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Microhabitat diversity of Svalbard Bryozoa

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Abstract

Bryozoans are one of the major macrofaunal groups of the high polar regions. Here we present data on the nature of bryozoan assemblages in the Svalbard Archipelago sampled over 6 years between 1997 and 2002. Samples were collected with use of Van Veen grab, dredge and Scuba diving at depths ranging from 0 to 268 m. Among examined material (5026 items) bryozoans were present on one type of abiotic (stones) and 40 types of biotic substrata. The biotic substrata we investigated included algae (12 taxa) and invertebrates (28 taxa: Hydrozoa, Gastropoda, Bivalvia, Polychaeta, Crustacea, Ascidiacea, other Bryozoa). Both a priori ANOSIM (Global $R=0.512$, $P=0.001$) and cluster analyses reveal differences between the assemblages on different types of substrata. Cluster analyses distinguish two distinct groups of substrata. The first (stable) included stones, molluscs and *Balanus balanus* whilst the second (flexible) consisted of algae, hydrozoans and bryozoans. Bryozoan assemblages which colonized different substrata, varied in terms of species composition and their dominance. Bryozoan species were categorized as generalists, low-specificity epibiotic species or locally abundant background species. No species were found to be substratum-specific to any type. Among substrata with the richest bryozoan fauna were stones (156 taxa), *Chlamys islandica* (68) and *Balanus balanus* (62). There were clear patterns in the distribution of substrata colonized by bryozoans within the fjord system: those shallow near the mouth were rich whilst those in deeper water were depauperate. We consider environmental gradients such as siltation and processes related to depth to be responsible for such patterns.

Keywords: Arctic, biodiversity, Kongsfjorden, substratum-bryozoan association

Introduction

Bryozoans are one of the few phyla in which virtually all representatives are primary or obligate sessile organisms. This means that they are directly dependent upon a substratum resource for at least the most significant stages of their life history. As with many benthic taxa, selection of the habitat is not a random process but rather the result of behavioural pattern (Hayward 1980). Thus the distribution of adults can largely be the result of choice exhibited by the prospecting larvae (Zimmer and Woollacott 1977). There are a number of factors influencing the selection of substrata by marine invertebrates. The most important

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seem to be: response to gravity, light, current, presence of surface film, and rugosity of substratum (Ward and Thorpe 1989).

The phenomenon of substratum preference is not only observed among the bryozoans. It is also a well-recognized behaviour among barnacles, brachiopods, polyplacophoran and gastropod molluscs, and tubeworms (*Spirorbis* spp.) (e.g. Pechenik and Eyster 1989). Some bryozoans benefit from host substrata in more ways than just as an attachment surface. *Membranipora membranacea* (L.), for example, intakes organic carbon from the kelp on which it lives (Manriquez and Cancino 1996).

Bryozoan abundance and taxonomic diversity can be directly related to substratum nature (Hayward and Ryland 1998). One of the most studied biotic substrata used by bryozoans are algae (e.g. Różycki and Gruszczyński 1986; Manriquez and Cancino 1996; Lippert et al. 2001). Some species of algae are used more than others (Ryland 1959). The most likely factors explaining the pattern of settlement is texture of thallus, age of the fronds and amount of mucus (Ryland 1959). Some bryozoan species-substratum associations are very selective either as commensal or mutualistic relationships (Cadee and McKinney 1994; Ross and Newman 1996). The broad range of substrata occupied by bryozoans includes, for example, crabs (Key et al. 1999), merostomata (Key et al. 1996) and isopod exoskeletons (Key and Barnes 1999), bryozoans (Barnes 1994), corals (Harmelin 1990), brachiopods (Barnes and Peck 1996), gastropods (Ryland 2001), and bivalves (Seed 1996).

In the Arctic little is known about microhabitat use by bryozoans other than that boulder fields can support rich and diverse assemblages (Dick and Ross 1988). Kluge's (1975) monograph is one of the most comprehensive on high arctic species but this merely indicates substrata on which given species were recorded. That Powell (1968) found 38 bryozoan species associated with scallop beds in arctic Canada shows that a substratum other than rock is also important there. Furthermore, in the Svalbard region, Różycki and Gruszczyński (1986) and Lippert et al. (2001) found that bryozoans were the most abundant epiphytes on nearshore algae.

Data about the other substrata occupied by bryozoans in the Arctic are lacking. Here we attempt a baseline study of the spectrum of substrata used by one of the most numerous components of nearshore Svalbard macrobenthos, the bryozoans. We attempt to describe the characteristics of bryozoan assemblages on the major different substrata used.

Material and Methods

Study area

We studied assemblages and potential substrata from eight localities in the Svalbard Archipelago (Wijdefjorden, Duvefjorden, Tommeloyane, Helleysundet, Boltodden, Hornsund, Bellsund, and Kongsfjorden; see Figure 1) but focused on the last of these (79°N, 12°E in West Spitsbergen).

Svalbard is influenced mainly by two water masses. The first is the West Spitsbergen current, which is a branch of the warm (4°C) and highly saline (35 PSU) Norwegian Current. This current moves along the western and northern parts of Spitsbergen (Loeng 1991). Transportation of these warm water masses causes a milder climate compared to other areas at similar latitude (Gammelsrod and Rudels 1983). The second water mass influencing this area is the East Spitsbergen Current. This cold, dense and highly saline water originates in the Arctic Ocean and travels along the east coast of Spitsbergen down to the southern tip of the island at which it is termed the Sorkapp Current. The Sorkapp

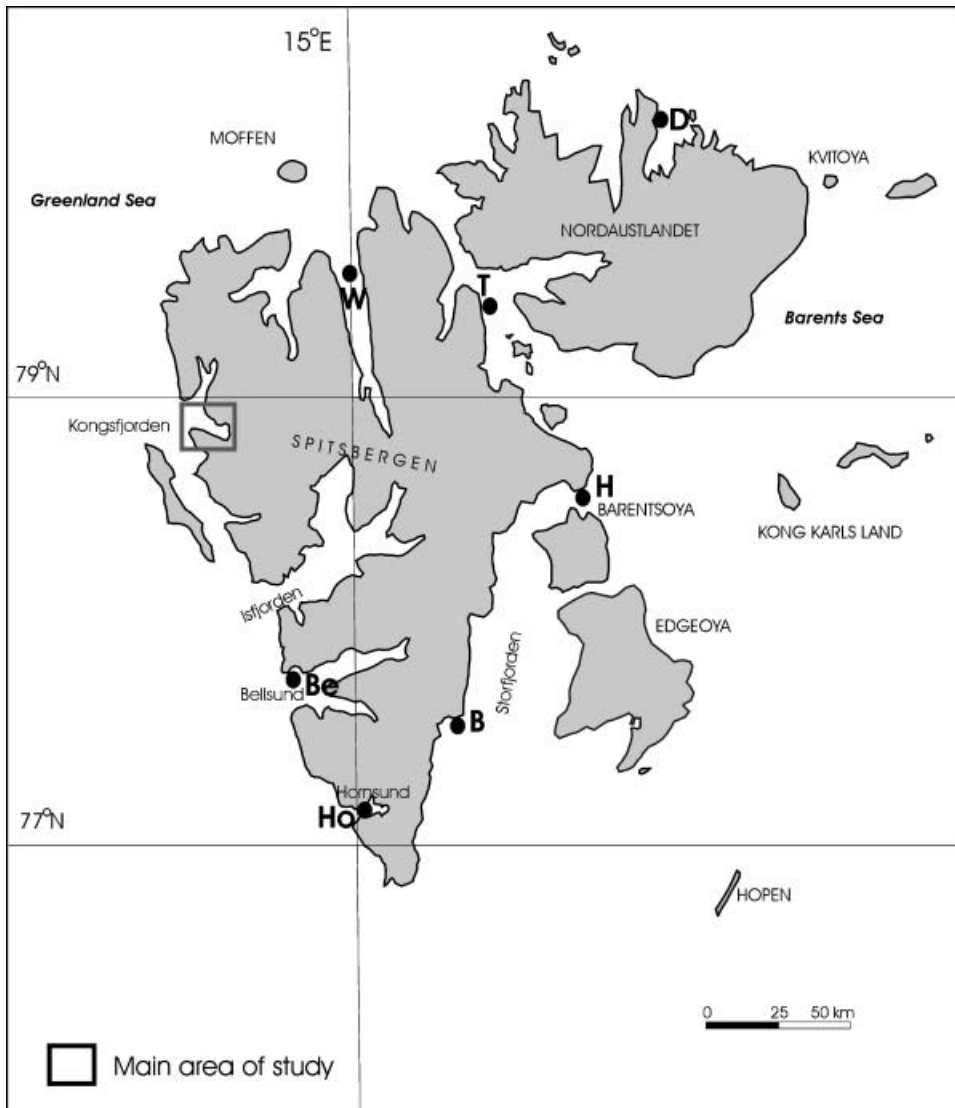


Figure 1. The position of study sites at Svalbard Archipelago. Framed main study site—Kongsfjorden; W, Wijdefjorden; D, Duvefjorden; T, Tommeloyane; H, Helleysundet; B, Boltodden; Ho, Hornsund; Be, Bellsund.

Current brings a watermass ranging in temperature from -1.5 to 1°C and salinity from 34 to 35 PSU to the western coast of Spitsbergen (Loeng 1991). As along most high polar shores, the Svalbard coast is subjected to ice scour from floating ice during the summer months. In winter the sea surface freezes on inner fjord areas forming fast ice. Fast ice occurs less often and less extensively in the central and outer parts of the fjords (Svendsen et al. 2002).

The main study site, Kongsfjorden, is 26 km long and on average 8 km wide. The whole area of the fjord is 208.8 km^2 . Its maximal depth is 428 m, average about 140 m. Of the total coastline length of the fjord (89.6 km) 15.9 km is glacier mouth. Typically important

factors influencing hydrography of the fjord are bathymetry, vicinity of the ocean, glaciers and local climate. Kongsfjorden does not typically have a fjord sill at the entrance, this absence causes strong influence of ocean waters on the hydrological regime (Węślawski et al. 1991). The fjord does have a range of bottom types from the soft fine, muddy sediments through sand and gravel to hard rock (Hop et al. 2002). Svendsen et al. (2002) provide a detailed description of the physical and environmental characteristics of the fjord.

Field sampling and data analyses

Sampling was carried out during the 1997, 1998, 2000, 2002 cruises of R/V *Oceania* and 1999, 2000, 2001 cruises of R/V *Jan Mayen*. Samples were collected from the intertidal to 268 m depth using three techniques: Van Veen grab, dredge and Scuba diving (hand picking and frame 0.25 m²). Of the 213 samples, 93 were collected by Scuba diving, 112 by grab and eight by dredge. Collected material was dried in the case of rocks, stones, shells, and barnacles. Algae and “bushy” bryozoan substrata were fixed in 4% formalin or 70% ethanol. All substrata were identified to the highest taxonomic resolution possible.

Frequency of occurrence was calculated by use of the equation:

$$F = n_i \times n^{-1} \quad (1)$$

where F is the frequency of given taxa (%), n_i is the number of samples where given taxa were present and n is the number of all samples.

To compare faunal composition of bryozoan assemblages between different substrata, we used the PRIMER software package. We calculated Bray-Curtis similarity measures using frequency of occurrence square-root transformed data (Bray and Curtis 1957). Using this matrix, samples were then classified into groups by hierarchical agglomerative clustering using group-average linking. We illustrated this divisive classification of samples using a standard dendrogram. One-way analyses of similarities (ANOSIM; Clarke and Green 1988) and multiple pairwise comparisons were used to test a priori differences between assemblages on different substrata. ANOSIM uses the test statistic R , which is calculated using average rank similarities among pairs of replicates (in this case e.g. species of algae) within each of two groups (e.g. algae–stones) minus the average rank similarity of replicates between groups and is scaled to give a value between -1 and 1 . Thus, $R=1$ when all similarities within groups are less than any similarity between groups, $R>0.75$ when there is large difference with the groups either well separated, $R>0.5$ when overlapping but clearly different, $R<0.25$ when groups are barely separable at all and $R=0$ when replicates within and between groups are equally similar. If $R \approx -1$, then pairs consisting of one replicate from each group are more similar to each other than are pairs of replicates from the same group (Clarke and Gorley 2001).

Results

From 213 samples, 5026 potential substrata for bryozoans were examined. On 3547 of them bryozoans were present. Those used consisted of loose rock and 40 biotic types. Twelve taxa of algae acted as hosts (Rhodophyta, Phaeophyta) along with 28 animal taxa [Annelida (Polychaeta), Bryozoa (Gymnolaemata), Chordata (Ascidiacea), Cnidaria (Hydrozoa), Crustacea (Cirripedia and Malacostraca), Mollusca (Monoplacophora, Gastropoda and Bivalvia)]. The bathymetric range in which most of the different microhabitats were found is shown in Figure 2. Accumulation curves for assemblages on

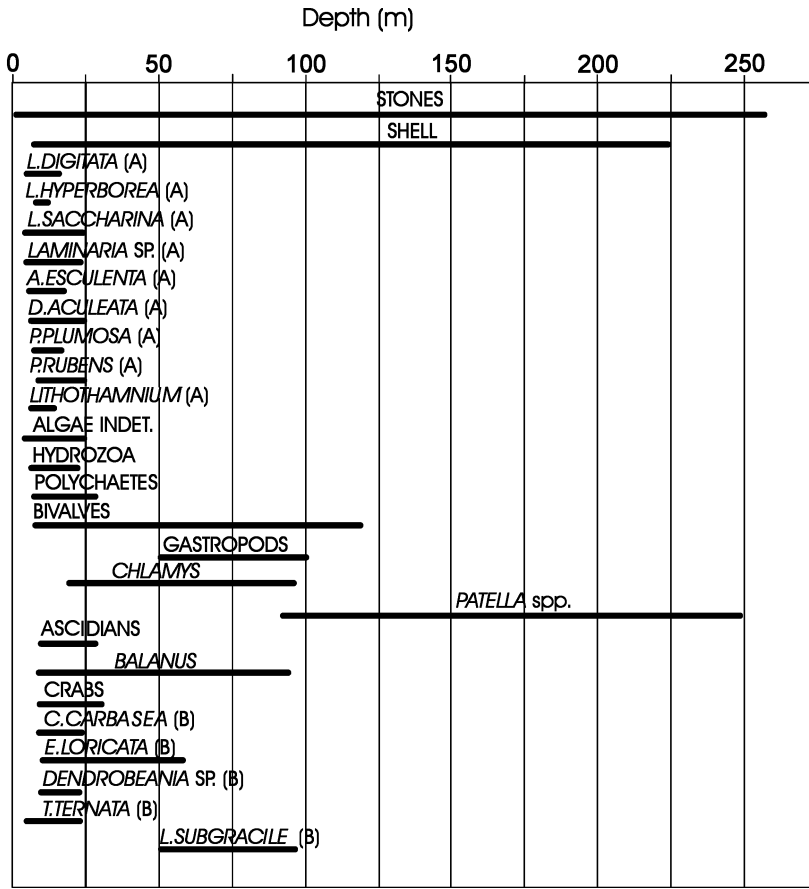


Figure 2. Depth range of substrata collected, A, algae; B, bryozoa.

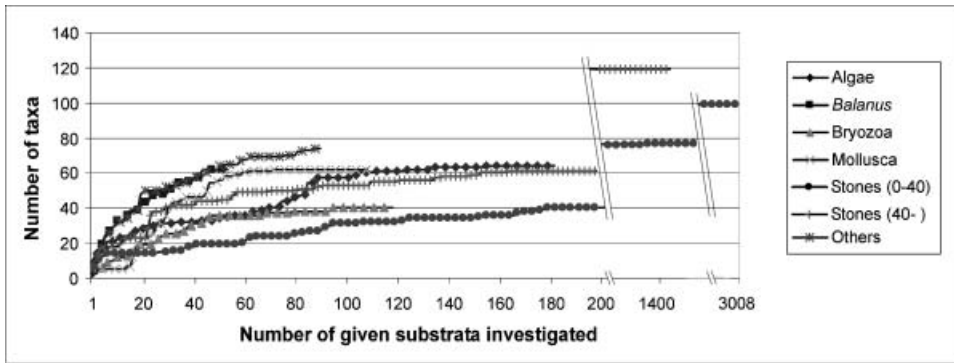


Figure 3. Accumulation curve for assemblages on major microhabitats.

many substrata (Figure 3) reached asymptote, suggesting that our sampling regime was sufficiently representative for the area.

In total 174 taxa of bryozoans were determined: 139 to species, 28 to genus, five to family, one to order and one to phylum level. The most frequently occupied substrata were

loose rock with 156 taxa of bryozoans recorded on them. On biotic substrata the number of taxa present varied from one to 68. They were most abundant on the bivalve *Chlamys islandica* (Møller) (68 taxa) and the cirriped *Balanus balanus* (L.) (62 taxa). Of the algae, *Phycodryas rubens* (L.) Batters (45 taxa) and *Alaria esculenta* (L.) Greville (29 taxa) hosted most.

Species frequency of occurrence of top 10 species in the main groups are presented in the Table I.

Despite some taxa occurring on various substrata, the assemblages were significantly different (ANOSIM global $R=0.512$, with associated $P=0.001$). Pairwise test for most of the groups of bryozoan assemblages are shown in Table II. Pairs which had significance levels (P) above 0.80 were not included (e.g. bryozoan–hydrozoan $R=-0.36$, $P=0.833$) in the table. These data due to their high type I error would be meaningless for ecological interpretations. Cluster analyses generally confirm dissimilarities and similarities calculated by a priori pairwise ANOSIM R statistics.

Cluster analyses (Figure 4) visualized the differences between the substrata. The most similar assemblages were constituted on *Balanus balanus* and *Chlamys islandica*—95%. At the level of approximately 40% similarity we could distinguish two groups of substrata: one more stable, including stones, *B. balanus* and molluscs, the other more flexible, including algae, hydrozoans and bryozoans.

Following Barnes and Clarke (1995) we classified bryozoan colonizers of substrata into four types: generalist, host-specific, low specificity and background species (Table III). No host-specific species were found.

Rank abundance plots (Figure 5) show that except on molluscs, shells and *Balanus* barnacles, assemblages were typically dominated by a few very abundant species. In most cases this differed between substrata and even between shallow and deep stones. The pioneer cheilostomes *Harmeria scutulata* (Busk), *Hippothoa arctica* Kluge, *Tricellaria ternata* (Ellis and Solander), and to a lesser extent *Celleporella hyalina* (L.), were the numerically dominant species.

Membranous, calcified and erect flexible morphological colony forms of bryozoans were present on all investigated types of substratum. Runner-like colonies were absent on hydrozoan and bryozoan substrata. Erect rigid forms were present only on more stable substrata types: stones, molluscs and *Balanus* (Table IV).

The dominant substrata used by bryozoans within the Kongsfjorden study site are shown in Figure 6. At the fjord mouth bryozoans mainly occur on stones but towards the middle fjord section this changes to algae. In the inner basin only bryozoans (*Alcyonidium disciforme*, Smitt) living on sediment were present. The least diverse microhabitats used by bryozoans were, therefore, at the two extremes of the fjord, the innermost and outermost sections. Diversity of microhabitat use decreased with depth, in many cases solely being stones. Bryozoans in the shallow area inhabited the most diverse type of substrata including rocks, algae, bryozoans, ascidians, hydrozoa, barnacles, molluscs, and crabs.

Bryozoan species playing important roles (dominants, most frequent ones) on certain microhabitats in Svalbard Archipelago are presented in Figure 7.

Discussion

Bryozoans from Svalbard waters are known to be species-rich (Gulliksen et al. 1999), our present study reveals that a rich diversity of substrata are also occupied by them. In a similar study in temperate waters Ward and Thorpe (1989) showed that the surface nature

Table I. Frequency of bryozoan occurrence on seven major groups of substrates. Since assemblages on stones from the zone between 0 and 40 m depth differ very much from the stones from the 40+ m depth (similarity less than 40%; see the Figure 4) they were treated separately.

Substrate	Frequency
Stones (0–40)	
<i>Harmeria scutulata</i> (Busk)	36
<i>Electra arctica</i> Borg	27
<i>Cribrilina annulata</i> (Fabricius)	22
<i>Cauloramphus intermedius</i> Kluge	21
<i>Tegella arctica</i> (d'Orbigny)	20
<i>Callopora</i> sp. Gray	19
<i>Cylindroporella tubulosa</i> (Norman)	19
<i>Stomachetosella cruenta</i> (Busk)	14
<i>Tegella retroversa</i> Kluge	11
<i>Microporella svalbardensis</i> Kuklinski and Hayward	11
Stones (less than 40)	
<i>Hippothoa arctica</i> Kluge	63
<i>Electra catenularia-similis</i> Kluge	25
<i>Hippothoa expansa</i> Dawson	16
<i>Electra arctica</i> Borg	10
<i>Schizoporella costata</i> Kluge	9.7
<i>Escharelloides spinulifera</i> (Hincks)	8.5
<i>Tubuliporidae</i> indet. Johnston	7
<i>Oncouseoecia diastroporides</i> (Norman)	6.6
<i>Callopora</i> sp. Gray	6.4
<i>Hippodiplosia obesa</i> (Waters)	6.4
Algae	
<i>Celleporella hyalina</i> (L.)	61
<i>Eucratea loricata</i> (L.)	24
<i>Lichenopora</i> sp. Defrance	23
<i>Tegella arctica</i> (d'Orbigny)	23
<i>Tricellaria ternata</i> (Ellis and Solander)	23
<i>Alcyonidium mytili</i> Dalyell	21
<i>Harmeria scutulata</i> (Busk)	21
<i>Callopora</i> sp. Gray	16
<i>Cribrilina annulata</i> (Fabricius)	16
<i>Dendrobeatia fruticosa</i> (Packard)	9
Hydrozoa	
<i>Tricellaria ternata</i> (Ellis and Solander)	75
<i>Cauloramphus cymbeaformis</i> (Hincks)	46
<i>Eucratea loricata</i> (L.)	46
<i>Celleporella hyalina</i> (L.)	33
<i>Carbasea carbasea</i> (Ellis and Solander)	21
<i>Harmeria scutulata</i> (Busk)	21
<i>Bowerbankia</i> sp. Farre	17
<i>Callopora</i> sp. Gray	13
<i>Lichenopora</i> sp. Defrance	13
<i>Tubuliporidae</i> indet. Johnston	8
Balanus	
<i>Callopora craticula</i> (Alder)	35
<i>Cylindroporella tubulosa</i> (Norman)	35
<i>Tegella arctica</i> (d'Orbigny)	35
<i>Tegella armifera</i> (Hincks)	29
<i>Schizomavella linearis</i> (Nordgaard)	27
<i>Tubuliporidae</i> indet. Johnston	23
<i>Scrupocellariidae</i> indet. Levensen	21

Table I. (Continued).

Substrate	Frequency
<i>Callopora lata</i> (Kluge)	15
<i>Callopora</i> sp. Gray	15
<i>Rhaphostomella ovata</i> (Smitt)	15
Bryozoa	
<i>Celleporella hyalina</i> (L.)	41
<i>Harmeria scutulata</i> (Busk)	37
<i>Tricellaria ternata</i> (Ellis and Solander)	28
<i>Cauloramphus cymbeaformis</i> (Hincks)	23
<i>Eucratea loricata</i> (L.)	16
<i>Callopora</i> sp. Gray	13
<i>Bowerbankia</i> sp. Farre	9
<i>Rhaphostomella bilaminata</i> (Hincks)	9
<i>Lichenopora</i> sp. Defrance	8
<i>Alcyonidium mytili</i> Dalyell	7
Molluscs	
<i>Celleporella hyalina</i> (L.)	35
<i>Callopora craticula</i> (Alder)	18
<i>Cylindroporella tubulosa</i> (Norman)	15
<i>Tegella arctica</i> (d'Orbigny)	15
<i>Schizomavella linearis</i> (Nordgaard)	12
<i>Tegella armifera</i> (Hincks)	12
<i>Alcyonidium mamiliatum</i> Alder	11
<i>Tubuliporidae</i> indet. Johnston	11
<i>Callopora</i> sp. Gray	8.7
<i>Scrupocellariidae</i> indet. Levinsen	8.7

Table II. ANOSIM pairwise statistic.

	R	P
<i>Balanus</i> -bryozoan	0.32	0.333
<i>Balanus</i> -algae	0.556	0.182
<i>Balanus</i> -stones	0.333	0.40
Mollusc-bryozoan	0.181	0.103
Mollusc-algae	0.644	0.009
Mollusc-stones	0.24	0.086
Bryozoan-algae	0.297	0.036
Bryozoan-stones	0.613	0.024
Bryozoan-ascidian	0.32	0.333
Hydrozoan-algae	0.071	0.364
Hydrozoan-stones	0.833	0.20
Algae-stones	0.803	0.003
Algae-ascidian	0.498	0.182
Stones-ascidian	0.75	0.20

(e.g. rough/smooth, convex/concave) rather than the type of substratum (e.g. rock or the shell of a particular mollusc species) was important for determining use by subtidal bryozoans. Our investigation supports this observation. The bryozoan community colonizing balanomorphs was similar to that on *Chlamys islandica* (see Figure 4). Although such substrata belong to different phyla (Crustacea, Mollusca), they are similar per se in shell surface structure. The same pattern was observed among algae and stones.

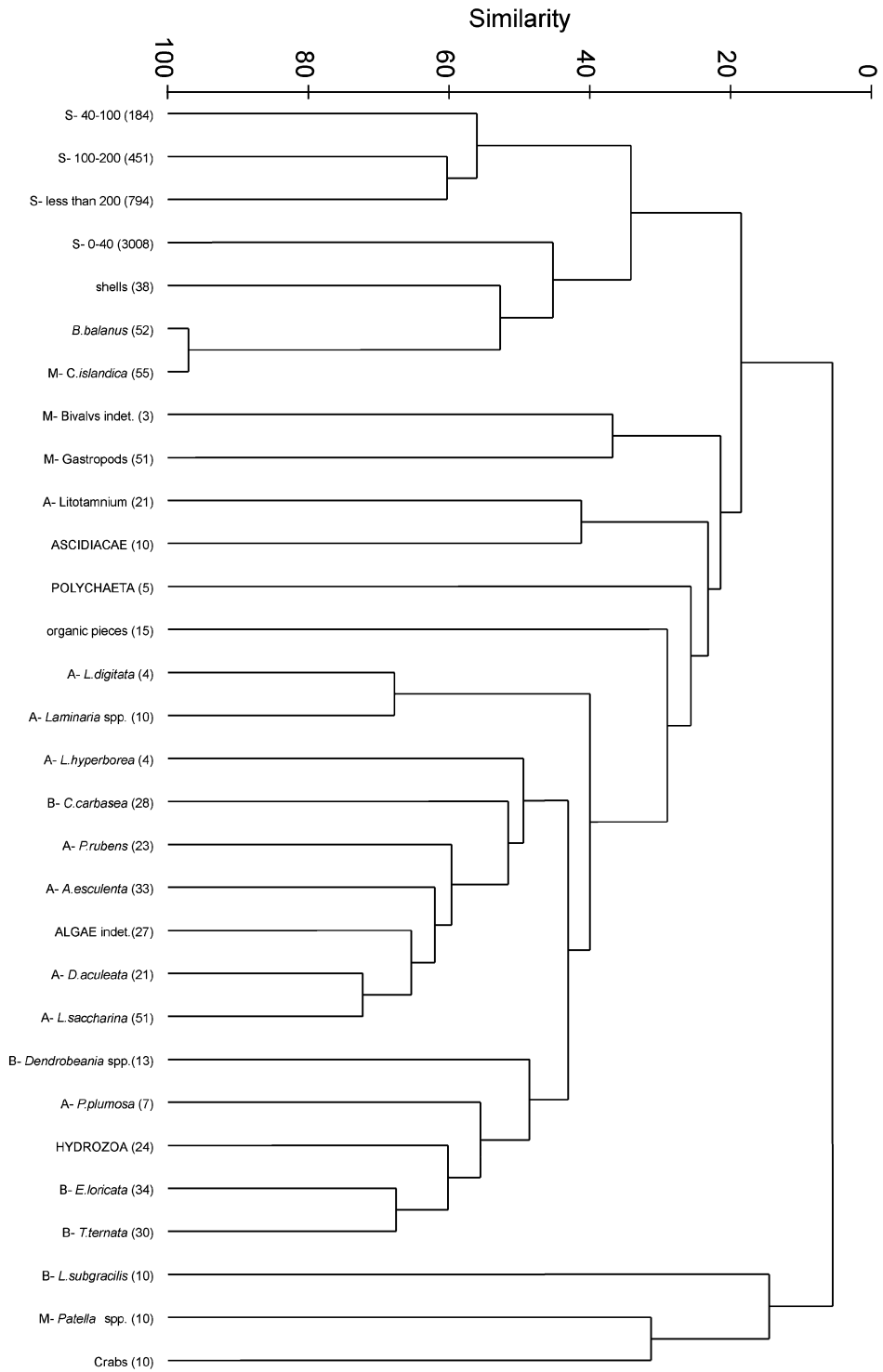


Figure 4. Cluster analyses based on frequency of occurrence data. S, stones; M, Mollusca; A, algae; B, Bryozoa; in brackets, number of individuals or pieces investigated.

Table III. A classification (according to Barnes and Clarke 1995) of some common Arctic bryozoans based on their occurrence as epifauna on biotic and abiotic substrata [in brackets: frequency of occurrence on the rocks (%)/frequency of occurrence on the animals and algae (%)].

Bryozoan species type	Exemplar species
Generalist	
Species which occur widely on rocks, stable hard substrata and animal, algal host	<i>Cribrilina annulata</i> (15/11) <i>Cylindroporella tubulosa</i> (14/9) <i>Harmeria scutulata</i> (24/15)
Host-specific species	
Species found only on specific animal host	Not found
Low-specificity epibiotic species	
Species which occur widely on organisms, algae but rarely on rocks	<i>Celleporella hyalina</i> (3/38) <i>Eucratea loricata</i> (2/13) <i>Tricellaria ternata</i> (2/17)
Background species	
Species which occur widely on rocks, but rarely on organisms, algae	<i>Electra arctica</i> (21/2) <i>Hippothoa arctica</i> (22/1)

In contrast to Antarctic studies (Barnes and Clarke 1995), no host-specific bryozoan was found in this study (see Table III). This may result from a longer period of evolution and isolation of the Antarctic ecosystem in comparison to the Arctic (Dunton 1992).

Cluster analyses reveal two major groups of substrata: flexible (algae, hydrozoa, bryozoan) and stable (stones, shells, molluscs etc.). Glasby (2001) found large differences in abundance of given taxa on fixed versus moving artificial substrata. Previous studies of epiphyte abundance on seagrasses and macro-algae would support his results (Trautman and Borowitzka 1999). This is seen in the present study as well, as it shows differences in community structure between natural moving substrata (algae, bryozoans) and stable, non-moving substrata (stones).

We suggest stony substratum per se is a much more stable substratum in comparison to all the flexible ones (algae, bryozoans, hydrozoans). There are many advantages to living on flexible substrata. Even if a given substratum is seasonal, usually its occurrence is predictable (e.g. algae). Stony polar substrata may be a focus of intense competition between encrusting organisms (Barnes and Kukliński 2003). Recruitment on flexible competitor-free substrata, therefore, is potentially beneficial. Manriquez and Cancino (1996) have also shown that bryozoans can absorb the exudates of algae. That might be especially advantageous in polar regions, where the food supply is highly seasonal. Settlement on algae in hydrodynamically favourable positions above a solid surface provides colonists with better flow and so higher nutrient supply and more efficient evacuation of waste (Wahl 1989).

Erect flexible and encrusting morphologies of bryozoans were present on all types of substrata, while erect rigid colonies only colonized stones, barnacles and molluscs. The solidity of the last three mentioned substrata is maybe why they are preferred by erect rigid morphological forms. Runner morphologies, in contrast, were absent on hydrozoans and bryozoans and dominated the morphological forms present on rocks below 40 m depth. Schäfer (1994) described these to be the primary macrobenthic colonizers of arctic rocks. Due to their primitive colony form (lowest integration within the colony), and fast, directional growth, they are very much adapted to inhabit unstable environments (e.g. small rocks, areas with high sedimentation rate) (McKinney and Jackson 1991; personal

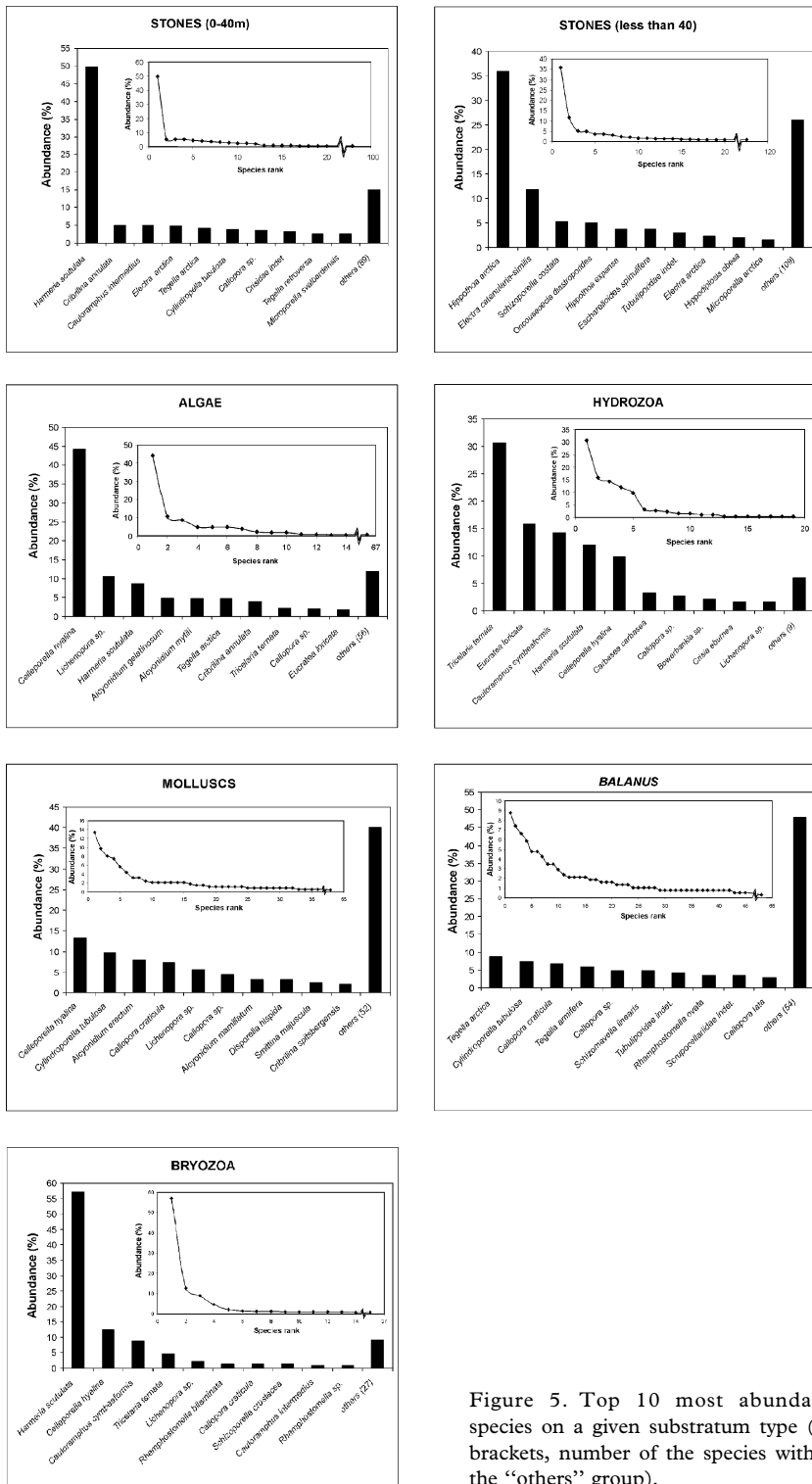


Figure 5. Top 10 most abundant species on a given substratum type (in brackets, number of the species within the “others” group).

Table IV. Proportion (%) of bryozoan morphologies present on a given substratum.

	Stones (0–40 m depth)	Stones (less than 40 m depth)	Algae	Hydrozoa	Mollusca	<i>Balanus</i>	Bryozoa
Membranous uncalcified	0.05	1.27	10.26	2.19	12.76	5.31	1.36
Runners	5.49	53.75	0.88	–	1.19	1.06	–
Encrusting	87.72	44.62	80.04	44.81	82.20	83.29	90.45
Erect flexible	6.74	0.03	8.81	53.01	2.37	10.08	8.19
Erect rigid	–	0.34	–	–	1.48	0.27	–

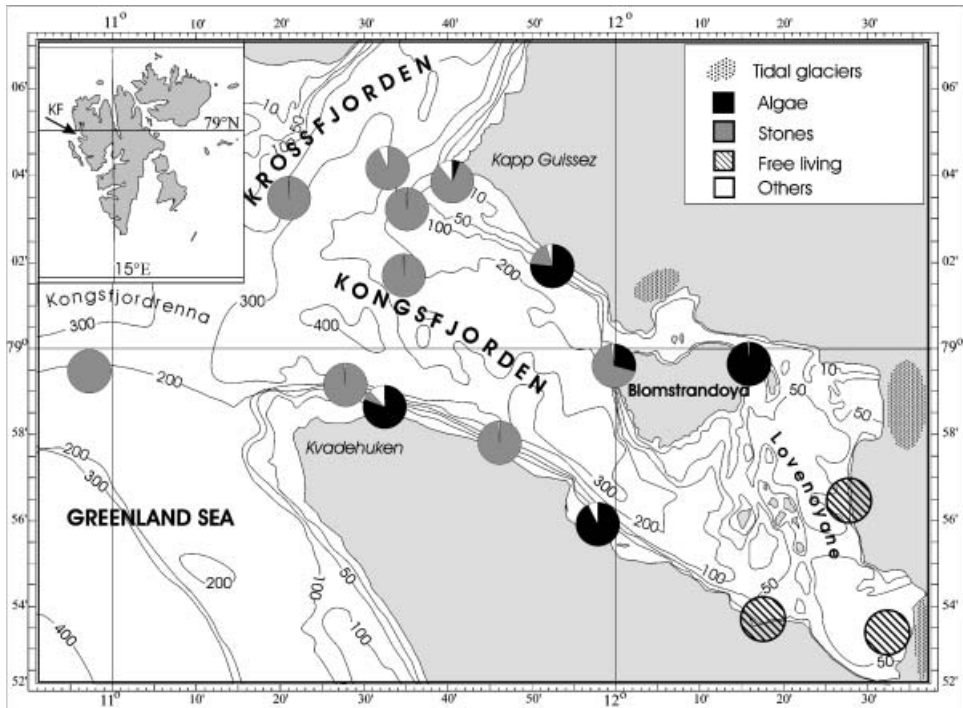


Figure 6. Quantitative ratio distribution of substrata colonized by bryozoans within Kongsfjorden. KF, Kongsfjorden.

observation). Their presence at these depths is probably indicative of disturbance in the area of occurrence, such as by seasonal input of fine sediment. Chemical and biological (e.g. avicularia presence) defence deployed by hydrozoans and bryozoans may explain the lack of runner morphologies colonizing them (Wahl 1989).

As we found across our Spitsbergen substrata, Lippert et al. (2001) found *Celleporella hyalina* dominated six algal species from the Kongsfjorden. This r-selected organism is abundant and widely distributed in the northern hemisphere (Hayward and Ryland 1999). The attributes of this species suit colonization of unstable substrata due to rapid patterns of growth and maturity (Seed and Hughes 1992).

The life history of *Harmeria scutulata*, which dominated shallow stones and bryozoan substrata, is largely unknown. Its lack of ovicells (personal observation) and high abundance

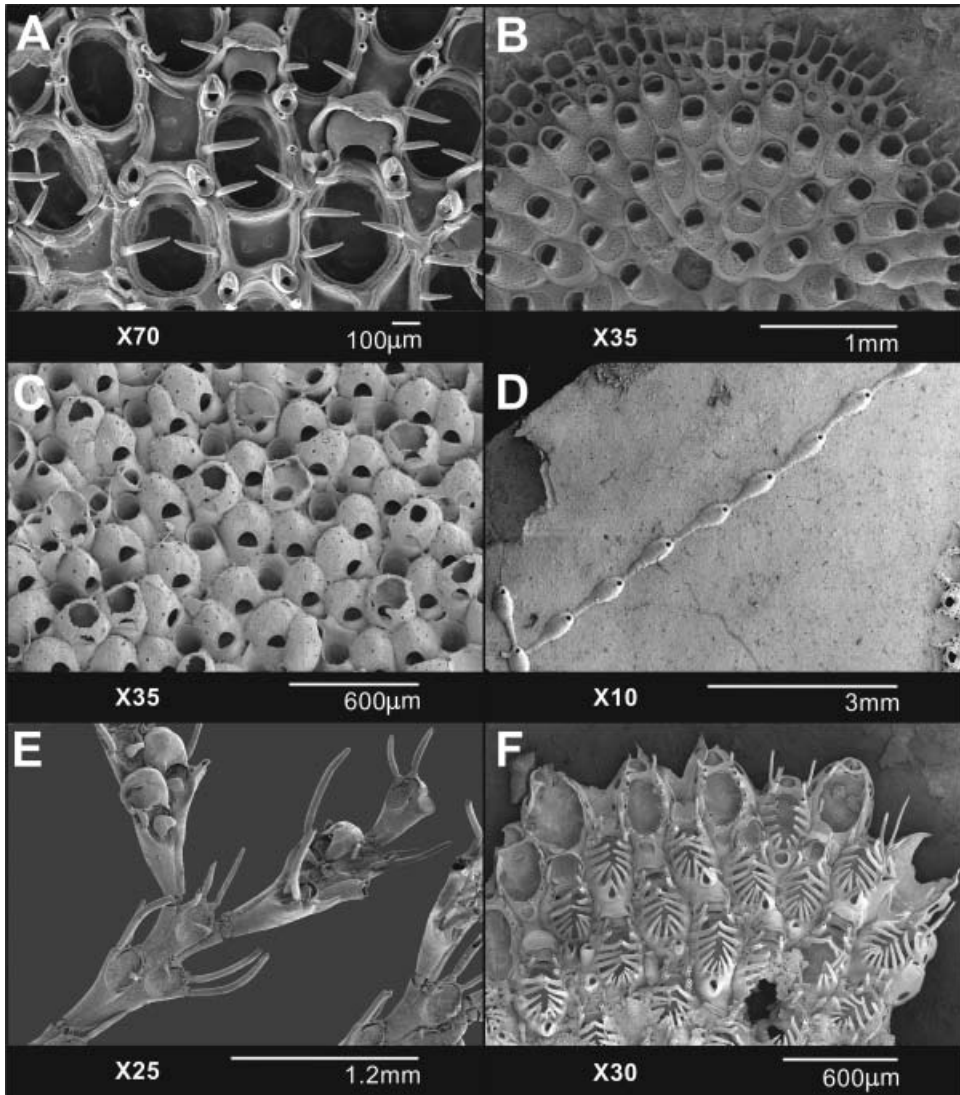


Figure 7. Species playing important role in certain microhabitats: (A) *Tegella arctica*—the most abundant species on *Balanus*; (B) *Harmeria scutulata*—the most frequently occurring species on stones (0–40 m) and the most abundant species on stones (0–40 m) and Bryozoa; (C) *Celleporella hyalina*—the most frequently occurring species on algae, bryozoans, molluscs, and the most abundant species on algae and molluscs; (D) *Hippothoa arctica*—the most frequently occurring and the most abundant species on stones (less than 40 m); (E) *Tricellaria ternata*—the most frequently occurring and the most abundant species on Hydrozoa; (F) *Callopora craticula*—the most frequently occurring species on *Balanus*.

(see Figure 5) would indicate an r-strategist. The habitat of this species is typically shallow waters repeatedly disturbed by ice-flows, fresh-water discharge and tides (Svendsen et al. 2002). Species with K-selected characters would seem unlikely to persist in such a disturbance regime. *Harmeria scutulata* certainly seems to be fast growing and able to colonize quickly. A strongly characteristic feature of the bryozoan communities we studied was the dominance of just a few species, despite the generally high levels of species richness

(Figure 5). This was especially true for stones (between 0 and 40 m depth, *Harmeria scutulata* 50% of all inhabiting species; stones below 40m depth, *Hippothoa arctica* 36%), algae (*Celleporella hyalina* 44%), hydrozoans (*Tricellaria ternata* 31%, *Eucratea loricata* 16%), and bryozoans (*Harmeria scutulata* 57%). Molluscs and barnacles were more evenly colonized by the bryozoan species, as has been found in both temperate and tropical equivalent habitats (Seed 1996).

Overall, all types of substrata in Svalbard waters are colonized by fast-growing bryozoans, which reach maturity very early (crucial for life-cycle closure) in the periodically food-limited and often highly physically disturbed Arctic environments.

Two gradients of substratum distribution were distinguished within our fjordic study area (Figure 6): the inner to the outer part of the fjord (geographic) versus that from the shallow to the deep part of the fjord (bathymetric). Such patterns are connected to clear environmental gradients (sedimentation, depth) along the fjord. The inner fjord has a much higher sedimentation rate, and a fine sediment bottom that is nevertheless more heterogeneous than the outer part (Svendsen et al. 2002). The deep outer region is mostly soft bottom with patchy stones or drop-stones occurrence where availability of substrata for bryozoans is very limited (Zaborska 2001). The shallow area was richer in substrata and sites potentially suitable for bryozoan colonization (Hop et al. 2002). The greatest difference between these two zones (shallow and deep), however, was the presence of algae in the shallow part, importantly adding three-dimensional structure to the system. We found algae to host different assemblages of Bryozoa than the other types of substrata (see Figure 4 and Table I).

Bryozoa are a very diverse group of macro-organisms (see Kluge 1975: 366 species) in comparison to the others in the Arctic (Gulliksen et al. 1999). One of their features which has made them so successful in that region is the ability to inhabit a wide range of substrata and to be highly successful as macrobenthic pioneer species, as identified here.

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References

- Barnes DKA. 1994. Communities of epibiota on two erect species of Antarctic Bryozoa. *Journal of the Marine Biological Association of the U.K* 74:863–872.
- Barnes DKA, Clarke A. 1995. Epibiotic communities on sublittoral macroinvertebrates at Signy Island, Antarctica. *Journal of the Marine Biological Association of the U.K* 75:689–703.
- Barnes DKA, Kukliński P. 2003. High polar spatial competition: extreme hierarchies at extreme latitude. *Marine Ecology Progress Series* 259:17–28.
- Barnes DKA, Peck LS. 1996. Epibiota and attachment substrata of deep-water brachiopods from Antarctica and New Zealand. *Philosophical Transactions of the Royal Society of London* 351:677–687.
- Bray JR, Curtis JT. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27:325–349.
- Cadee GC, McKinney FK. 1994. A coral-bryozoan association from the Neogene of northwestern Europe. *Lethaia* 27:59–66.
- Clarke KR, Green RH. 1988. Statistical design and analysis for a 'biological effects' study. *Marine Ecology Progress Series* 46:213–226.

- Clarke KR, Gorley RN. 2001. PRIMER v5: user manual/tutorial. Plymouth: PRIMER-E. 91 p.
- Dick MH, Ross JRP. 1988. Intertidal Bryozoa (Cheilostomata) of the Kodiak vicinity, Alaska. Center for Pacific Northwest Studies, Western Washington University, Occasional Paper 23:1–133.
- Dunton KH. 1992. Arctic biogeography: the paradox of the marine benthic fauna and flora. *Trends in Ecology and Evolution* 7:183–189.
- Gammelsrod T, Rudels B. 1983. Hydrographic and current measurements in the Fram Strait, August 1981. *Polar Research* 1:115–126.
- Glasby TM. 2001. Development of sessile marine assemblages on fixed versus moving substrata. *Marine Ecology Progress Series* 215:37–47.
- Gulliksen B, Palerud R, Brattegaard T, Sneli J. 1999. Distribution of marine benthic macroorganisms at Svalbard (including Bear Island) and Jan Mayen. Trondheim: Directorate for Nature Management. Research report for DN 1999–4.
- Harmelin JG. 1990. Interactions between small sciaphilous scleractinians and epizoa in the Northern Mediterranean, with particular reference to bryozoans. *Marine Ecology* 11:351–364.
- Hayward PJ. 1980. Invertebrate epiphytes of coastal marine algae. In: Price JH, Irvine DEG, Farnham WF, editors. *The shore environment*. London: Academic Press. p 761–787.
- Hayward PJ, Ryland JS. 1998. Cheilostomatous Bryozoa Part I. Aeteoidea–Cribriloidea. In: Barnes RSK, Crothers JH, editors. *Synopses of the British fauna (new series)*. 2nd edn, nr 10. p 1–366.
- Hayward PJ, Ryland JS. 1999. Cheilostomatous Bryozoa Part II. Hippothooidea–Celleporoidea. In: Barnes RSK, Crothers JH, editors. *Synopses of the British fauna (new series)*. 2nd edn, nr 14. p 1–416.
- Hop H, Pearson T, Hegseth EN, Kovacs KM, Wiencke C, Kwaśniewski S, Eiane K, Mehlum F, Gulliksen B, Włodarska-Kowalczyk M, et al., 2002. The marine ecosystem of Kongsfjorden, Svalbard. *Polar Research* 21:167–208.
- Key MM, Barnes DKA. 1999. Bryozoan colonization of the marine isopod *Glyptonotus antarcticus* at Signy Island, Antarctica. *Polar Biology* 21:48–55.
- Key MM, Jeffries WB, Voris HK, Yang CM. 1996. Epizoic bryozoans, horseshoe crabs, and other mobile benthic substrates. *Bulletin of Marine Science* 58:368–384.
- Key MM, Winston JE, Volpe JW, Jeffries WB, Voris HK. 1999. Bryozoan fouling of the blue crab *Callinectes sapidus* at Beaufort, North Carolina. *Bulletin of Marine Science* 64:513–533.
- Kluge GA. 1975. *Bryozoa of the northern seas of the USSR*. New Delhi: Amerind Publishing. 711 p.
- Lippert H, Iken K, Rachor E, Wiencke C. 2001. Macrofauna associated with macroalgae in the Kongsfjord (Spitsbergen). *Polar Biology* 24:512–522.
- Loeng H. 1991. Features of the physical oceanographic conditions of the Barents Sea. In: Sakshaug E, Hopkins CCE, Oritsland NA, editors. *Proceedings of the Pro Mare Symposium on Polar Marine Ecology*, Trondheim, 12–16 May 1990. *Polar Research* 10:5–18.
- Manriquez PH, Cancino JM. 1996. Bryozoan-macroalgal interactions: do epibionts benefit? *Marine Ecology Progress Series* 138:189–197.
- McKinney FK, Jackson JBC. 1991. *Bryozoan evolution*. Chicago: The University of Chicago Press. 238 p.
- Pechenik JA, Eyster LS. 1989. Influence of delayed metamorphosis on the growth and metabolism of young *Crepidula fornicata* (Gastropoda) juveniles. *Biological Bulletin* 169:417–424.
- Powell NA. 1968. Studies on Bryozoa (Polyzoa) of the Bay of Fundy region: II—Bryozoa from fifty fathoms, Bay of Fundy (I). *Cahiers de Biologie Marine* 9:331–347.
- Ross A, Newman WA. 1996. A new sessile barnacle symbiotic with bryozoans from Madagascar and Mauritius (Cirripedia: Balamorpha): a unique case of co-evolution. *Invertebrate Biology* 115:150–161.
- Różycki O, Gruszczyński M. 1986. Macrofauna associated with laminarians in the coastal waters of West Spitsbergen. *Polish Polar Research* 7:337–351.
- Ryland JS. 1959. Experiments on the selection of algal substrates by polyzoan larvae. *The Journal of Experimental Biology* 36:613–631.
- Ryland JS. 2001. Convergent colonial organization and reproductive function in two bryozoan species epizoic on gastropod shells. *Journal of Natural History* 35:1085–1101.
- Schäfer P. 1994. Growth strategies of arctic Bryozoa in the Nordic Seas. In: Hayward PJ, Ryland JS, Taylor PD, editors. *Biology and palaeobiology of bryozoans*. Proceedings of the 9th International Bryozoology Conference. Fredensborg: Olsen and Olsen. p 173–176.
- Seed R. 1996. Patterns of biodiversity in the macro-invertebrate fauna associated with mussel patches on rocky shores. *Journal of the Marine Biological Association of the U.K* 76:203–210.
- Seed R, Hughes RN. 1992. Reproductive strategies of epialgal bryozoans. *Invertebrate Reproduction and Development* 22:291–300.

- Seed R, Wood V. 1994. Recruitment and mortality of *Alcyonidium hirsutum* (Fleming) and *Flustrellidra hispida* (Fabricius) (Bryozoa: Ctenostomata) within a *Fucus serratus* L. community. *Cahiers de Biologie Marine* 35:305–326.
- Svendsen H, Beszczyńska-Møller A, Hagen JO, Lefauconnier B, Tverberg V, Gerland S, Ørbæk JB, Bischof K, Papucci C, Zajaczkowski M, et al., 2002. The physical environment of Kongsfjorden-Krossfjorden, an Arctic fjord system in Svalbard. *Polar Research* 21:133–166.
- Trautman DA, Borowitzka MA. 1999. Distribution of the epiphytic organisms on *Posidonia australis* and *P. sinuosa*, two seagrasses with differing leaf morphologies. *Marine Ecology Progress Series* 179:215–229.
- Wahl M. 1989. Marine epibiosis: I, Fouling and antifouling: some basic aspects. *Marine Ecology Progress Series* 58:175–189.
- Ward MA, Thorpe JP. 1989. Assessment of space utilisation in a subtidal temperate bryozoan community. *Marine Biology* 103:215–224.
- Węśławski JM, Jankowski A, Kwaśniewski S, Swerpel S, Ryg M. 1991. Summer hydrology and zooplankton in two Svalbard fiords. *Polish Polar Research* 12:445–460.
- Zaborska A. 2001. Lithology of the fiordic bottom sediments, Kongsfjorden (Spitsbergen) [MSc thesis]. Gdynia (Poland): University of Gdańsk. (Pol).
- Zimmer RL, Woollacott RM. 1977. Metamorphosis, ancestrulae, and coloniality in bryozoan life cycles. In: Woollacott RM, Zimmer RL, editors. *Biology of bryozoans*. London: Academic Press. p 91–142.