johnston, 1847)	BA, at	1.8	Incrusting
<i>Turbicellepora avicularis</i> (Hincks, 1880)	B, at	0.9	Massive

Table 1.

Species composition, biogeographic structure, frequency of occurrence and constitution of bryozoan species. A – arctic, B - boreal, BA – boreo-arctic, SBA – subtropic-boreo-arctic, at – atlantic, cp – circumpolar, at –

valve did not exceed five, and usually only one to two species were found on one valve. The abundance of bryozoan colonies on brachiopod shells was low and varied from one to four in most cases on

M. cranium and from one to eight on *D. septigera*, presumably due to the larger adult shell size of the latter. No preference in distribution of bryozoan colonies between brachial and pedicle brachiopod

Colony constitution	Occurrence/ depth range of records in entire study area, m	Tempe- rature of occur- rence, °C	<i>Dallina</i> <i>septigera</i>	<i>Macan- drevia</i> <i>cranium</i>	<i>Terebra- tulina</i> <i>retusa</i>
Flexible, weakly calcified	99/32-1112	5.5-7.1	+	+	
Flexible, weakly calcified	30/78-914	4.0-4.7		+	
Flexible, calcified	-	-		+	
Unilaminate cemented, calcified sheet	104/50-1098	2-8.4	+	+	+
Radial calcified sheet	51/77-710	1-8.4	+	+	
Unilaminate cemented, calcified sheet	90-702			+	
Unilaminate cemented, calcified sheet	7/135-702	2.8-7.9	+	+	
Unilaminate cemented, calcified sheet	24/135-914	1-4	+	+	
Multilaminate branched, cemented calcified	23/107-509	4.0		+	
Uniseriably branched	44/38-300	8.8-8.4		+	
Unilaminate cemented, calcified sheet	31/70-509			+	
Unilaminate sheet, weakly calcified	65/90-1083		+	+	
Funnel-shaped, calcified form	89/65-997	3.7-8.3	+	+	
Unilaminate cemented, calcified sheet	2/405-509	1.0-4.0		+	
Multilaminate cemented, calcified	47/21-276	3.4		+	

as on shells of different brachiopod species.
atlantic, ws – widespread.

valves was found, but all branched species were recorded close to the valve's umbo, while dominant incrusting species occupy the central part of the brachiopod valves most extensively (Fig. 2). If colonies

developed at the margin of the valve, this had a negative influence on the growth of the valve, the outline becoming more rounded in profile (Fig. 3).

Diplosolen obelia and *Disporella hispida*



Fig. 2. Ordinal locations of dominant epibiont bryozoans on brachiopod valves
A – *Diplosolen obelia*; B – *Disporella hispida*; C – *Ramphonotus minax*. Foto J. Åsheim.

had the highest frequency of occurrence on the brachiopods. *Ramphonotus minax* was met relatively often, whereas the other 12 species were found only sporadically (Table 1). No clear preference for certain brachiopod species was found for the 3 most frequent bryozoan species, while the rare species mainly appeared on *M. cranium*. Only *D. obelia* occurred on valves of *T. retusa*. In general, the bryozoan epifauna was present over a wide depth range, whereas the range of each single bryozoan species varied considerably from the shallow shelf to depths of more than 1000 m. This is evident for the dominant

D. obelia, *D. hispida* and *R. minax*, the rest of the species occurring in restricted depth intervals. A relatively high number of taxa was found from 200 to 500 m, and the richest fauna was registered in a narrow depth range of 400–450 m at the edge of the outer shelf (Table 1, Fig. 4).

The calculations of Chekanovski-Sørensen similarity indexes show a presence of only two bryozoan faunal associations on the brachiopods (Fig. 5). The association of *D. obelia* and *D. hispida* occurred on all depths. The other, more rare species association, comprising *Ch. barelii*, *P. skenei* and *S. landsborovii*, appeared at depths from 300 to 400 m (Fig. 5). The rest of the bryozoan species did not show a significant linkage neither with the epifaunal associations nor with each other.

The biogeographic analysis of the epibiont bryozoan fauna shows the dominance of boreo-arctic species above other groups. The share of boreal species together with subtropic-boreal species was somewhat smaller, and the share of the arctic species was very low (Fig. 6).

Variation of the biogeographic groups



Fig. 3. Shell forms of *Macandrevia cranium* and *Dallina septigera* with epibionts.

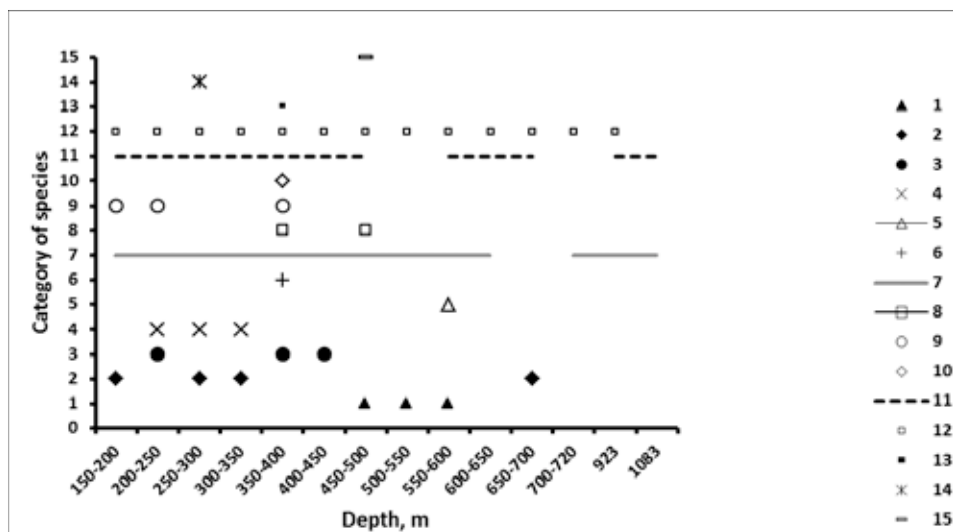


Fig. 4. Records of epibiontic bryozoans on brachiopods at different depths. Category of species: 1 - *Escharoides bidenkapi*; 2 - *Bicellarina alderi*; 3 - *Escharella octodentata*; 4 - *Pyripora catenularia*; 5 - *Turbicellepora avicularis*; 6 - *Chartella barelii*; 7 - *Ramphonotus minax*; 8 - *Smittina landsborovii*; 9 - *Reteporella beaniana*; 10 - *Palmiskenia skenei*; 11 - *Disporella hispida*; 12 - *Diplosolen obelia*; 13 - *Entalophoecia deflexa*; 14 - *Plagioecia patina*; 15 - *Crisia* sp.

along the depth gradient in the study area is shown on Fig. 7. It shows the correlation of the arctic forms to areas deeper than 500 m, and the occurrence of boreal and boreo-arctic species over a large depth gradient (Fig. 7).

Calculation of Pearson correlation coefficients between number of species and their abundance, and an analysis of the influence of environmental factors and amount of substrate is given in Table 2. A significant relationship was found between the abundance of epibiont bryozoans and the amount of brachiopod substrates, and between the share of arctic epibiont species and the number of brachiopod specimens, but with an inverse correlation. In addition, a significant correlation was found between the share of arctic and boreal species and

the number of bryozoan species, as well as between the share of biogeographic groups and abundance of bryozoans recorded on brachiopod valves. In both these cases the relationships were inverse (Table 2).

Discussion

Species composition of the epibiont bryozoan fauna

The number of bryozoan species registered on artificial or biological substrates does not exceed 500 species worldwide (Nikulina, 2004). In the Faroes the bryozoan fauna on brachiopods is not rich either (Table 1), as the species number is only one eighth of the total number known from the area (Hayward, 1994, Hayward identifications for the database of the BIOFAR project). However, this is in accordance with the results presented in

	Bryozoan species number	Bryozoan abundance on brachiopods	Depth, m	Near bottom water temperature, °C	Abundance of brachiopods
Bryozoan species number	1	0.28	0.04	-0.28	0.32
Bryozoan abundance on brachiopods	0.28	1	-0.01	-0.023	0.61
Share of arctic species	0.93	-0.71	0.39	0.38	-0.60
Share of boreal species	-0.68	-0.50	0.2	0.11	-0.41

Table 2.

Pearson correlation between species richness, abundance of all bryozoans colonies and certain species and biogeographic forms and environmental factors and brachiopod shells number.

publications for the Mediterranean Sea and for the Brazilian shelf and continental slope (d'Hondt, 1984; Rodland *et al.*, 2004). The diversity in each area does not exceed 15 taxa: about 15 bryozoan morphospecies on three species of brachiopods from the Brazilian area (Rodland *et al.*, 2004) and 12 species on one brachiopod species from the Mediterranean Sea (d'Hondt, 1984). The occurrence of bryozoans on brachiopods is probably accidental because no significant relationship was found between the number of species and brachiopod abundance (Table 2).

Our results and published information (d'Hondt, 1984) indicate that the species composition of epibiont bryozoans is different in different areas of the world and depends on the surrounding benthic faunal assemblages and the identity of the host. However, there are common features in the bryozoan epifauna of both areas. One is the dominance of a single species, as well as the presence

of subdominant forms. In the Faroese area the stenolaemate bryozoan species *Diplosolen obelia* and *Disporella hispida* dominate on *Macandrevia cranium*, with a similar frequency of occurrence (86 %) as that found for *Microporella ciliata* in the Mediterranean Sea on the brachiopod *Gryphus vitreus* (d'Hondt, 1984). In both areas the subdominant species (in the Corsica area *Diaperoecia major*, now *Annectocyma major* (d'Hondt, 1984), and in the Faroe Islands *Disporella hispida*) was represented with a similar frequency of occurrence of ≤ 50 %. The dominant epibiont species *D. obelia* was widespread on other substrates in the Faroese area (Table 1), whereas in the Corsica area the dominant bryozoan was only found as an epibiontic form (d'Hondt, 1984). The species composition of the rest of the epibiontic bryozoans was different for the two areas. In both areas incrusting forms dominate (58 %) the epibiontic bryozoan fauna.

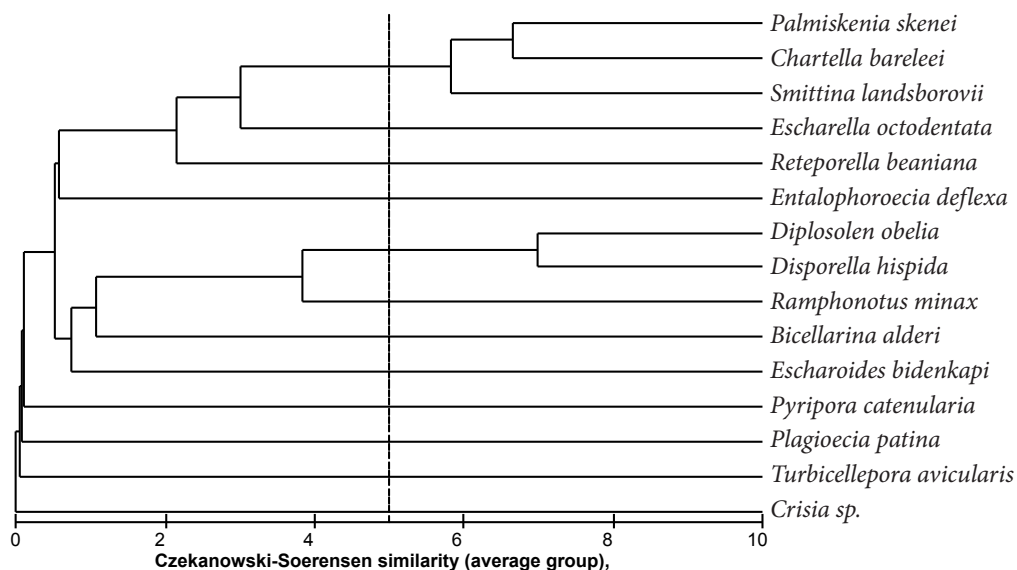


Fig. 5. Faunal complexes of bryozoans on brachiopod valves in the Faroese area.

In the Faroes the dominant incrusting species, *D. obelia* and *D. hispida*, form a faunal subgroup (Fig. 5) and were not found on other substrates at the same stations (BIOFAR database), a fact pointing to their substrate selectivity. The other faunal subgroup, including *P. skenei*, *S. landsborovi* and *C. barelii* (Fig 5), was found on brachiopods in a narrow depth range at the continental shelf break (Fig. 4) (Table 1), which might indicate a scarcity of substrates for these species. The rest of the epibiont bryozoans did not fit into any group (Fig. 5). Some of them were very rare in the study area as a whole (Table 1), and they only occasionally settled on the brachiopods. The rarely occurring settling on brachiopods of species such as *Bicellarina alderi* – elsewhere common in the Faroese area (BIOFAR database) – is caused by their substrate selectivity and

the unsuitability of the brachiopod valves as substrate for flexible, weakly calcified colonies in an environment of currents, the usual habitat of brachiopods.

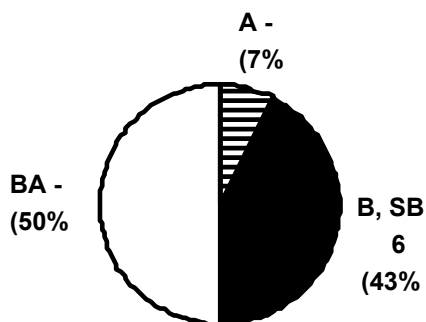


Fig. 6. Number and proportion of different biogeographic groups of epibiont bryozoans found on brachiopods. A – arctic; B, SB – boreal and subtropical-boreal species; BA – boreo-arctic species.

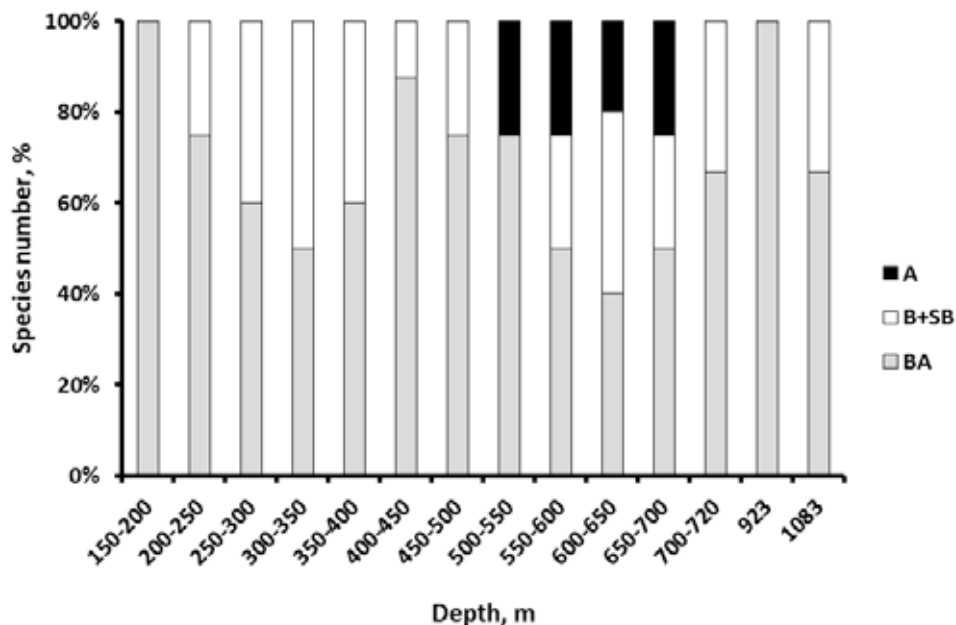


Fig. 7. Variation of proportion among different biogeographic groups of bryozoans - brachiopod epibionts. A – arctic; B, SB – boreal and subarctic-boreal species; BA – boreo-arctic species.

Relationships between epibiont bryozoans and substrate

Bryozoans have been found as sessile epibiont animals on different substrates and sediments (Kluge, 1962; Hayward and Ryland, 1998; 1999; Thomsen, 1977; d'Hondt, 1984; Denisenko and Savinov, 1984; Cadee and McKinne, 1994; Taylor, 1994). A special effort to understand patterns of bryozoan distribution on organic substrates has been carried out by d'Hondt (1984) and Hageman *et al.* (2000). Most of these investigations, however, provide no information that helps us to understand whether there is a relationship between the substrate type and the bryozoan species composition.

By settling on the surface of brachiopods,

bryozoans are provided with additional living space for their colonies, lifting them above the sea bottom and keeping them from being buried, thus keeping the zooids from dying due to covering by re-suspended sediment. Also, the brachiopod's ability to rotate around the pedicle (Richardson, 1986 in Thomsen, 1990) helps them avoid sedimentation. On the other hand the bryozoan colonization of secondary space gives them an advantage in feeding, enhancing food catching from the near bottom water layer. This is especially important for the two species, *D. hispida* and *D. obelia*, which are characterized by small zooids and lack of morphological structures for cleaning the zooids. Another indication of

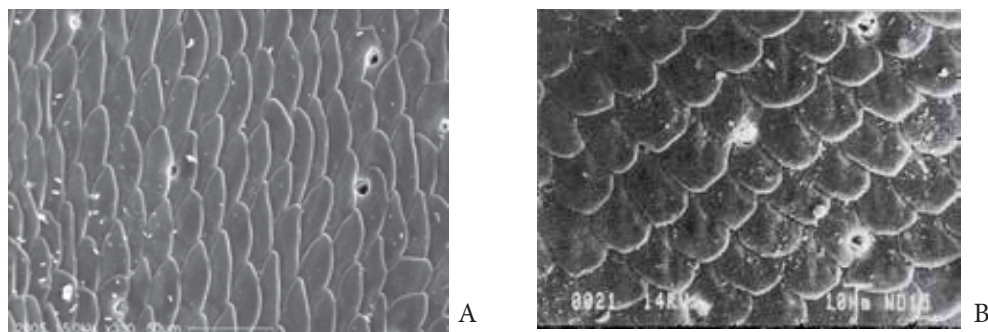


Fig. 8. Microstructure of the *Terebratulina retusa* (A) and *Macandrevia cranium* (B) (after Thomsen, 1989).

the suitability of brachiopods as substrates for bryozoan epibionts is the presence of a significant correlation between colony abundance, mainly by dominant species, and brachiopod abundance (Table 2).

Brachiopods also represent a possibility of getting additional space for colony development for the more rare bryozoan species. The absence of a significant relationship between the abundance of brachiopods (substrate amount) and the number of bryozoan species (Table 2) indicates, however, accidental settlement.

As in the present study, bryozoan epibionts are not generally found on all the recorded brachiopod species in a given area. In the Mediterranean Sea bryozoans were mainly present on *Gryphus vitreus*, whereas four other brachiopod species (*Terebratulina retusa*, *Crania* (now *Novocrania*) *anomala*, *Megathiris detruncata* and *Megerlia truncata*) were only sporadically colonized (Logan, 1979; d'Hondt, 1984). On the outer part of the Brazilian shelf, bryozoans were mainly found on one brachiopod species, *Argyroteca* sp., among four brachiopod species (*Bouchardia rosea*, *Argyroteca* cf. *cuneata*, *Terebratulina* sp., and *Platidia anomioides*) (Rodland *et al.*, 2004). Bryozoans from the Faroe Islands prefer two brachiopod species (*Macandrevia cranium* and *Dallina septigera*) among six species for settlement. Bryozoan selectivity can perhaps be explained by differences in the microstructure of the brachiopod valves, e.g. presence/absence of punctae, and/or the external morphology (ornamentation)

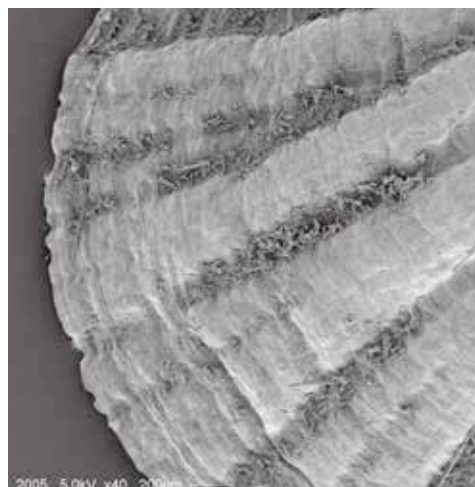


Fig. 9. Surface of *Terebratulina retusa* valve. Sponges are seen in grooves rims (after Tendal and Thomsen, 2005.).

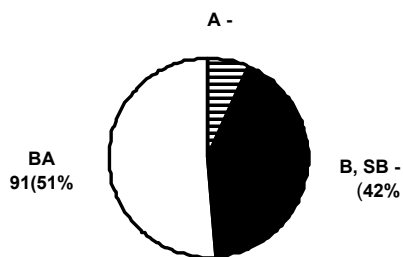


Fig. 10. Biogeographic structure of the bryozoan fauna of the BIOFAR study area.

Species number and share of biogeographic groups. A – arctic; B, SB – boreal and subtropic-boreal species; BA – boreo-arctic species.

in different brachiopod species (Fig. 8; cf. Tendal and Thomsen 2005).

The exterior of the valves of *T. retusa* is characterized by radial ribs (Fig. 9), whereas *M. cranium* and *D. septigera* have rather smooth surfaces. Bryozoan larvae prefer uneven surfaces for settlement (Denisenko, 1990), but a surface which is very ornamented, e.g. with sharp ribs and deep grooves, becomes dirty quicker than a less rough surface and thus prohibits colony development. Therefore, the smooth surfaces of *M. cranium* and *D. septigera* are well suited for settling bryozoans. In the ribbed *T. retusa*, the grooves between the radial ribs are occupied by poriferans even in young specimens (Tendal and Thomsen, 2005). These patterns can explain why one of the widest distributed bryozoan species, *D. obelia*, was only sporadically found on *T. retusa*. A similar pattern influencing brachiopod epibionts was found in Palaeozoic species (Alexander

and Scharpf, 1990). Epibionts, including bryozoans, inhibit the growth of the brachiopods (Fig. 4), a phenomenon also seen in the bivalves *Chlamys islandica* (Denisenko and Denisenko, 1991) and *Modiolus modiolus* (Dinesen, 1999; K. Bille Hansen, pers comm, 2007).

The interrelationship between in-crusting species and substrate/host animals cannot be classified as commensalism (for definition see Morton and Depledge 1989), because it is beneficial for the bryozoans but may be harmful to the host (Cadee, 1991). The negative influence is probably small and less than the influence of boring fungi, which easily destroy brachiopod shells (Zezina, 1976; Thomsen, 1989; Tendal and Thomsen, 2005).

We have not paid particular attention to substrate competition between different systematic groups, but competition between bryozoans was observed on both *M. cranium* and *D. septigera*. Due to the low number of epifaunal species on these two brachiopod species and also the low abundance of bryozoan colonies on the valves (usually only one colony and on average not more than four in the case of *D. septigera*), it was rare. Overgrowth of colonies was obvious in a few cases. The margins of bordering colonies usually corresponded to the form of the neighboring colonies. On *T. retusa* poriferans are the main epibiont group (Tendal and Thomsen, 2005) and competition for space between them and bryozoans can only be found on young individuals. Poriferans may later overgrow bryozoan colonies and cause their death. Overgrowth and destruction

of smaller epibiont organisms have also been reported from the Greenland Sea (Kuklinski and Bader, 2007).

The frequency of colonization of *M. cranium* and *D. septigera* was similar and the number of epibiont species at a given station was dependent on the abundance of the brachiopods which was evident by significant values of the Pearson correlation coefficient (Table 2).

Biogeographic pattern

The biogeographic distribution pattern of the bryozoans on brachiopods at the Faroe Islands (Fig. 5) corresponds to the variation of proportion of the biogeographic groups

of the whole bryozoan fauna (Fig. 10), and the dominance of boreal and boreo-arctic species is a general feature. Boreal and boreo-arctic species were recorded from a wide range of depths (Table 1, BIOFAR database), whereas arctic species were restricted in depth distribution (Fig. 11). The reasons seems to be that boreal brachiopods are rare at depths greater than 500 – 600 m north of the Ridge (Thomsen, 2001) and that the distribution of stenothermic arctic species was restricted to depths below 500 m in the northern part of the study area (Fig. 7), where the temperature was below 4°C and the Faroe–Iceland Ridge prevents the

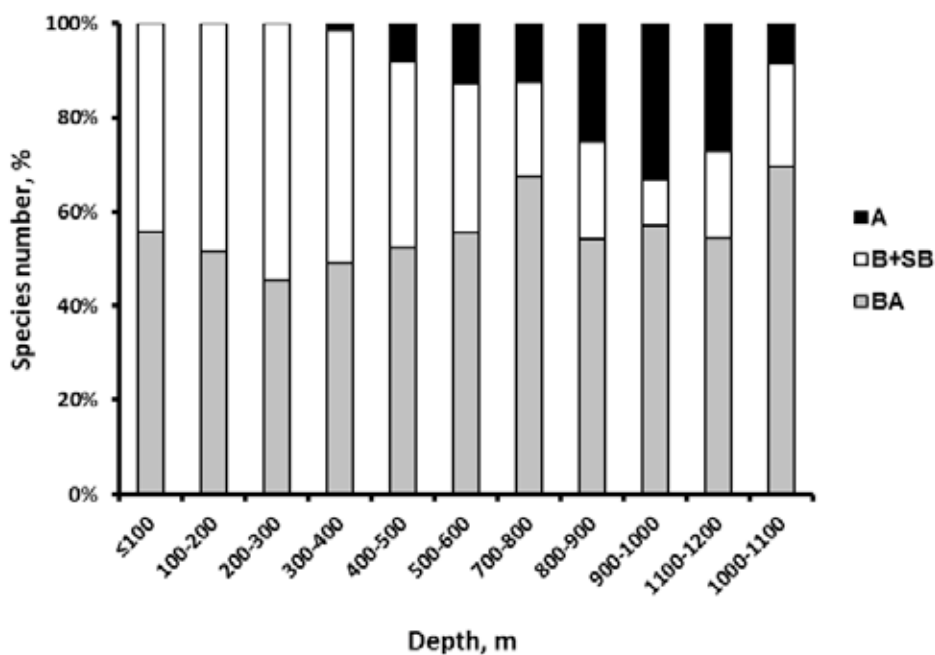


Fig. 11. Proportion of different biogeographic groups of the bryozoan fauna in BIOFAR samples at different depths in the Faroe area.

penetration of warm Atlantic water into deeper areas of the Norwegian Sea.

Relationship to environments

Although relationships between variations in environmental factors and the distribution of bryozoan fauna have been demonstrated for other regions (Denisenko, 1990; 2008; 2010; Kuklinski and Bader, 2007), the Pearson correlation did not show significant values in the present study. This absence of correlation might be explained in three different ways. One is that the epibiont bryozoan fauna shows high variability along the depth gradient (Fig. 4) and has a wide depth distribution in the study area as a whole (Table 1). The second is that the presence of available space for larval attachment and colony development plays a more important role for species expansion than variations in depth or water temperature. The third is that the hydrographic regime, which is very heterogenic in the area, causes differences in the spatial distribution of species with different biogeographic origins. The first explanation is supported by the fact that the share of different biogeographic groups of bryozoans significantly correlated within the study area (Table 2).

Conclusion

The bryozoan epibiont species on brachiopods around the Faroes are few in number, with incrusting species being the most diverse among the growth-forms. The density of the species and their colonies on the brachiopod valves is low. Their settlement can be regarded as

occasional because their colonies occupied the biogenic substrate when other suitable substrates were absent. This postulate is also supported by the absence of a significant relationship between number of species and brachiopod abundance. *Diplosolen obelia* and *Disporella hispida* are the most common epibionts on brachiopods and there is significant degree of correlation between bryozoan abundance and brachiopod abundance.

Bryozoans species were mainly found on two of the six species of brachiopods present in the Faroe area. Their preference of the valve surfaces of *Macandrevia cranium* and *Dallina septigera* seems to be related to the external morphological structure of these brachiopods..

In spite of the dominance of boreal and boreo-arctic species, the presence of arctic bryozoans is marked. Their occurrence is related to the heterogeneity of the environment and a significant relationship has been found between these bryozoans and the abundance of brachiopods, even though this abundance is low in cold water areas.

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