

Hard-bottom benthic ecosystem in Kongsfjorden, a glacial fjord in the Arctic

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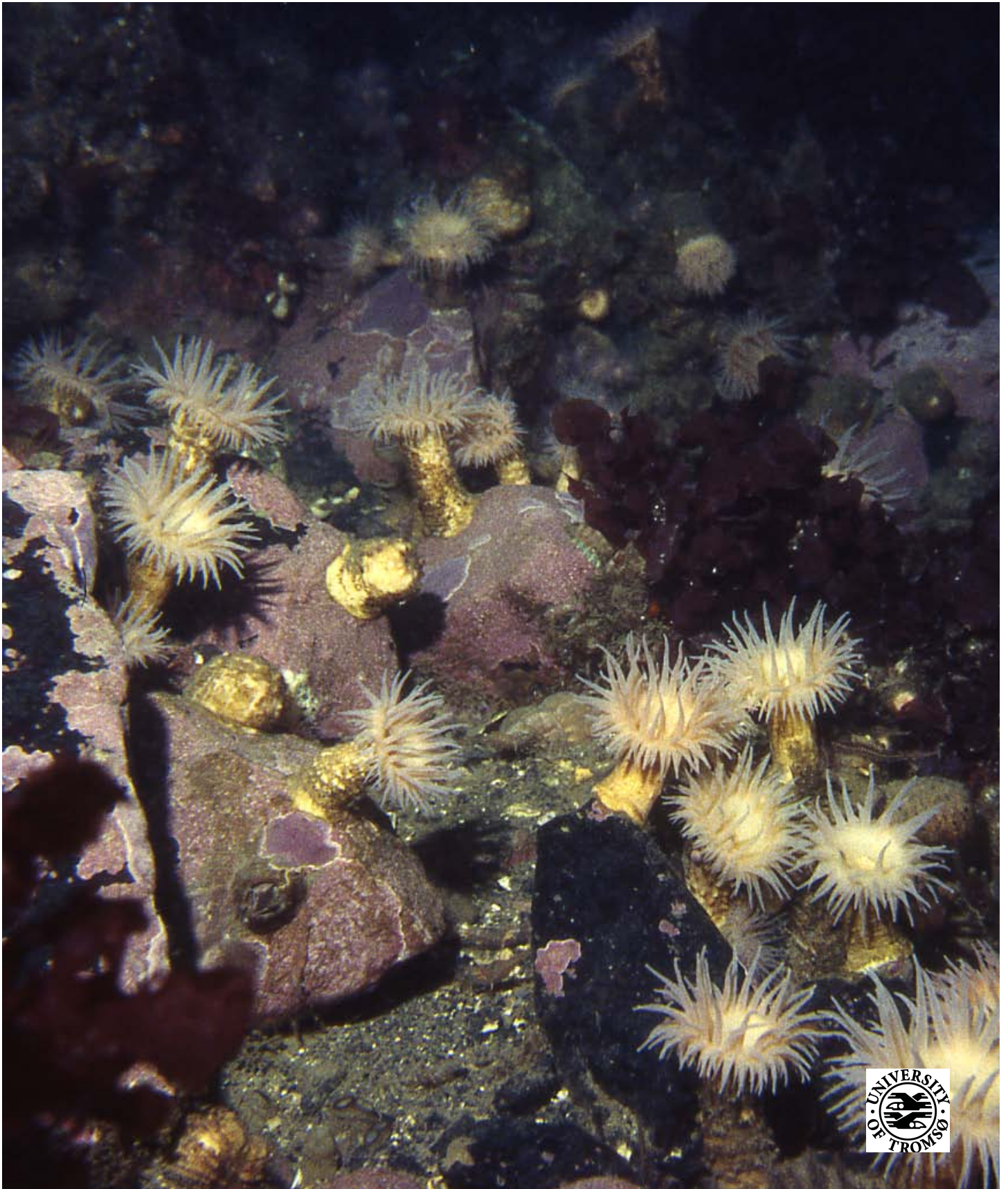


Photo on front page: Haakon Hop.

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"...whether there be knowledge, it shall vanish away".
1 Corinthians 13:8

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Summary

Subtidal hard-bottom habitats constitute substantial parts of the Arctic fjord ecosystem. There is a deficiency in complex surveys of the composition of hard-bottom fauna in the Arctic. The aim of this study was to increase the understanding of how animals are distributed on hard-bottom and their role in the marine ecosystem in the Arctic.

A baseline study of hard-bottom zoobenthos in relation to environmental gradients in Kongsfjorden, a glacial fjord in Svalbard, is presented, based on sampling in 1996 and 1998. The inventory resulted in a total of 403 species in 62 samples from 0 to 30 m depth along five transects. Because 32 taxa could not be identified to species level and because 11 species are probably new to science, the total number of identified species was 360. Of these, 47 species are new for Svalbard waters. Bryozoa was the most diverse group concerning species.

Species richness, frequency of species occurrence, mean abundance and biomass generally decreased towards the tidal glaciers in the inner Kongsfjorden. The diversity was consistently low at shallow depths, whereas the non-linear patterns of species composition of deeper samples indicated a presence of complicated hydrographical conditions between surface and deeper water masses at 15-20 m depth. Decreased species richness and occurrence on most shallow parts of transects were accompanied with high peculiarity of species composition. Overall faunal depletion towards the inner part of the fjord as well as a decrease in diversity at 15-20 m depth was not accompanied by more pronounced faunal peculiarity. Among eight environmental factors, depth and distance from the glacier were most important for explaining variance in the composition of the zoobenthos.

Groups of “colonial” and “solitary” species differed in diversity, biogeographic composition and distribution by location and depth as well as in relation to other environmental factors. “Solitary” species made a greater contribution than “colonial” species to total species richness, total occurrence and biomass in samples, and were more influenced by the depth gradient.

Biogeographic composition was sensitive to variation of environmental characteristics over the studied depth range and revealed features of both Arctic and sub-Arctic properties of the fauna. Shifts in climate-related environmental variables are expected to influence the biota. Such impact on composition, distribution of zoobenthic species will likely result in shifts in ecosystem functioning.

The contribution of the survey to total inventory of species in the Svalbard marine ecosystem cannot be counted as complete as indicated by the cumulative species count. For some taxonomic groups, like Bryozoa, our data showed good correspondence with estimations made by other authors in similar habitats and depth ranges. The probable underestimation of diversity for some other groups, like Echinodermata, can be reduced by improvement of sampling procedures.

A list of recorded species with distribution and abundance characteristics is given in the Appendix. We contributed to the knowledge of Kongsfjorden ecosystem not only with the biotic data, but also with a description of physical environment at sampling sites.

Seven community types were identified on hard substrata in Kongsfjorden. The method of adequate determination of community types included consideration of the species' potential role in community, accounting for dominant species and similarity in species composition. Special attention should be paid to define the dominant taxa to avoid mixing of different community types.

“The *Symplectoscyphus* community”, “The *Balanus* community” and “The Branched bryozoans community” were named after the foundation species, which are primarily responsible for establishing the associations. “The Amphipoda community” and “The Bivalvia community” received names taken into account the role of these taxa in total similarity of samples of these community types. “The Developed fauna” community and “The Impoverished fauna” community types did not have clearly dominant taxa, critically differing in the values of species diversity and abundance. Amphipoda and *Symplectoscyphus* communities were specific for most shallow habitats on upper limits of the infralittoral. Bivalvia community was typical at the deeper parts of transects where gravel substrata predominate. Branched bryozoans community occupied depth 2.5 – 10 m. In inner part of the fjord at the same depth range, it was replaced by the “Developed” community type. *Balanus* community was represented at the range of depths from 5 m to 30 m, being most widely distributed on hard-bottom in

Kongsfjorden. Patches of bedrock with extremely low benthic diversity can occasionally be found in the variety of transects and depths. “The Impoverished fauna” community type is most “artificial” because of different causes of low diversity in samples. Macroalgal species were not among factors best matching patterns of zoobenthos distribution. Variables with the highest impact were: depth, *Balanus* and branched bryozoans biomass.

Specific approach to the diversity study of hydroids in Kongsfjorden allowed evaluation of the role of this particular taxon in hard-bottom habitats and estimation of importance of abiotic factors in validation of species separation for taxonomic purposes.

The studied habitats and transects should be counted as useful for climate change-related monitoring of diversity on hard-bottom and research on ecosystem functioning. Future studies could reveal new species at these sites related to altered distribution ranges and invasions of species.

List of papers

- I. Voronkov A., Hop H., Gulliksen B. 2013. Diversity of hard-bottom fauna relative to environmental gradients in Kongsfjorden, Svalbard. *Polar Research*. doi: 10.30402/polar.v32i0.11208.
- II. Voronkov A., Hop H., Gulliksen B. Zoobenthic communities on hard-bottom habitats in Kongsfjorden, Svalbard. Manuscript submitted to *Marine Biology Research*.
- III. Voronkov A., Stepanjants S.D., Hop H. 2010. Hydrozoan diversity on hard bottom in Kongsfjorden, Svalbard. *Journal of the Marine Biological Association of the United Kingdom*. 90:69-84.



Divers before sampling in turbid waters at the mountain base of Colletthøgda, (inner-fjord transect OSS1), Kongsfjorden, Svalbard. (Photo: Andrey Voronkov)

Paper III is reprinted with the permission of The Marine Biological Association of the United Kingdom.

Introduction

The basic attribute of marine ecosystems is their community-associated species composition (Bluhm et al. 2011). Information on species composition together with data on the abundance and biomass promotes a variety of function-related studies of marine ecosystems. Society is faced with recent global environmental and anthropogenic changes and interested in the predictions of consequences in order to reduce potential negative feedbacks from the nature. The most pronounced changes have occurred in the Arctic marine ecosystem (Wassmann et al. 2011). Within this context, a number of scientific projects (e.g. MarBEF, CoML) prioritized attention to biodiversity assessments, particularly in the Arctic (e.g. ArctEco, ArcOD (Gradinger et al. 2010)). Implementation of such projects has the goal to fill the gap of insufficient knowledge of the biodiversity in the Arctic subtidal hard-bottom areas (Hop et al. 2011).

Hard-bottom zoobenthic surveys in the Arctic before the era of scuba diving are very limited (e.g. Spärck 1933; Thorson 1933, 1934; Madsen 1936). The use of scuba equipment opened broad possibilities for subtidal biological investigations. However, there are logistic challenges due to difficult conditions of distant Arctic ecosystems. Specially trained and equipped scuba divers must be involved in such investigations. The identification of fauna down to species level usually requires participation of several taxonomic specialists. A complex data set, distinguishing colonial from solitary organisms, and needs for analyses using multivariate statistical techniques to achieve evaluation of biodiversity make estimations very challenging.

Another question lies outside of the problems of biological material accessibility and scientific complexity of material processing. It is hidden in the area of scientific training. There are not so many scientists anymore who can be inspired by classic zoological sample treatment routines. Actually, collection, primary processing (sorting), preservation, identification, labeling, cataloguing, depositing to museum's collections, collection of the data from other specialists, and incorporation of the data into user friendly database with quality control on each stage of the process involves much work time and are not regarded as the most exciting. Comprehensive zoobenthic surveys are rare, or, if performed, sometimes not of the best quality and results often remain unpublished.

For these reasons, only a limited number of complex faunistic surveys of the composition of hard-bottom fauna in the Arctic have been carried out and published data are often fragmentary (Propp 1971; Gulliksen 1978, 1979; Gulliksen et al. 1980; Golikov & Averintsev 1977; Averintzev 1992; Golikov et al. 1993; Jørgensen & Gulliksen 2001; Chenelot et al. 2011).

The objective of the present study is to contribute to the knowledge on the biodiversity of the subtidal hard-bottom in a fjord ecosystem in the Arctic, namely in Kongsfjorden on Svalbard.

Kongsfjorden is located on the north-western part of Spitsbergen (Svalbard archipelago) at 79°N latitude. It is a glacial fjord influenced by both Arctic and Atlantic waters masses. The warm West Spitsbergen Current interacts with local environmental conditions to create ecologically important gradients in temperature, salinity, turbidity, and concentrations of organic and inorganic suspended and sedimented particulate matter (Svendsen et al. 2002; Cottier et al. 2005). The development of national and international research programs (e.g., Swerpel & Weslawski 1989; Warwick et al. 2003), better logistic infrastructure and the establishment of the Kings Bay Marine Laboratory (2005) give us unique possibility to use the fjord as a reference ecosystem. Both the physical and the biological environment has received a considerable amount of research attention (Hop et al. 2002, 2006; Svendsen et al. 2002), which is a promising advancement for marine ecological and diversity investigations.

The present investigation is a combination of study performed using classic faunistic methods and contemporary methods of diversity and community analysis. Contemporary methods of data analysis and presentation of results were mastered during the study at the University of Tromsø, in discussions and communication with specialists who belong to the national Norwegian and international scientific community. The classic methods used in the present research are based on a long tradition of taxonomic and faunistic studies at the Zoological Institute in St.-Petersburg, Russia.

The specific of the present study is that it has certain descriptive components in addition to explanatory ones. The descriptive character of the work presumes that descriptions could be quite extensive. The performance of the project included the process of overcoming the contradiction between needs of extensive descriptions and common journal rules, which require papers to be as compact as possible.

Collected data on zoobenthos distribution have multidisciplinary importance. From one side, they improve the knowledge on the ecosystem, and from another they can be used for taxonomic purposes, for example, as instrument for illustration of species distinctness.

The culture of collection and treatment of the collected samples is something that disappear very fast if there is no direct transfer of such scientific knowledge from generation to generation of benthologists. So, this baseline study can be viewed partly as promoting the transfer of the traditional habits and standards of faunistic research to future generations of marine zoologists.

Objectives

The overall aim of this study is to present detailed background information on benthic biodiversity in a fjord ecosystem in the Arctic.

Specific objectives were:

1. To describe the species composition and abundance of hard-bottom benthos in Kongsfjorden, Svalbard in spatial gradients of environmental conditions (Paper I);
2. To determine zoobenthic communities on hard-bottom in Kongsfjorden, and to describe their composition and variability (Paper II);
3. To provide an example of a biodiversity study, which estimates the role of a particular taxon (Hydrozoa) in hard-bottom habitats and evaluates the importance of abiotic factors in separation of species for taxonomic purposes (Paper III);
4. Estimate potential relationships of diversity to environmental changes, with emphasis on climate-related changes (Paper I).

Material and methods

Physical environment and considered gradients

The physical environment of Kongsfjorden is described in details in Paper I. The most important features, related to our study were as follows: Kongsfjorden, a glacial fjord 32 km in length, and width across the opening about 17 km, has gradients in environmental parameters. This happens mainly because of: 1) absence of a sill at the fjord's mouth, which creates conditions for penetration of warm and saline Atlantic waters into the fjord system; 2) Coriolis effect of rotational dynamics and local winds, which makes for definite currents circulation pattern and tidal waves, and 3) presence of negative net balance tidal water glaciers in inner part of the fjord, which supply fresh water and suspended particulate matter to the fjord system. Hard substrata, represented by bedrock in shallow parts, are typical for exposed locations, such as land points, rocky outcrops and rocky islands along the northern coast of Kongsfjorden. The coast also contains gravel and boulder beaches, which could be considered hard substrata, as well as sandy beaches in more sheltered areas.

Environmental gradients are described in accordance with the classification presented in Table 1 (Paper I). Gradients considered were: distance of sampling area from the Kronebreen glacier, depth, and the main character and composition of the substratum. The gradients in the amount of silt on substratum, substratum angle, currents and wave activity were described as relative characteristics, without precise measurements, using method and in accordance to the classification presented in Table 1 (Paper I). Substratum types were distinguished according to a classification that has been used to describe the marine ecosystem of Kongsfjorden (Hop et al. 2002). Therefore, in our work we contributed to the knowledge of Kongsfjorden ecosystem not only with the biotic data, but also with a description of physical environment at sampling sites. Most of previous hydrographic studies were devoted to estimations of patterns on scale of the whole fjord, hundreds or tens of metres (Svendsen et al. 2002). Data on environmental gradients structure are collected from localities distant from shores due to depth limits for research vessels. There is evident lack of information about features of local environmental conditions, with no detailed information on very local scale for Kongsfjorden. We can presume, that decrease in the faunal diversity at depth 15-20 m, differences in zoobenthic species composition between habitats at 5-10 m depth and those at 25-30 m depth, as well as singularity of fauna composition in upper parts of the transects are evidences of stratified or more complicated structures of the physical environment, which are still not well documented in Kongsfjorden. There is clear need for detailed hydrographic study of near-shore shallow (0-50 m depth) areas, also on a seasonal aspect.

Collection details and data preparation

Benthic samples from hard substrata in Kongsfjorden were collected by diving expedition organized by the Norwegian Polar Institute in August-September 1996 and 1998. Investigations were carried out on 5 transects: Kapp Mitra (abbreviated MITR), Kapp Guisnez (GUIS), Hansneset (HANS), Juttaholmen (JUTT) and Colletthøgda near Ossian Sars Mountain (OSSI). Transects are placed along the main fjord's axis that corresponds to the gradient of environmental conditions. Transect MITR is from the most outer part of the fjord near the opening to the open sea (Fram Strait/Greenland Sea), the transect OSSI correspondingly is from most inner part of the fjord, which is close to the tidal glaciers Kongsvegen and Kronebreen, as well as Kongsbreen (Lefauconnier et al. 1994; 1999; Fig. 1).

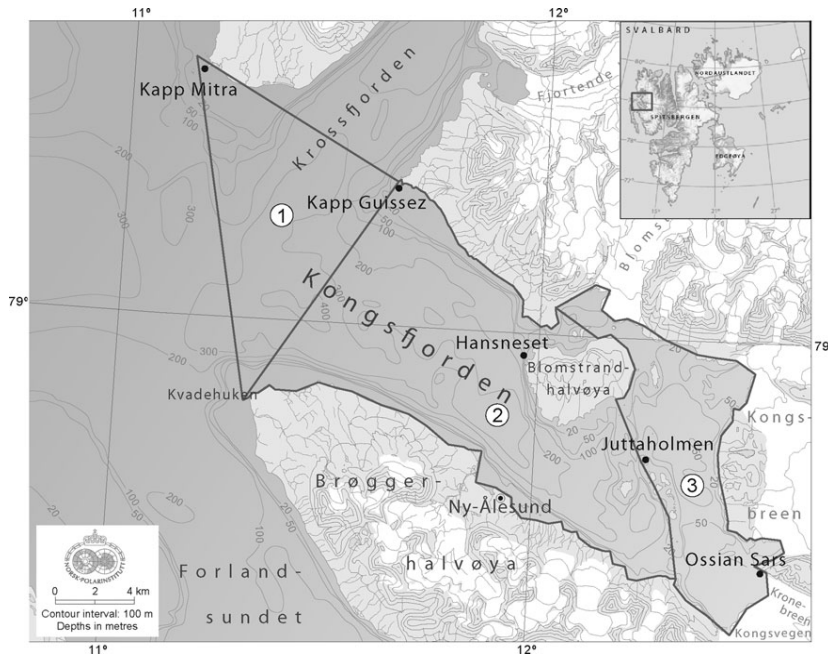


Fig. 1. Kongsfjorden with locations of the sample transects (black dots). Lines define the outer (1), middle (2) and inner (3) parts of the fjord (modified after Hop et al. 2002).

Hard-bottom is recognized as bedrock, rock or coarse gravel, including pockets or thin layers of softer sediments often found on the surface of rocky substrata.

Samples were collected from the tidal zone, depths ca. 0 m down to 30 m, which is usually regarded as the safety limit for scuba diving without use of special breathing mixtures. In some parts of the fjord hard substrata extend to 50 m depth and deeper. Thereby this is a study of the upper 30 m hard-bottom belt of five locations in Kongsfjorden. In the inner part of the fjord sampling was restricted to 15 m depth at JUTT and 5 m at OSSI because hard substrata were covered with a thick layer of sediments below these depths. Samples from 0 m depth on transect MITR were not collected because the site is extremely exposed to wave impact and unsafe to sample when vessel-time was available. General sampling design included the collection of benthic flora and fauna by scuba divers from square frames 0.25 m² from each of depths 30 – 25 – 20 – 15 – 10 – 5 – 2.5 – 0 m on each transect. From each of these depths, where the hard substrata were found, two samples were collected. Sampling depths should be considered as presented depth plus-minus 0.5 m because of absence of correction in relation to tides (Svendsen et al. 2002)). Digital video recording of each transect was conducted along a line (nylon rope) from the surface to the maximum sampling depth.

The collection sites were selected on the basis of the topography given in sea charts, the type of substratum in the tidal zone and observations made during exploratory dives before sampling was carried out. The samples were collected from definite depths, based on the diver's depth-loggers, and characteristic habitats and communities generally found at those depths. Frames were dropped to the bottom when arriving at the assigned depth and flipped sideways 1-3 times to assure some level of randomness in samples ("haphazard sampling"). Hard-bottom habitats are often very heterogeneous, and differences between communities from the same depth and transect were sometimes very significant. Therefore, data about samples from the same depths on transects were not combined, but considered separately. In the further analysis we used data from a total of 62 samples.

Macrobenthic organisms were handpicked from the hard surfaces. Algae and organisms attached to the surface were cut loose with a diver's knife. Animals attached to algae were included; all macroalgae attached to the bottom within the sampling frame were removed and collected. Collected material was, often together with parts of the substratum, placed into diver's sampling bags

with a mesh size of 1 mm. Small motile and sessile organisms were collected using an underwater suction pump (Lønne 1988). Stones, empty shells etc. within the frames were examined for epibionts.

Based on the experience from the present study, we can suggest some improvements of the sampling procedures for future research. Our sampling design, which used standard two 0.25 m² square frames at each depth on transects, lowers the chance of recording large and sparsely distributed individuals. It leads to the situation, when the diversity of some groups, such as Echinodermata, can be underestimated. It also makes accounting of fouling species more difficult. A sampling design that includes more frames of different sizes (0.25-0.01 m²), together with recordings of large rare individuals or colonies along transects, may yield a more complete inventory of species (e.g., Scarlato et al. 1967).

Benthic animals were taxonomically sorted in the laboratory to phyla and preserved in 4% formaldehyde or 75% alcohol. Organisms were later identified to the lowest possible taxa by specialists. Abundance and biomass were measured and biomass (g m⁻²) was considered as wet weight of whole individuals or colonies. Hard parts, such as shells, were included in the wet weight. The weight of encrusting bryozoan species was estimated as a colony's size multiplied by the weight of 1 mm² of the colony. Abundance was estimated as number of individuals (ind. m⁻²). A list of taxa identified in survey, with taxonomic authorities and year for descriptions, is given in the Appendix. Identification specialists are listed in "Acknowledgments".

Biogeographic characteristics of "colonial" and "solitary" species and affiliation of species with different functional groups were used in the description of biodiversity. Biogeographic types of species were defined based on the distribution patterns for shelf species found in the Eurasian Arctic seas (Sirenko et al. 2009). In addition, data on macroalgal species composition and biomass for HANS (Hop et al. 2012) and for other sites (H. Hop and N.A. Kovaltchouk, unpubl. data) were used in estimations of relative importance of different factors for zoobenthic communities' distribution.

All collected data were incorporated into Excel spreadsheets, with joint biotic and environmental data. The data-files are user-friendly and have wide potentials for future use in comparative investigations.

Data analysis

To adequately describe the fauna, it is necessary to consider different scales of diversity measures (Gray 2000). We present an analysis of the data of the hard-bottom zoobenthos in Kongsfjorden at the sample level and in terms of combined data for transects and depths, and also presenting general features of diversity in the fjord as a sum of data from the transects and depths.

Comparisons of zoobenthic diversity were done mainly based on species richness (SR), average occurrence (AO) and frequency of species occurrence (FO) in the samples. Species richness was determined as the total number of species in a sample or in a group of samples. The AO for a set of samples was the total number of species records averaged per sample. The FO was the number of species records expressed as a percentage of all species records in a set of samples. The coefficient of variation applied is the ratio of the standard deviation to the mean.

Using diversity indices directly based on abundance data is difficult for hard-bottom samples due to the frequent occurrence of colonial animals. Difference in the number of samples from transects and depths as well as unequal number of samples within different community types limit the statistical treatment of combined data.

Obtained data were treated by methods of univariate and multivariate statistics. Multidimensional scaling, BIO-ENV, SIMPER, ANOSIM and cluster analysis were conducted using the statistical package PRIMER 5.2.9 (Clarke & Gorley 2001; Clarke & Warwick 2001). Canoco for Windows 4.55 was used to conduct Canonical Correspondence Analysis and CanoDraw for Windows 4.14 to create resulting plots from the analysis (ter Braak & Smilauer 2002).

Multidimensional scaling, or Kruskal's non-metric MDS, represented our samples (or data summarized by transects or depths) as points in two-dimensional space. Relative distances between points are in the same rank order as the relative dissimilarities of the samples, measured from the Bray-Curtis coefficients.

Hierarchical agglomerative cluster analysis (based on group-average link) was conducted for species lists to illustrate if there are groups of samples with similar species composition, and, if yes, what is the character of differences between these groups. In all our MDS analyses the stress, or distortion between the similarity rankings and the corresponding distance rankings in the ordination plot, was low. In this case, Clarke & Warwick (2001) advice to use MDS instead of cluster analysis. However, for Paper III, MDS ordination is > 0.1 , which makes the use of the cluster analysis reasonable. Also, dendrogram labelling options better demonstrate relation of sample groups to depth and distance from glaciers gradients.

Primer's ANOSIM, a non-parametric analysis of Bray-Curtis similarity (Bray & Curtis 1957), was used to show the significance of differences between community types, defined *a priori*. The null hypothesis, which postulates no difference in species composition between community types, was tested. A test statistic (R) reflected the observed difference between community types, contrasted with differences among samples within each community type. Positive values (up to 1.0) could indicate that the similar samples are within the selected groups, values close to zero indicate that high and low similarities are mixed and there is no relation to the group, and negative values (to -1.0) indicate that the most similar samples are outside of the groups. To test the statistical significance, ranked similarities within and between groups were compared with the similarity generated for the samples randomly assigned to groups. The observed value of R was compared against the random distribution to assess how significant is the difference. Pairwise R values also gave an absolute measure of how far the groups are separated from each other.

SIMPER, Similarity Percentages routine, was used to determine the species that were most important in creating the observed pattern of similarity between groups of samples. This method calculates Bray-Curtis similarity for each sample in one group compared to each sample in another. The mean similarity between compared groups, calculated for each species, gives in turn the relative contribution (%) of species to total similarity.

The BIO-ENV procedure was conducted to match biotic to environmental pattern. The routine calculates a measure of agreement between fixed biotic dissimilarity matrix and each of the possible abiotic (or biotic if they are used as environmental factors) triangular matrices. A standard Spearman rank correlation coefficient was computed for all possible combinations of environmental variables. Results showed which variables and in which combination are required to maximize the matching coefficient.

Canonical correspondence analysis (CCA) was used to relate the species and samples data to environmental variables. The method operates on data on occurrences or abundances (biomass) of species and data on environmental variables at sites, and extracts from the measured environmental variables' synthetic gradients (ordination axes) that maximize the niche separation among species (ter Braak & Verdonschot 1995). Results of the analysis were visualized by plotting of ordination diagram using CanoDraw for Windows 4.14 program. On the ordination diagram, samples and species are represented by dots and environmental variables by arrows, reflecting relative position of samples and species against environmental variables. The length of arrows reflects how much weight has the variable in explanation of variability between samples and species (Jongman et al. 1987). Monte-Carlo permutation test determined the statistical significance of the relation between the species and the set of environmental variables, testing the null hypothesis that there is no relation. A test statistic, F_0 , was calculated, which expresses how strongly the species data respond to the environmental data. Reference distribution for the test statistic under the null hypothesis was checked against F_0 , calculating the probability (P-value) that F_0 or larger values occur in the reference distribution.

Results and discussion

Diversity of hard-bottom fauna

Hard substrata are indispensable parts of the Kongsfjorden ecosystem. Investigation of the hard-bottom zoobenthos in Kongsfjorden was started in 1962 by the French expedition Recherche Cooperative sur Programme 42. Extensive biological samples from different transects and points in Krossfjorden, Kongsfjorden and the Forlandsundet area were collected (Lagardere 1968). Unfortunately, most of data collected by the expedition remain unpublished. The only published work presents the diversity of Crustacea in the fjord at a depth range of 5 to 40 m. Next phase of investigations of the Kongsfjorden macrobenthos started in the late 1970'ties. Since that time several works containing zoobenthic species lists have been published (Ambrose & Leinaas 1988; Hansen & Haugen 1989; Włodarska-Kowalczyk et al. 1998; Jørgensen & Gulliksen 2001; Lippert et al. 2001; Kendall et al. 2003; Weslawski et al. 2003, 2006; Laudien et al. 2004; Lippert 2004; Sahade et al. 2004; Wessels et al. 2004, 2006; Włodarska-Kowalczyk & Pearson 2004; Bick & Arlt 2005; Kaczmarek et al. 2005; McMahon et al. 2006; Carlsen et al. 2007; Beuchel & Gulliksen 2008; Kedra et al. 2011). Special attention has been paid to specific benthic taxa: benthic Foraminifera (Elverhøi et al. 1980); Porifera (Assmann 2004); Hydrozoa (Ronowicz 2007; Ronowicz et al. 2008; Voronkov et al. 2010); Mollusca (Włodarska-Kowalczyk 2007); Crustacea (Blazewicz-Paszkowycz & Sekulska-Nalewajko 2004); Bryozoa (Gontar et al. 2001; Kuklinski 2002, 2005; Kuklinski & Barnes 2005a, b; Kuklinski et al. 2005, 2006; Kuklinski & Bader 2007); and Sipuncula (Kedra & Murina 2007; Kedra & Włodarska-Kowalczyk 2008). However, the inventory of the fauna cannot be considered as complete. Main attention has been paid to soft-bottom benthos, and faunal diversity on hard substrata is clearly underestimated. Part of our study presented below contributes to the aim of diversity evaluation of Kongsfjorden hard-bottom subtidal zoobenthos. Specific tasks include:

- general considerations of zoobenthos composition in samples;
- analysis of zoobenthos distribution along fjord's axis and in a depth gradient;
- estimations of abundance and biomass on transects and depths;
- determining of relative importance of different environmental factors with regard to zoobenthic species.

General characteristics of zoobenthos composition in samples

In our Kongsfjorden samples, 360 species were identified. In addition, our samples contained 32 taxa that lacked obvious characteristic identification features and could not be identified to species level but should be considered as separate species. Eleven species are new or probably new to science. The total SR of our samples was around 403 species (Supplementary Table S1). The cumulative species count curve (Clarke & Warwick 1994) is not asymptotic, which implies that total SR has the potential to rise with increased sampling effort.

Our samples contain 22.1% of the total number of species of zoobenthic invertebrate macroorganisms recorded to the date in Svalbard waters. The majority of species we found have been recorded previously for Svalbard area. Compared to the list of the marine macro-organisms in Svalbard waters, published by Palerud et al. (2004) and it's previous version (Gulliksen et al. 1999) that also include Jan Mayen area and contain some synonyms, 47 species from our samples should probably be considered new for the area (Supplementary Table S1).

The 403 species represented 11 phyla of animals. In our samples for majority of main supraspecific taxa, the number of species is < 50 % of total number of species recorded in specific taxa in the Svalbard area, except for Bryozoa and some taxa with low species richness. More extensive sampling will reduce the underestimation of diversity on hard substrata. Our data on species composition showed good correspondence with estimations made in other studies in similar habitats and depth ranges (Assmann 2004, Kuklinski et al. 2005, Ronowicz 2007). The diversity of some groups, such as Echinodermata, seems to be underestimated in our survey, probably because of our

sampling design. Among important taxa, bryozoans showed the highest SR and predominated among species that were most widely distributed at the collection sites.

Despite several studies on the soft-bottom fauna in Kongsfjorden (e.g., Kendall et al. 2003; Laudien et al. 2004; Włodarska-Kowalczyk & Pearson 2004; Kaczmarek et al. 2005), there is still no complete published list of soft-bottom species. Comparing soft- and hard-bottom fauna in terms of diversity is therefore difficult. It is known that biodiversity and density are generally higher on coasts compared to off-shore areas (Gray 1997; Weslawski et al. 2003), although the magnitude of difference may vary depending on scale and geographic position. Based on dredged samples from a single expedition, Kaczmarek et al. (2005) reported the presence of 123 taxa in a soft-bottom association at depths ranging from 5 to 50 m. This is 3.3 times lower than the number of species we recorded on hard-bottom in our study.

Zoobenthos distribution along fjord's axis

Species richness varied within the fjord and was highest along transects from the outer and middle parts of fjord. The number of species in samples varied broadly, even among samples from the same transect and depth. This resulted in a high variance when averaging species richness data by transects and depths. Generally, the mean number of species per sample was reduced on transects close to the Kronebreen glacier compared to transects further out in the fjord. Decreased diversity in the inner parts of fjords has been demonstrated by many studies of the soft-bottom (e.g., Schmid & Piepenburg 1993; Kendall 1994; Włodarska-Kowalczyk & Pearson 2004; Kaczmarek et al. 2005) and intertidal habitats (Brattegard 1966). However, the decrease, according to our data, was not gradual. Lower diversity on the GUIS transect compared to HANS was probably related to less abundant *Balanus balanus* associations at GUIS. The reason for such limited distribution of this highly important habitat-forming species is not clear, but could also reflect patchiness in the hard-bottom environment. Decreased diversity on hard bottom in the inner part of the fjord was associated with a high percentage of species widely distributed on transects. These species are common and can resist chronic natural disturbance connected with glacier run-off to inner fjord habitats (Włodarska-Kowalczyk et al. 2005). Therefore, the total faunal depletion was not accompanied by significant strengthening of faunal peculiarity.

Fisher's F-test indicated that Bray-Curtis dissimilarity of transects, based on the presence/absence of species and standardized occurrence of species in samples on transects, was insignificant for samples from the MITR, GUIS and HANS transects. Differences in species composition between the JUTT and OSSI transects were significant ($P < 0.05$) and they differed significantly from other transects as well.

The contribution of the main zoobenthic taxa to SR was consistent among the MITR, GUIS and HANS transects. There were no significant differences between these three transects and the JUTT transect with regard to richness of higher taxa despite a considerably lower total number of species at JUTT. This similarity in the number of supraspecific taxa applied to levels from phyla to order. Transect OSSI, which was the transect closest to a glacier, was much poorer in SR and in number of supraspecific taxa, with presence of only six phyla of a total of 11.

Zoobenthos distribution related to depth

The composition of zoobenthos varied with depth. The SR was minimal at 0 m depth, comprising 42 species of a total of 360 recorded for hard-bottom habitats and maximum at 5 m depth, where 282 species of a total of 360 were recorded.

Ice-scouring effect on intertidal and upper subtidal habitats is well-documented for soft-bottom (Conlan et al. 1998) and hard-bottom (McCook & Chapman 1993; 1997) both in Arctic and Antarctic (Pugh & Davenport 1997). In Kongsfjorden ice-scouring also should be considered as one of the main factors contributing to low diversity of epifaunal species in upper parts of studied transects.

Samples taken at 0 m depth exhibited taxonomic uniqueness not only at the species level but also at higher taxonomic levels. At 2.5-30 m depth, all the main taxa were presented, and there were no considerable differences in the number of supraspecific taxa from phylum to order. The differences were chiefly seen at the family to species levels.

There was a high percentage of species that were found only at 0 m depth and the neighbouring depth. This indicates that decreased diversity in the shallowest habitats is caused by factors other than those that account for the decreased diversity in the inner part of the fjord and at 15-25 m depth. The “specialization” of species in relation to conditions at shallow depth in Kongsfjorden was more pronounced than in relation to glaciomarine conditions. However, high peculiarity at this depth was accompanied by a high percentage of “common” species. This emphasized the high natural disturbance in this habitat.

The patterns of zoobenthic response to the depth gradient were generally similar for SR and occurrence, and they appeared to be non-linear with considerable decrease in the diversity at 15-20 m depth (Fig. 4, Paper I). When comparing species composition at different depths, it is clear that the highest singularity occurred in the list of species from 0 m depth. Samples from 15 m depth, in contrast, were most similar to the samples from all other depths. The MDS plot based on Bray-Curtis similarity illustrated greater differences in species composition with increasing separation in depth.

Such pattern of species composition in relation to the depth gradient may be attributed to the stratified hydrographical structures of the upper 30 m water layer, with a transitional zone between surface and deeper water masses at 15-20 m depth. Hydrographical studies in the upper 30 m depth layer in near-shore areas in the fjord are a topical problem, given that there is no consensus regarding the structure and processes in the upper 30 m water layer. It was observed, that ecocline (halocline, thermocline and pycnocline) divide habitats and create discontinuity for marine benthic communities. Physical and chemical factors in this case define the faunal structure up from the ecocline, whereas biological processes are the main factors responsible for the faunal composition in the relatively more stable environment below the ecocline (Rosenberg & Möller 1979).

There are also evidences that a significant part of pelagic production may occur in the cline (Richardson & Christoffersen 1991, Nielsen et al. 1994). Josefson et al. (1995) investigated whether there was any increase in the input of energy to the benthos in the area where cline comes into contact with the bottom. The data collected did not support the hypothesis of a direct positive relation between cline production and growth of infaunal bivalve molluscs, which was used as a proxy for benthic energy demand. From the other side, there was no evidence of negative relation between cline and benthos. Further studies could support the hypothesis that the decreased diversity at 15-20 m depth is the result of unstable conditions or elucidate other possible reasons.

Abundance on transects and at depths

For “solitary” species, the mean abundance in samples was highest in the outer part of the fjord and decreased towards the inner glaciers. Polychaeta Sabellida contributed most to the decrease in mean abundance. For the second important group, Amphipoda Gammaridea, its relative contribution to total abundance on transects generally increased towards the inner-fjord glaciers. Joint abundance of other “solitary” animals showed a tendency to decrease towards the inner part of the fjord. The four outer transects were more or less similar in the composition of taxa with regard to total abundance.

The abundance of “solitary” organisms at different depths varied significantly. Mean abundance was minimal in samples from 0 m depth and increased with depth, resembling patterns described for SR and AO for the whole material. In contrast to SR and AO, there was no increase in abundance values at 25-30 m depth. Thus, the decrease in relative abundance was gradual from 5 to 30 m depth if we consider the relation of mean abundance to AO. The deepest habitats contained more species compared to the 15-20 m depth range, although in the deepest habitats the species present were less abundant. When fouling Polychaeta Sabellida was excluded from consideration, the mean abundance decreased with increasing depth from 0 to 30 m. High abundance at shallow depth mainly involved Amphipoda Gammaridea. The abundance of remaining “solitary” macrobenthos

increased from 0 to 5 m depth and then gradually decreased to 30 m depth. Depths from 5 to 30 m were similar in the composition of dominant supraspecific taxa with regard to total abundance. Species and higher taxa composition at 0 and 2.5 m depth were significantly different.

The composition of dominant species with regard to abundance changed with depth. At 0 m depth, *Ischyrocerus anguipes*, *Gammarus setosus*, *Gammarellus homari* and *Caprella septentrionalis* dominated. From 2.5 m depth and deeper, Spirorbidae g. spp. and crustaceans were most abundant in samples. The dominance of molluscs *Margarites helicina*, *Hiatella arctica* and *Musculus* spp. became evident at 2.5 m, but even more so at 5 m depth. From 10 m and deeper, most abundant after Spirorbidae g. spp. were *Balanus balanus*, *Hiatella arctica* and *Tonicella* spp.

The properties of the hard-bottom communities of the fjord, as described here, are valid for August-September. Seasonality is a characteristic feature of Svalbard fjords (Weslawski et al. 1988; Kedra et al. 2011). Even though benthic communities are more stable seasonally than pelagic communities, seasonal migrations and presence/absence of juveniles in samples may change some diversity patterns, especially in sense of abundance and biomass. To clarify this it necessary to include seasonal aspects in future hard-bottom studies in Kongsfjorden.

Biomass on transects and at depths

Crustaceans formed more than a half of the total biomass (53.7%) in hard-bottom samples from Kongsfjorden. Most (96.8%) crustaceans comprised barnacles *Balanus* and *Semibalanus* (soft parts together with their massive calcareous shell). The weight of zoobenthos in samples fluctuated widely, from 0.7 g m⁻² at 0 m depth on the inner transect OSS1 to 10554.9 g m⁻² at 10 m depth on the outer transect MITR. The variation was high because of high patchiness in community distribution even on the same transect and at the same depth. The biomass of organisms was considerably lower in the inner part of the fjord.

The mean biomass in samples increased steeply from 0 to 10-15 m depth and then decreased gradually to 30 m depth. The dominant species with regard to biomass at 0 m depth included the amphipods *Gammarellus homari*, *Ischyrocerus anguipes* and *Gammarus setosus*. At 2.5 m, amphipods gave way to the molluscs *Hiatella arctica*, *Margarites helicina* and *Buccinum glaciale*. At greater depths (5-30 m), *Balanus balanus*, *Hiatella arctica* and *Strongylocentrotus* spp. were most dominant regarding biomass.

Our biomass data do not allow the direct estimation of differences in the content of organic carbon in samples. Species have different fractions of organic carbon content in relation to biomass. However, combining data on these fractions and data on weights distribution could allow the estimation of organic carbon budgets in different parts of the fjord and at different depths.

Relative importance of different factors

In the analysis we considered a number of variables (Tab. 1, Paper I) to estimate the relative importance and correlation of environmental factors with regard to species occurrence. The analysis does not pretend to be comprehensive, since it does not include some factors whose effect is well-known and proved, such as ice-scour activity or sea urchin grazing activity. Relative importance and correlation of selected environmental characteristics were estimated using CCA and Monte-Carlo permutation tests (ter Braak & Smilauer 2002). The factor of depth, and, secondly, factors of distance from the glacier, substratum type and amount of silt were important for explaining the variance in zoobenthos composition in samples from hard substrata in Kongsfjorden. For the total biomass and the total species occurrence in the samples, these four factors displayed a high level of significance.

According to Kaczmarek et al. (2005), the composition of soft- and hard-bottom faunal associations in Kongsfjorden is primarily dependent on the bottom type, with the depth gradient having little effect. However, our data provide evidence that the main factor structuring diversity of the benthos on hard substrata is depth. The type of substratum, which partly is related to depth and angle of the substratum, is also important, but less so than the depth. Glacier-induced sedimentation is often

mentioned as a main reason for the decrease of diversity of soft-bottom fauna in inner parts of Arctic and sub-Arctic fjords (Holte et al. 1996; Kaczmarek et al. 2005; Włodarska-Kowalczyk et al. 2005). Our data support this. The impact of the amount of silt on the rock surface is high for species composition, abundance and biomass. The angle of the hard substratum surface may also, as mentioned, be of great importance for faunal composition (Jørgensen & Gulliksen 2001). Our data indicate that the factor of substratum inclination is not very important, but the sampling site used by Jørgensen & Gulliksen (2001) included steeper rock walls with overhangs, habitats found in less degree at our transects. The only significant influence the substratum angle had in our study was on the composition of “colonial” species, with higher diversity in steep relief habitats.

“Colonial” versus “solitary” species.

Substratum availability and competition for space are among the most important factors affecting distributional patterns of hard-bottom zoobenthos (Dayton 1971; Paine 1974). The adaptive significance of solitary and colonial strategies in competition has been the topic of several studies on marine hard substrata. In such investigations species were counted as colonial if members of the colony were spatially connected to each other and had common ancestry due to asexual reproduction (Boardman et al. 1973). Solitary species are comprised of distinct individuals that are capable to perform all individual functions (Jackson 1977). Jackson (1977) concluded, based on his investigation of cryptic environments in coral reefs in Jamaica, that solitary animals are relatively more abundant in early stages of succession on hard substrata. His explanation was that solitary animals, most of which have small size, rapid growth and short generation times, employ opportunistic strategy to occupy and dominate communities. Gulliksen et al. (1980) concludes that solitary opportunistic species prefer to inhabit new lava grounds on Jan Mayen probably because the new habitats experience less predator pressure. As succession proceeds, colonial animals become dominant in competition with solitary ones, because their indeterminate growth allows effective substratum occupation without requiring sexual reproduction, and colonial forms are less susceptible to overgrowth (Jackson 1977). Osman's (1977) experiments were in agreement with Jackson's conclusions even though they were conducted in temperate environments near Woods Hole, Massachusetts. However, experimental studies in Puget Sound on Pacific coast of North America showed opposite results (Schoener & Schoener 1981; Greene & Schoener 1982; Greene et al. 1983). Abundance of solitary animals gradually increased through time until they became dominant. Development of fouling communities was variable at study sites, but dominance of solitary species at latest stages of succession was consistent. Regardless of observed patterns and offered explanations, these and similar studies (e.g., Woodin & Jackson 1979; Sutherland 1978; Schmidt 1982) emphasized, that classification based on morphology, rather than one based on how closely related forms are taxonomically, may be an appropriate method for assessing the competition patterns on hard substrata.

Previous studies, mentioned above, considered “colonial” and “solitary” groups of species in general, according to the definition given by Boardman et al. (1973). However, there is different nature of coloniality for different “colonial” taxa in samples, for example in case of sponges and in case of tunicates. It is desirable to analyze groups with different nature of coloniality separately if the intention is detailed analysis of “colonial” and “solitary” life strategies with regard to their coexistence on hard bottom. We did not have such a purpose in our study, and limited our estimations to general distributional patterns.

The initial point for consideration of colonial and solitary species in our study was to use abundance data for estimation of biodiversity patterns on hard substrata in Kongsfjorden. However, due to simultaneous presence of both “colonial” and “solitary” organisms in samples, the use of abundance data cannot characterize the general pattern of zoobenthic diversity on hard substrata. Separation of “colonial” and “solitary” species allowed making some conclusions on abundance in gradients of environmental conditions, and also emphasized the different relations these two functional groups had to their respective environments. Abundance data for colonial species can be estimated from data on number of colonies and area of colony surface (Gontar et al. 2002, 2004). However, in

our case, it was carried out only for encrusting bryozoans (Voronkov et al. 2013). For other groups, it was difficult because of high diversity and big volume of collected samples.

As “colonial” organisms in our samples are regarded: all Porifera species, all Cnidaria Hydrozoa Thecophora species, a major part of Cnidaria Hydrozoa Athecata species, all Bryozoa species, all Ascidiacea Aplousobranchia species and a minor part of Ascidiacea Stolidobranchia species. All other benthic animals were counted as “solitary” organisms.

“Colonial” forms were represented in all samples except for three. Samples without “colonial” species were situated on different transects at 0 m depth. Bryozoa Cheilostomata formed 68.6% of total biomass of colonial organisms. However, high biomass was apparent only for a small number of species. In Bryozoa Cheilostomata high biomass was formed by 3 species of 96. Branched colonies of *Tricellaria ternata* (Ellis et Solander, 1786), *Eucratea loricata* (Linnaeus, 1758) and *Dendrobeania murrayana* (Johnston, 1847) constitute together 77.6% of total biomass of branched and encrusting colonies of Bryozoa Cheilostomata.

Polychaeta was the most abundant “solitary” group and constituted 81.9% of total abundance. Within polychaetes 98.9% were sabellids with an average per sample abundance reaching 7207.7 ind.m⁻². The part of all other groups in total abundance of “solitary” organisms was 18.1%. More than half of them, 59.4% were Crustacea (79.8% of them were crustaceans from order Amphipoda) and 30.8% were molluscs. Echinodermata, the rest of Polychaeta and all other “solitary” groups together represented the remaining 9.8%.

Species richness as well as general occurrence in samples was higher for “solitary” species. However, relative occurrence, which is relation of SR to AO, was higher for “colonial” species, i.e., “colonial” species occurred in samples relatively more frequently than did “solitary”.

Total biomass of “solitary” species was 4.4 times that of the biomass of “colonial” species. It was on average 835.8 gm⁻² per sample. Organisms, attributed as “colonial”, formed 18.6% of total biomass, which is equivalent to 191.5 gm⁻² on average per sample. The largest biomasses of “colonial” species were skewed to more shallow depths compared to “solitary” ones.

Coefficients which recount wet weight to organic carbon content for each species can be applied to our data to improve the understanding of relative importance of “solitary” and “colonial” species in carbon budget of the ecosystem.

Generally the mean number of species per sample was lower on transects close to the glacier. However, “colonial” and “solitary” species showed some differences in distribution along fjord’s axis. The SR and FO of “colonial” species were relatively low at transect GUI. Low value of SR was compensated by high SR of “solitary” species on GUI, so that total SR was almost the same as at MITR and HANS. Relatively low occurrence in samples on GUI was a characteristic for all “colonial” groups, Bryozoa, Chordata, Cnidaria and Porifera. However, Cnidaria Hydrozoa contributed most to the deficiency. Relative SR for this group at GUI was intermediate between MITR and HANS, but FO was much less (3.7% vs 8.3% and 6.5% in MITR and HANS, respectively). The reason why “colonial” species had relatively low occurrence at GUI is not clear. Whether the fauna development is in some special state in process of natural succession or the difference is a result of a temporary or permanent impact of environmental disturbance - these are the topics for further analyses and experiments on the hard-bottom Kongsfjorden ecosystem.

Groups of “colonial” and “solitary” species showed some differences also in biogeographic patterns. “Colonial” species in general have relatively narrower and more northern distributional ranges on hard-bottom in Kongsfjorden. The “solitary” species accounted for the decrease with depth in the occurrence of boreal species, and the concomitant increase with depth in species with wider distribution ranges. In terms of their biogeographic composition, “colonial” species showed less variation with respect to the depth gradient.

Factors of depth and distance from glacier together with factors such as substratum type and amount of silt on the substratum surface explained most of variation in presence of different species, biomass and abundance of “solitary” species. Factors related to water movement (waves, strength of water currents), and substratum inclination had little importance for zoobenthos distribution compared to the factors mentioned above. The “colonial” part showed some peculiarity. “Colonial” species

composition was stronger linked to distance from glacier and angle of substratum inclination than to primary substratum type and amount of silt on substratum surface. “Colonial” organisms were more diverse in the outer part of the fjord and in habitats with steep relief. Differences in “colonial” biomass distribution along fjord’s axis were not significantly related to the distance from the glaciers.

Zoobenthic communities

Rocky-shore organisms are particularly useful for experimental manipulations in the investigation of benthic community structure. Because of this, more is known about the species interactions of rocky-shore communities than of almost any other ecosystem (Barnes & Hughes 1999). However, it is valid mostly for intertidal habitats. Much less is known about the ecology of rocky subtidal communities, simply because such habitats are less accessible than intertidal ones (Witman & Dayton 2001).

The community concept in marine ecology has long history. In 1913 C.G.J. Petersen first used the term “community” to describe composition and distribution of animals of the seabed off Denmark (Petersen 1913). Since that time the term was very much in use, despite that different ecologists give sometimes different meaning to it (Hiscock & Mitchell 1980). MacGinitie (1939) defined a community as “...an assemblage of animals or plants living in a common locality under similar conditions of environment and with some apparent association of activities and habits” (ICES 2008). We use the term “community” rather than “assemblage” to describe a group of co-occurring benthic species in samples assuming that species occurrences are a product of close associations.

The study is conducted on the zone referred as a lower part of littoral zone, whole infralittoral and upper part of circalittoral zone according to of the European Nature Information System (EUNIS) habitat classification (Davies et al. 2004). EUNIS code and names for studied habitats are: A1 “Littoral rock and other hard substrata”, A3, “Infralittoral rock and other hard substrata” and A4, “Circalittoral rock and other hard substrata”. Zone A1 has upper limit by the top of the splash zone and the lower limit by the top of kelp zone. Deeper, zone A3 is dominated by seaweeds and limited by the lower limit of the kelp growth. Upper part of the animal-dominated circalittoral zone A4 is limited by the presence of the foliose red algae. Lower circalittoral, where the light intensity is not enough to support persistent growth of red algae, lies outside of the frames of the present study.

Hard-bottom habitats have been studied previously in Kongsfjorden with description of different aspects of benthic fauna. However, there have been no published attempts to summarize data on diversity of faunal associations along fjord’s axis with consideration of environmental variables. Based on our extensive Kongsfjorden hard-bottom biodiversity dataset, we aimed to:

- determine zoobenthic communities on the hard-bottom in Kongsfjorden;
- define indicator species responsible for showing main differences between zoobenthic communities in Kongsfjorden;
- describe the composition of the zoobenthic communities, their properties and variability;
- reveal the environmental variables determining distribution of the zoobenthos, including data on key zoo- and phytobenthic species in the analysis.

It is critically important to make data comparable with studies conducted in other marine ecosystems (e.g., Hiscock & Mitchell 1980), and we have therefore described procedures for the determination of the communities in details. The approach to the segregation of the hard-bottom zoobenthic communities included consideration of species potential role in community, accounting for dominant species and similarity in species composition.

Two key groups of zoobenthos that influence the hard-bottom ecosystem of Kongsfjorden included: barnacles (*Balanus balanus*) and branched bryozoans (*Tricellaria ternata* and *Eucreatea loricata*). These three species were identified as key foundation species, which are also dominant in most of the studied habitats. The foundation hydroid species *Symplectoscyphus tricuspoidatus* var. *acuminatus* was dominant in its representative community, but more extensive sampling is necessary to determine its role in the fjord ecosystem. Mentioned species were representative for three types of communities: the “*Balanus* community”, the “Branched bryozoans community” and the

“*Symplectoscyphus* community” and were represented in most of our hard-bottom samples. There were 17 samples from total 62 without evidently dominant species or taxa with no developed foundation species. Two such communities were observed: the “Developed fauna community” and the “Impoverished fauna community”. The “Developed fauna community” differed by high SR, abundance and biomass of zoobenthos in contrast to the “Impoverished” one, with extremely low diversity and biomass. High SR, AO and abundance of bivalve molluscs were recorded at the bottom of transects in specific gravel habitats. The corresponding community received the name “Bivalvia community”. Hyperbenthic amphipods were dominant in a shallow-water community, the “Amphipoda community”.

In calculations of the similarity in species composition based on species biomass we used square root transformation of the data. However, most adequate description of the samples dissimilarity was obtained on species lists with extra removal of large and heavy, not numerous individuals of some sessile or motile species, which presence within sampling areas was rare. Primer’s ANOSIM test confirmed the statistical significance of differences between communities determined using the described approach.

Hiscock & Mitchell (1980) pointed attention to the necessity of inclusion of the habitat data in determining of the communities, summarizing in their work wide range of important environmental variables. Many of them coincide with variables that we used for analysis of communities distribution (Tables 2 and 3, Paper II).

We attempted to identify environmental variables which most match zoobenthic patterns using BIO-ENV procedure. As a basis for the analysis we used a “biotic” dissimilarity matrix which includes data on all zoobenthic species composition except *Balanus balanus* and branched bryozoans *Eucratea loricata* and *Tricellaria ternata*. As “abiotic variables” we choose standard environmental variables (Table 1, Paper I) plus biomass of main foundation species *B. balanus* and branched bryozoans *E. loricata* and *T. ternata*. In the list of “abiotic variables”, the biomasses of most abundant algal species were included as well. These were dominant kelp species: *Alaria esculenta*, *Alaria grandifolia*, *Laminaria digitata*, *Laminaria saccharina* and *Saccorhiza dermatodea*. Also combined data on biomass of different branched bryozoan species, on *Balanus* spp. and on kelp species were included as environmental variables.

As result of the BIO-ENV analysis, the kelp species or combined kelp species biomass were not among variables that best explained distributional patterns of zoobenthos. Variables which exhibited highest match with the zoobenthic species distribution were: depth, *Balanus* and the biomass of branched bryozoans. Inter-relation of these variables gave Spearman rank correlation level 0.771.

Some of the authors give evidences of the familiar associations between different species of coastal marine macroalgae and invertebrate animals as a result of selective larval settlement (Hayward 1980). Kortsch et al. (2012) concluded, that “simultaneous changes in the abundance of benthic invertebrates suggest that the macroalgae played a key structuring role in these communities”. However, other data show little influence of the seaweed diversity on the diversity of associated faunal assemblage (Bates and DeWreede 2007), and our data agree with this conclusion. It supports the doubts with regard to the validity of algal species use as descriptors for zoobenthic communities, despite that algae often dominate in abundance or biomass in different hard-bottom habitats. Distinguishing community types based on algal dominance rather tends to obscure the faunal data and decrease the significance of estimations.

The CCA plot showed how considered environmental factors were related to communities (Fig. 7, Paper II). “Amphipoda”, “*Symplectoscyphus*” and “branched Bryozoa” communities were located in shallow and steep habitats, with little siltage due to exposure by currents and waves. “*Balanus*” and “Bivalvia” communities occupied deeper and more level habitats. The “Developed fauna community” occurred in shallow-water habitats, replacing the “Branched Bryozoa” community in the inner part of the fjord. Specific environmental conditions there can support high diversity and production characteristics, but prevent growth of abundant branched bryozoan colonies. Most of samples with “impoverished” community were close to the glacier, and influenced by heavy siltation.

Our data indicated definite links between different species in most of the studied habitats. Relation of one species to another makes use of the term “community” reasonable. However, answer to the question - how “natural” is the term “community” applied to the description of diversity on hard substrata in Kongsfjorden - has no simple answer. In “*Balanus*”, “Branched bryozoan” and “*Symplectoscyphus*” communities, species occurrence was a product of close association. For other communities, it was difficult to estimate how close relations were between species. Additional effort should be put into verifying categories of assemblage. Because we examined only five transects from the whole fjord, there is a chance that more extensive sampling can extend the list of foundation species in Kongsfjorden and therefore improve our knowledge on diversity of communities.

Analysis of selected taxa

There are two different approaches to diversity-related marine ecological research of hard substrata. First one includes the collection of the data required to prove or reject a theory or a hypothesis. Number of samples collected must meet minimal requirements of the significance. Treatment is often limited to identifications of higher taxonomical levels. Some surrogacy methods are also in use (Włodarska-Kowalczyk & Kedra 2004). Another approach includes extensive, but rational sampling within the area of interest, using standard sampling design, complete treatment and identification to species level. In the first case the data are hardly possible to use for any other calculations except the proposed hypothesis. Comparability possibilities are limited due to specialized sampling design and methods of treatment. In the second case, the dataset is more rich and suitable for different kinds of treatments and comparisons. Both approaches are valid, but the second approach is expected to be more rational in sense of relation between effort and resulting efficiency, especially if the work is a part of effective research network.

The second approach was much in use in the Russian school of marine research (Sirenko 1998). Such method of ecosystems investigation was used at the Laboratory of Marine Research, the Zoological Institute in St.-Petersburg, Russia (LMI ZIN). It allowed performing of thorough diversity and ecology assessments of many ecosystems of Russian Arctic (Franz Josef Land, the Laptev Sea, Wrangell Island and De Long Strait of the Chukchi Sea, the White Sea, Chauna Bay of the East-Siberian Sea, Jarnyshnaya Inlet of the Barents Sea, the East-Siberian and the Chukchi Seas) and Far East seas (the Sea of Japan and the Sea of Okhotsk) (Golikov 1977, 1985, 1988, 1990, 1994a, b, c; Sirenko 2001, 2004a, b; Sirenko & Vassilenko 2008). Unfortunately, these studies are not well known because the results were published in the Russian language.

Our study was performed in traditions and with participation of taxonomists from LMI ZIN. Therefore, in addition to the principal results of the study, i.e. description of diversity in environmental gradients and definition and description of zoobenthic communities, the possibility was available to conduct a variety of additional analyses based on collected data.

Hydrozoans are widely distributed on hard substrata, and this group was particularly studied in our survey (Paper III). The knowledge of hydroid distribution and ecology in coastal areas, especially in the upper sublittoral (0–30 m) is generally lacking, although recent studies have been performed in Svalbard waters, including Kongsfjorden (Ronowicz 2007; Ronowicz et al. 2008). It stems, in part, from the fact that in ecological studies of the entire benthic community there is usually limited emphasis on species inventory. In the case of Hydrozoa, one of the main reasons they are usually not accurately represented in ecological studies is that they are difficult to sample and identify; the majority of hydroids are delicate and require the use of special sampling and preservation methods to obtain identifiable samples. At the same time, taxonomists are usually not interested in the role of hydroids in the structure and function of communities. For hydroids (that are mainly colonial organisms), the quantification of characteristics such as biomass is especially important in order to estimate their role in benthic communities. The main purpose of Paper III was to present an integrated description of hydroids on hard substrata in Kongsfjorden that combines data on the species composition with the description of the role of each of the species in the community.

Despite that Hydrozoa colonies are widely distributed on rock and gravel substrata in Kongsfjorden, hydroids were generally not dominant or subdominant in zoobenthic communities. The exception is the species *Symplectoscyphus tricuspoidatus* var. *acuminatus*, colonies of which were sometimes abundant enough to determine the community structure and characteristics of benthic diversity. Of the 23 species recorded in this study, *Laomedea flexuosa*, *Phialella quadrata* and *Halecium tenellum* as well as representatives of family Stylasteridae were recorded from Svalbard waters for the first time. The most frequently occurring species included: *Orthopyxis integra*, *Lafoea dumosa*, *Campanularia volubilis*, *Filellum serpens*, *Symplectoscyphus tricuspoidatus* var. *acuminatus* and *Halecium labrosum*. These species primarily account for the dissimilarity in species composition among samples from different transects, depths and community types.

Hydroid diversity was highest in the zoobenthic community structured by branched bryozoans. The abundance and distribution of hydroids were reduced, to some extent, in the inner part of the fjord compared to the outer fjord. Species richness of hydroids was high at shallow depths, decreased at around 15 m and then increased again to 30 m depth. Species with low-boreal–Arctic and panoceanic distributional ranges were the most frequently occurring species. Depth, type of background substratum and amount of silt on its surface were the main factors influencing hydroid distribution. Description of all recorded taxa distributions together with data on their habitat and associations in zoobenthic communities are presented in Appendix 2, Paper III.

Another three publications based on our samples, were devoted to different aspects of diversity and ecology of bryozoans in Kongsfjorden. Two articles (Gontar et al. 2001, 2002) describe the main features of bryozoan diversity, species distribution and production characteristics in relation to environmental gradients. The articles include a comprehensive list of identified taxa and contain detailed biogeographic characteristics of each species. Updates to the existing species inventories for Kongsfjorden and Svalbard waters are also presented. In the discussion of species distribution it was assumed, that low salinity during summer is the main reason for low diversity of bryozoans on shallow depths in Kongsfjorden. It was concluded, that bryozoans could serve as environmental bioindicators. Observed consistent decrease in species richness at 15–20 m depth at different transects was counted as related to different water masses. The third article (Gontar et al. 2004) deal with an analysis of cover of encrusting bryozoan colonies. This was an attempt to apply the concept of territoriality to colonial species in fouling epifaunal communities. Territoriality is a type of intraspecific or interspecific active relations which lead to dispersion of individuals or colonies in a space. Cover of a colony was counted as one of the basic features of territoriality of bryozoans in a limited space. General equations of relation between cover and biomass of different bryozoan species were calculated to show differences in the species' abilities to occupy the substratum. It was also concluded that variability in the parameters of equations calculated for different samples was related to the level of environmental stress. Variability was higher where the pressure of glacial induced sedimentation was more pronounced.

These three bryozoan articles are not included in my PhD thesis even if I am a co-author. The main reason is that my input to the articles was limited to sampling and early processing of the samples.

Our extensive species and environmental dataset also provides possibility for more detailed analysis and specific publications on other taxonomic groups.

Hard-bottom ecosystem and environmental changes

Our biodiversity assessment gives us possibility to make some preliminary considerations to possible effect of environmental changes on hard-bottom ecosystem in Kongsfjorden, especially related to possible climate-related changes. A connection to the problem of the effect of climate-related environmental changes on zoobenthos composition and distribution is provided through the available data on the species biogeographic characteristics.

Biogeographic characteristics of species are the generalized patterns of the distribution of organisms. The formation of distribution areas depends on organisms' ability to spread, which is limited by morphological and functional attributes of their organization (Golikov et al. 1990). The presence of organisms in an area implies that the environmental conditions do not exceed the limits of their resistance. Difference in species distribution is expected to reflect the difference in the ecophysiological optima of organisms and species. Analyses of how environmental factors influence the biogeographic structure of biotas are essential for understanding of the processes underlying global diversity patterns and for predicting large-scale biotic responses to global change (Belanger et al. 2012). The number of well-documented climate-related changes already taken place in benthic systems is surprisingly low (Wassmann et al. 2011).

One of the most effective approaches to recording and understanding of such changes is monitoring. Valuable data, obtained from underwater photographs based on a non-destructive sampling technique at permanently marked and long-term monitoring sites, were analyzed by Beuchel et al. (2006); Beuchel & Gulliksen (2008) and Kortsch et al. (2012). They found that considerable part of interannual variability in abundance and species diversity was related to climatic changes linked to North Atlantic Oscillation Index (NAO) and its local manifestations. NAO and diversity were negatively correlated, and drastic shifts in diversity patterns coincided with a shift of a NAO from positive to negative mode (Beuchel et al. 2006). According to Kortsch et al. (2012), co-occurring changes in the abundance of benthic invertebrates are related to the key role that macroalgae play in hard-bottom benthic communities. The biotic changes observed have a climate-driven nature, and the ecological processes that are expected to be drivers of the observed biotic changes are likely to promote the "borealization" of studied Arctic marine communities in the coming years. These important results were obtained from consideration on a scale related to alpha diversity.

Our analysis of biogeographic structure of the fjord hard-bottom habitats, which deals with differences among sites, provide basis for climate-related monitoring in context of beta and gamma diversity. Our specific tasks were:

- to describe the biogeographic composition of zoobenthos in hard-bottom habitats in Kongsfjorden;
- to estimate what kind of environmental conditions, Arctic or moderate, most influence the biogeographic composition of hard-bottom zoobenthos in Kongsfjorden;
- to estimate the relative importance of environmental factors with regard to distribution of species with different biogeographic characteristics;
- to find spatial biogeographic faunal patterns, which may reveal particularities within environmental gradients.

Conclusions on biogeographic composition were based on substantial part of the material. Only 10% of species and 18% of identifications to the supraspecific level were not involved in the analysis. Species were distributed into seven categories according to classifications given in Sirenko et al. (2009). About half (51.4%) of total 403 species had a boreal-Arctic distribution. Species with even wider distribution ranges (subtropical-Arctic, subtropical-Boreal and pan-ocean species) included 7.2% in total. Of the species with more narrow distributional ranges, Arctic, high-boreal-Arctic and boreal species represented the remaining 41.4%.

Different researchers use different systems to analyse the biogeographic composition of the fauna, and the sampling ranges and habitats do also vary; this makes it difficult to compare results directly. In spite of this, we suggest the position of Kongsfjorden as intermediate between boreal and Arctic fjord environments. Golikov et al. (1985) estimated that boreal species comprise 33-38% of

species on hard substrata, and Arctic species as 1-2%, in different parts of the Chupa Inlet of the White Sea. The percentage of boreal species in High-Arctic shallow habitats (0-36 m) in Franz Josef Land was 1-3% (Golikov & Averincev 1977) and Arctic species comprised 14-19%. In our Kongsfjorden study, boreal species represented 9.7% and Arctic species 16.6%. The relatively high contribution of boreal species is due to the influence of the warm West Spitsbergen Current. This influence does not, however, exclude the occurrence of Arctic species, and the relatively high percentage of Arctic species is a feature of the Arctic location of the fjord. The relative importance of Arctic and high-boreal-Arctic biogeographic groups was higher in the inner part of Kongsfjorden, indicating that the inner part of this fjord is more Arctic, whereas the outer part is more boreal or sub-Arctic. This was most notable at the OSSI transect, which situated closest to the Kronebreen glacier.

The biogeographic composition at the other transects was rather similar in spite of differences in species composition. This illustrates the similarity of Kongsfjorden, which has sub-Arctic characteristics on account of transformed Atlantic water advected into the fjord (Svendsen et al. 2002; Hop et al. 2006), to eastern Atlantic fjords, where the increased percentage of species with northern distributional ranges in the innermost parts is a common feature (Brattegard 1966). This differs from the western Pacific boreal gulfs and bays, where continental climatic conditions support the dominance of warm-water species in inner parts (Golikov & Scarlato 1965, 1967, 1968; Scarlato et al. 1967). The absence of significant differences in biogeographic composition in the four outer transects probably indicate that limits of zoobenthic species resistance are broad and that the observed along-fjord gradients in environmental conditions not are strong enough to structure the hard-bottom benthos. From a benthic point of view, the North Atlantic water influence is relatively similar for outer and middle parts of the fjord, including the transect JUTT on the border between middle and inner parts of the fjord. This may to some extent reflect the water circulation in Kongsfjorden with topographical steering and turning of the incoming current in mid-fjord near HANS (Willis et al. 2006).

In a study by Golikov & Averincev (1977), the authors stated, that at sites with High-Arctic conditions the proportion of widespread boreal-Arctic species was larger compared to localities with moderate Arctic conditions. Arctic environmental conditions predominate in the inner part of Kongsfjorden, but we did not record a larger proportion of boreal-Arctic species. In our samples, boreal-Arctic species contributed more to total biomass in the outer part of the fjord, whereas the percentage of Arctic and high-boreal-Arctic species was more pronounced in the inner fjord's basin.

Data on SR, FO, total biomass and abundance showed that species with different latitudinal preferences were distributed unevenly related to depth. The proportion of boreal species generally decreased with increasing depth. The tendency to a decrease in the percentage of boreal species on hard substrata with increasing depth has also been described for Chupa Inlet in the White Sea (Golikov et al. 1985) and for Ramfjorden in mainland Norway (Soot-Ryen 1924). In Kongsfjorden, we also observed a corresponding increase in the percentage of boreal-Arctic species with depth, whereas other groups showed no clear tendencies. We also noted a decrease in the percentage of groups with narrow distributional ranges (Arctic, high-boreal-Arctic and boreal) with increasing depth. Shallow habitats, especially the shallowest (0 m depth), showed singularity in terms of zoobenthos biogeographic composition. A contrast in biogeographic composition between the shallowest depths and the 5-30 m depth range was also apparent for relative biomass. Decrease in the percentage of boreal species and an increase in the percentage of species with the widest distributional ranges from 2.5 m depth and deeper were due to the abundance of "solitary" organisms. The biogeographic composition of hard-bottom zoobenthos is likely sensitive to the presence of separate water layer(s) at shallow depths. However, the decrease in species diversity at 15-20 m depth was not reflected in the biogeographic composition.

Species with a boreal-Arctic distributional range contributed considerably to the total biomass on each of transects. However, their contribution to the biomass found on the innermost transect OSSI was much less compared to the other transects. Species with a more northern distributional ranges formed almost half (44.6%) of the total biomass on OSSI. The Arctic species on OSSI were mostly "colonial" species, whereas the high-boreal-Arctic species were mainly "solitary." Arctic species also

made a relatively high contribution to the total biomass on the JUTT transect in the inner part of the fjord.

There were no Arctic species with very high abundance; the most abundant were species with boreal-Arctic and boreal distributional ranges. Thus, the upper 30 m of the hard-bottom environment of Kongsfjorden was inhabited by a fauna largely comprised of warm-water species.

Canonical Correspondence Analysis was used to estimate the relative importance of environmental factors with regard to distribution of species with different biogeographic characteristics. The analysis revealed, that the factor of exposure to wave impact was of highest importance explaining most of variation in biogeographic composition of benthic species in samples ($F=10.38$, $p=0.002$). Factors of depth, water current flow and amount of silt on rock explained less variation, although the importance was statistically significant ($F=2.42$, $p=0.032$; $F=2.32$, $p=0.044$; and $F=2.27$, $p=0.046$, respectively). Level of exposure to waves can hardly be counted as direct factor influencing variation in biogeographic composition. However, we presume that variation in wave impact, being not linear, better than depth or other factors correspond to variation pattern in the factor responsible for biogeographic variation. Temperature plays a critical role in large-scale estimations (Golikov et al. 1990, Belanger et al. 2012). It is, most likely, valid also for local-scale environments, with possible interaction with wave impact.

Thus, the biogeographic composition of hard-bottom zoobenthos is sensitive to variation in environmental conditions in Kongsfjorden. In relation to the changes in climate, the species composition, and, correspondingly, the biogeographic composition of zoobenthos in the fjord will likely change. Biogeographic composition deals mostly with temperature resistance limits, but because the benthic ecosystem is well “buffered” having high percent of species with wide distributional ranges, and, consequently, wide tolerance ranges, the system will likely change slowly or with delayed response.

Changes of zoobenthos composition and production characteristics will happen not only because of direct shifts in temperature and consequent shift in average ecophysiological optimum for the ecosystem (most pronounced in outer parts of the fjord). Also increase in stress caused by mineral sedimentation and water turbidity, a consequence of glaciers melt, as it was concluded by Włodarska-Kowalczyk & Weslawski (2001), will negatively affect the diversity of the fjord ecosystem. Our data confirm considerably lower diversity on hard substrata in areas affected by heavy sedimentation and high turbidity.

This baseline study should be useful for future studies assessing the influence of climate change on species distributions and structure of benthic communities. The presented research adds very much to the value of the studied habitats from a scientific point of view. The studied locations should be counted as useful for monitoring of diversity and research on hard-bottom ecosystem functioning, and deserve special protection as experimental fields.

Final remarks

Philosophy is "love of wisdom" (φιλοσοφία = φιλία (love) and σοφία (wisdom), Ancient Greek).

As far back as a half thousand years before Common Era, Heraclitus of Ephesus (Ἡράκλειτος ὁ Ἐφέσιος), a pre-Socratic Greek philosopher, taught: "Being wise is the highest virtue, wisdom is to speak the truth and agree with it own actions, asking nature to know the truth" (Stob. Serm., III, cit. from: Suvorov 1905, p. 24).

Fast changes in social human live during last centuries, development of technologies etc drastically change the common human's intellection from contemplation of nature to complete dominance of "things" creation. Even in an academic environment there is a clear shift for scientific work from promoting of wisdom by rational means to just acquiring of knowledge.

I consider it an honour to me to be a part of the community which keeps traditions established long time ago by people who set the wisdom as a highest priority for themselves. The sign of it is that in the community, which follows the European science and academic tradition, the degree, to which I apply for, still has a name "Philosophiae Doctor degree".

I agree very much with Professor Nicholas Maxwell, Senior Research Fellow at University College in London who promotes the idea of ... "a revolution in the aims and methods of academic inquiry, so that the basic aim becomes to promote wisdom by rational means, instead of just to acquire knowledge. Acquiring scientific knowledge, dissociated from a more basic concern for wisdom, leads, via technology and industry, to an enormous increase in the power to act. This has led to much that is good, but also to much that is harmful" (Maxwell 1984, in Preface to the second edition).

I hope that the knowledge I acquired during present PhD study and which is represented in my thesis, will serve not to multiply facts collection only but to promote the truth in favour of those, who are ready to "agree with it own actions".

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Tromsø
2014

Supplementary Table S1.

List of species from hard substrata in Kongsfjorden, Svalbard. Species ¹ are new for Svalbard area compared to the list of species in Palerud et al. (2004). Species ² have extended distributional areas north of Jan Mayen and Bjørnøya compared to the list of species in Gulliksen et al. (1999). Values in the column headed “Min – max depth” indicate species distributional ranges for each transect. “Count” indicates occurrence in samples. “N, ind. (col.)” indicates the number of individuals (colonies) in samples. “Mean biomass (g m⁻²)” is the mean biomass in samples for each transect. “X” signifies species presence in samples when it was impossible to count the number of individuals or number of colonies. “Diverse” is organisms not identified to species level.

Taxa	Min - max depth					Count					N, ind. (col.)					Mean biomass (g m ⁻²)					Min - max of depth Sum	Count Sum	N Sum	Sum of mean biomass (g) Sum		
	MITR	GUIS	HANS	JUTT	OSSI	MITR	GUIS	HANS	JUTT	OSSI	MITR	GUIS	HANS	JUTT	OSSI	MITR	GUIS	HANS	JUTT	OSSI						
Phylum PORIFERA																										
Class CALCAREA																										
1 <i>Clathrina blanca</i> (Miklucho-Maclay, 1868) ¹			30					1										0.02					30	1	1	0.02
2 <i>Leucandra egedii</i> (Schmidt, 1870)			15 - 25					3										0.20					15 - 25	3	5	0.20
3 <i>Leucosolenia complicata</i> (Montagu, 1818)	2.5 - 25	2.5 - 15	1.3 - 30	0 - 2.5		4	6	4	2		X	X	X	X				0.02	1.61	0.61	0.02		0 - 30	16	X	2.26
4 <i>Sycon arctica</i> (Haeckel, 1870) ²			10 - 25	2.5				2	1														2.5 - 25	3	10	1.40
5 <i>Sycon protectum</i> Lambe, 1896 ¹	10 - 25	15				2	1				3	3						0.84	3.20				10 - 25	3	6	4.04
6 <i>Sycandra utriculus</i> (Schmidt, 1869) ²	2.5 - 20	2.5 - 15	2.5 - 30	2.5 - 10		7	6	11	6		153	217	34	49				8.02	7.09	0.91	2.02		2.5 - 30	30	453	18.05
Class DEMOSPONGIAE																										
7 <i>Halichondria panicea</i> (Pallas, 1766)	5 - 15		10 - 25	2.5 - 5		3		2	2		X		X	X				1.01		1.64	185.40		2.5 - 25	7	X	188.05
8 <i>Haliclona aqueductus</i> (Schmidt, 1862) ¹	5 - 25	5 - 15	10 - 30	5		4	3	10	2		X	X	X	X				2.67	12.56	71.63	0.50		5 - 30	19	X	87.36
9 <i>Haliclona cinerea</i> (Grant, 1827)		5	15 - 30	5			1	4	1			X	X	X					1.20	12.66	5.08		5 - 30	6	X	18.94
10 <i>Haliclona oblonga</i> (Hansen, 1885) ¹		2.5						1				X							4.80				2.5	1	X	4.80
11 <i>Hymeniacidon assimilis</i> (Levinsen, 1886) ¹				10					1					X							6.40		10	1	X	6.40
12 <i>Myxilla incrustans</i> (Johnston, 1842)	10	5	10 - 30	5		1	1	2	1		X	X	X	X				35.60	0.40	15.10	8.20		5 - 30	5	X	59.30
Phylum CNIDARIA																										
Class SCYPHOZOA																										
13 <i>Halicyclystus auricula</i> (Rathke, 1806)				5					1					1							80.00		5	1	1	80.00
14 <i>Eleutherocarpidae</i> g. sp.		2.5						1				1							0.04				2.5	1	1	0.04
15 <i>Eleutherocarpidae</i> g. sp.1		2.5						1				1							0.02				2.5	1	1	0.02
16 <i>Manania</i> sp.n., aff.				5					1					1							0.40		5	1	1	0.40
Class HYDROZOA																										
Order Anthoathecata																										
17 <i>Candelabrum phrygium</i> (Fabricius, 1780)	5 - 10	5 - 15	1.3 - 2.5			2	2	2			2	3	3					0.60	1.40	1.80			1.3 - 15	6	8	3.80
18 <i>Eudendrium vaginatum</i> Allman, 1863	2.5 - 5							3			X							0.93					2.5 - 5	3	X	0.93
19 <i>Garveia</i> sp.						5								1							0.04		5	1	X	0.04

89	<i>Chaetozone setosa</i> Malmgren, 1867				10	5				1	1				1	2			0.03	0.02	5 - 10	2	3	0.06					
90	<i>Cirratulus cirratus</i> (O.F. Müller, 1776)	25	5					1	1			1	1					0.14	0.04		5 - 25	2	2	0.17					
91	<i>Paraonidae</i> g. sp.		2.5 - 10	5															0.01	0.01	2.5 - 10	3	8	0.02					
92	<i>Tharyx</i> sp.		20 - 30	5															0.07	0.01	5 - 30	4	21	0.07					
Order Flabelligerida																													
93	<i>Brada inhabilis</i> Rathke, 1843	30																			30	1	1	0.16					
94	<i>Flabelligera affinis</i> M. Sars, 1829	15 - 30	2.5	5 - 25	5 - 10			3	1	2	2		5	2	3	2			1.12	0.18	4.48	0.07	2.5 - 30	8	12	5.84			
Order Opheliida																													
95	<i>Ophelia limacina</i> (Rathke, 1843)	15 - 30	15 - 25																			15 - 30	5	21	3.52				
96	<i>Scalibregma inflatum</i> Rathke, 1843				2.5																0.01	2.5	1	1	0.01				
Order Capitellida																													
97	<i>Branchiomaldane</i> sp.		5																			5	1	2	0.01				
98	<i>Capitella capitata</i> (Fabricius, 1780)	5	2.5 - 10	2.5 - 25	2.5 - 5	2.5 - 5		1	3	3	2	2	1	15	4	2	5				0.01	0.02	0.01	0.01	0.01	2.5 - 25	11	27	0.05
99	<i>Heteromastus filiformis</i> (Claparede, 1864)	30																				30	1	1	0.01				
100	<i>Nicomache minor</i> Arwidsson, 1906	25																			0.61	25	1	5	0.61				
101	<i>Petaloproctus tenuis</i> cf. var. <i>borealis</i> Arwidsson, 1907		15																				15	1	1	0.09			
102	<i>Rhodine gracilior</i> (Tauber, 1879)	30																			0.10	30	1	1	0.10				
Order Terebellida																													
103	<i>Amphitrite cirrata</i> O.F. Müller, 1771	15 - 20		10 - 20																		10 - 20	6	14	5.95				
104	<i>Baffinia hesslei</i> (Annenkova, 1924)	5 - 25	5 - 10	10																	0.08	0.13	0.09	5 - 25	6	16	0.30		
105	<i>Eupolyornia nesidensis</i> (Delle Chiaje, 1828)		15																			15	1	1	0.10				
106	<i>Laphania boeckii</i> Malmgren, 1866	30	20		5 - 10																0.15	0.19	0.02	5 - 30	5	9	0.36		
107	<i>Leaena ebranchiata</i> (M. Sars, 1865)		30																			30	1	1	0.02				
108	<i>Lysippe labiata</i> Malmgren, 1866		20 - 25		10																0.08		0.02	10 - 25	3	7	0.10		
109	<i>Neoamphitrite affinis</i> Malmgren, 1866				2.5																		2.5	1	1	0.27			
110	<i>Nicolea zostericola</i> Oersted, 1844	5	30																		0.08	0.01		5 - 30	2	8	0.08		
111	<i>Polycirrus</i> sp.	15 - 30	5 - 25	10 - 30	10	5															0.08	0.23	1.05	0.07	0.01	5 - 30	13	16	1.43
112	<i>Terebellides stroemi</i> M. Sars, 1835	25	20 - 30	25																	0.14	2.33	0.05	20 - 30	7	18	2.52		
113	<i>Thelepus cincinnatus</i> (Fabricius, 1780)	5 - 25	2.5 - 15	2.5 - 30	2.5																20.43	7.05	1.30	0.01	2.5 - 30	25	108	28.79	
114	<i>Trichobranthus glacialis</i> Malmgren, 1866		25																			25	2	2	0.05				
Order Sabellida																													
115	<i>Bispira crassicornis</i> M. Sars, 1851	15 - 30		10 - 30																		10 - 30	5	11	4.70				
116	<i>Branchiomma infaricata</i> Krøyer, 1856				2.5																	2.5	1	1	0.02				
117	<i>Bushiella (Jugaria) granulata</i> (Linnaeus, 1758)	20		10 - 30																	0.03	0.30		10 - 30	8	112	0.33		
118	<i>Bushiella (Jugaria) quadriangularis</i> (Stimpson, 1854)	25	10	10 - 20	5																	0.03	0.08	0.01	0.09	5 - 25	5	13	0.21
119	<i>Chitinopoma serrula</i> (Stimpson, 1854)			10 - 30	5																		5 - 30	6	11	0.06			
120	<i>Chone infundibuliformis</i> Krøyer, 1856	15 - 30	5 - 25	5 - 25	5																0.22	0.22	0.14	0.02	5 - 30	16	31	0.60	
121	<i>Circeis armoricana</i> Saint-Joseph, 1894 ¹	25	10	10 - 30	2.5 - 15																0.01	0.12	0.06	0.04	2.5 - 30	17	135	0.22	
122	<i>Circeis spirillum</i> (Linnaeus, 1758)	5 - 30	2.5 - 30	2.5 - 30	2.5 - 10																0.06	0.14	0.03	0.02	2.5 - 30	27	292	0.24	

123 <i>Paradexiospira (Paradexiospira) violacea</i> (Levinsen, 1883)	2.5 - 5	5 - 30	5 - 30	2.5		2	5	5	1		4	86	11	1		0.04	0.37	0.04	0.01		2.5 - 30	13	102	0.45
124 <i>Paradexiospira (Spirorbides) vitrea</i> (Fabricius, 1780)	10	10 - 30	10 - 30			1	3	7			4	9	23			0.02	0.01	0.03			10 - 30	11	36	0.06
125 <i>Pileolaria berkeleyana</i> Rioja, 1942 ¹	25	5 - 30	10 - 30			2	4	6			2	14	19			0.10	0.35	0.39			5 - 30	12	35	0.83
126 <i>Protula tubularia</i> (Montagu, 1803)			30					1					1					1.20			30	1	1	1.20
<i>Spirorbidae</i> g. sp.	2.5 - 30	2.5 - 30	2.5 - 30	2.5 - 10	5	12	13	14	7	2	37277	42545	29331	6334	3	11.12	12.02	8.97	2.28	0.01	2.5 - 30	48	115490	34.40
127 <i>Spirorbis spirorbis</i> (Linnaeus, 1758)			5 - 20					3					3					0.03			5 - 20	3	3	0.03

Phylum ARTICULATA

Class CRUSTACEA

Subclass MAXILLOPODA

Order Cirripedia

128 <i>Balanus balanus</i> (Linnaeus, 1758)	2.5 - 30	2.5 - 20	5 - 30	2.5 - 10		11	7	11	3		1245	477	1174	17		1499.81	779.35	1129.86	5.66		2.5 - 30	32	2913	3414.69
129 <i>Balanus crenatus</i> Bruguiere, 1789	5	5 - 10				1	2				18	43				144.32	52.54				5 - 10	3	61	196.86
130 <i>Semibalanus balanoides</i> (Linnaeus, 1767)	10	0		0		1	2		1		2	15		4		2.03	6.93		1.09		0 - 10	4	21	10.05

Subclass MALACOSTRACA

Order Mysidacea

131 <i>Mysis oculata</i> (Fabricius, 1780)			20	5				1	1				2	2							0.07	0.23		5 - 20	2	4	0.30
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Order Cumacea

132 <i>Lamprops fuscata</i> Sars, 1864		10		2.5	2.5 - 5		1		1	3		1		1	32			0.01		0.01	0.08		2.5 - 10	5	34	0.10
133 <i>Leucon nasicooides</i> Lilljeborg, 1855	20 - 30	30				3	1				5	1						0.01	0.01			20 - 30	4	6	0.02	

Order Isopoda

134 <i>Janirata tricornis</i> (Krøyer, 1849)	25		10 - 30	5		1		3	1		1		11	6				0.03		0.05	0.17		5 - 30	5	18	0.25
135 <i>Munna fabricii</i> Krøyer, 1846	25	5 - 25	10 - 15	5	5	1	3	3	1	1	1	8	5	1	1			0.01	0.01	0.01	0.01	0.01	5 - 25	9	16	0.01
136 <i>Munna groenlandica</i> Hansen, 1916 ¹	5 - 15	5 - 25	20 - 30			2	3	2			9	4	5					0.01	0.01	0.01		5 - 30	7	18	0.01	
137 <i>Munna kroyeri</i> Goodsir, 1842 ¹	25 - 30	30				3	1				6	6						0.01	0.01			25 - 30	4	12	0.02	
138 <i>Munna pellucida</i> Gurjanova, 1930 ¹	5 - 25		15 - 25	10		3		2	1		5		3	1				0.01		0.01	0.01	5 - 25	6	9	0.01	
139 <i>Munna spitzbergensis</i> Gurjanova, 1930		2.5						1				1							0.01			2.5	1	1	0.01	

Order Decapoda

140 <i>Hyas araneus</i> (Linnaeus, 1758)	5 - 25	5 - 30	2.5 - 20	15		7	6	6	1		18	10	7	1		27.95	22.23	53.01	7.60		2.5 - 30	20	36	110.79	
141 <i>Eualus gaimardi</i> (Miln-Edwards, 1837)		15 - 25	5 - 30			2	3					3	3					0.42	2.22			5 - 30	5	6	2.64
142 <i>Lebbeus polaris</i> (Sabine, 1824)	20 - 25	10 - 30	10 - 30	5		3	3	10	1		5	12	44	7		0.52	0.32	1.22	0.38		5 - 30	17	68	2.43	
143 <i>Sclerocrangon boreas</i> (Phipps, 1774)		10 - 30						5				18						14.91				10 - 30	5	18	14.91
144 <i>Spirontocaris phippisii</i> (Krøyer, 1841)	25	15 - 25				2	2				3	9						0.80	1.25			15 - 25	4	12	2.05
145 <i>Pagurus pubescens</i> Krøyer, 1838	20 - 30	5 - 30	15 - 30	2.5		4	8	3	1		7	19	4	2		2.46	7.60	0.27	9.60		2.5 - 30	16	32	19.93	

Order Amphipoda

146 <i>Anonyx sarsi</i> Steele et Brunel, 1968	10 - 14	0 - 15	5		5	2	4	1		1	4	41	7		1	1.47	0.12	0.09		0.01	0 - 15	8	53	1.69	
147 <i>Apherusa corbeli</i> Lagardere, 1968																						5	1	1	0.01
148 <i>Apherusa glacialis</i> (Hansen, 1887)			0					1						1						0.01		0	1	1	0.01
149 <i>Apherusa sarsi</i> Shoemaker, 1930		30					1					6						0.39				30	1	6	0.39

150 <i>Atylus carinatus</i> (Fabricius, 1793)	10					1					1										10	1	1	0.48
151 <i>Bathymedon obtusifrons</i> (Hansen, 1887)			30				1					1									30	1	1	0.01
152 <i>Calliopius laeviusculus</i> (Krøyer, 1838)		2.5				1						1									2.5	1	1	0.06
153 <i>Caprella septentrionalis</i> Krøyer, 1838	2.5 - 15	0 - 15	0 - 15	0 - 5	0 - 5	5	9	10	6	3	115	351	444	51	31	0.47	1.62	2.47	0.20	0.65	0 - 15	33	992	5.41
154 <i>Deflexilodes norvegicus</i> (Boeck, 1861)		25				1						1									5 - 25	2	2	0.03
155 <i>Deflexilodes tessellatus</i> (Schneider, 1883)			25										2								25	1	2	0.02
156 <i>Deflexilodes tuberculatus</i> (Boeck, 1871)	25	25 - 30	10 - 30	2.5 - 10		1	3	3	3		2	17	6	10		0.02	0.08	0.02	0.03		2.5 - 30	10	35	0.15
157 <i>Gammarellus homari</i> (Fabricius, 1779)	2.5 - 10	0 - 15	0 - 25	0		6	7	10	1		355	180	555	27		5.08	4.15	6.20	0.89		0 - 25	24	1117	16.32
158 <i>Gammarus oceanicus</i> Segerstrale, 1947	2.5					1					10					2.94					2.5	1	10	2.94
159 <i>Gammarus setosus</i> Dementieva, 1931		0 - 30	2.5	0 - 5	0		3	1	4	2		5	1	10	1155		0.04	0.54	0.02	11.38	0 - 30	10	1171	11.99
160 <i>Gammarus wilkitzkii</i> Birula, 1897	2.5		0.5 - 1.3			1		2		1	4		4		1	0.22				0.10	0 - 2.5	4	9	0.60
161 <i>Gitanopsis arctica</i> G.O. Sars, 1892		15				1						1									15	1	1	0.01
162 <i>Gitanopsis inermis</i> (G.O. Sars, 1883)			15 - 30	5				3	2				10	12					0.01	0.02	5 - 30	5	22	0.03
163 <i>Guerneia nordenskioldi</i> (Hansen, 1888) ¹		25				1						1									25	1	1	0.01
164 <i>Halirages fulvocincta</i> (M. Sars, 1858)	15	10 - 30	0 - 10	2.5 - 5		1	6	8	3		1	25	140	5		0.01	0.14	0.54	0.12		0 - 30	18	171	0.80
165 <i>Hyperideia</i> g. sp.	30		0			1					1			1		0.01			0.02		0 - 30	2	2	0.04
166 <i>Ischyrocerus anguipes</i> Krøyer, 1838	2.5 - 20	0 - 15	0 - 30	0 - 10	0 - 5	7	7	9	3	4	2163	1389	3309	342	51	2.79	1.17	2.61	1.93	0.15	0 - 30	30	7254	8.66
167 <i>Ischyrocerus megacheir</i> Boeck, 1871	5 - 20		10			2		2			35		26			0.10		0.18			5 - 20	4	61	0.28
<i>Ischyrocerus</i> spp.	2.5 - 25	5 - 30	2.5 - 30	2.5 - 5	2.5 - 5	4	7	9	6	2	81	176	249	13	35	0.12	0.08	0.17	0.02	0.37	2.5 - 30	28	554	0.75
168 <i>Maera prionochira</i> Bruggen, 1907		20				1						1									20	1	1	0.01
169 <i>Megamoera dentata</i> (Krøyer, 1842)	15 - 30	10 - 30	15 - 25	5 - 10		3	6	4	5		6	12	12	5		0.16	0.11	0.09	0.03		5 - 30	18	35	0.39
170 <i>Metopa glacialis</i> (Krøyer, 1842)	5 - 10	5				3	1				6	2				0.01	0.02				5 - 10	4	8	0.03
171 <i>Metopa pusilla</i> G.O. Sars, 1892	2.5 - 5		2.5			2		1			17		2			0.01		0.01			2.5 - 5	3	19	0.03
172 <i>Metopa sinuata</i> G.O. Sars, 1892	5 - 15	2.5	1.3 - 5			3	1	3			15	1	8			0.01	0.01	0.01			1.3 - 15	7	24	0.02
173 <i>Monoculodes latimanus</i> (Goes, 1866)		30	25 - 30	5 - 15		2	2	4			4	5	7				0.02	0.05	0.04		5 - 30	8	16	0.11
174 <i>Odius carinatus</i> (Bate, 1862)	10	2.5 - 30	20			1	5	1			1	8	1			0.01	0.01	0.01			2.5 - 30	7	10	0.03
175 <i>Onisimus edwardsi</i> Krøyer, 1846	2.5 - 15	2.5 - 25	1.3 - 15	0 - 5		4	5	6	5		10	27	67	22		0.27	0.67	0.41	0.21		0 - 25	20	126	1.56
176 <i>Onisimus litoralis</i> (Krøyer, 1845)	2.5	2.5		0		1	1			1	1	5		1		0.01	0.14		0.20		0 - 2.5	3	7	0.35
177 <i>Parapleustes assimilis</i> (G.O. Sars, 1882)	5		5			1		1			2			1		0.01			0.01		5	2	3	0.01
178 <i>Parapleustes bicuspis</i> (Krøyer, 1838)	2.5 - 25	5 - 20	1.3 - 25	2.5 - 5		8	6	12	2		29	137	131	33		0.04	0.30	0.16	0.36		1.3 - 25	28	330	0.86
179 <i>Parapleustes</i> cf. <i>gracilis</i> (Buchholz, 1874)			5					1						1					0.01		5	1	1	0.01
180 <i>Paroedicerus lynceus</i> (M. Sars, 1858)				5 - 15	2.5 - 5			4	4					12	23				0.17	0.51	2.5 - 15	8	35	0.68
181 <i>Pleustes (Pleustes) panoplus</i> (Krøyer, 1838)		10 - 15	0 - 10				3		8			4		89				0.12	0.38		0 - 15	11	93	0.50
<i>Pleustidae</i> g. spp.	5	2.5	0 - 10	5		2	1	5	1		11	28	37	2		0.03	0.24	0.09	0.01		0 - 10	9	78	0.36
182 <i>Pleusymtes glaber</i> (Boeck, 1861)	2.5 - 25	2.5 - 15	0 - 25	2.5 - 5		9	7	10	4		113	68	88	14		0.12	0.10	0.09	0.02		0 - 25	30	283	0.32
183 <i>Pleusymtes glabroides</i> (Dunbar, 1954)	5 - 20	2.5 - 15	1.3 - 20	0 - 2.5	2.5 - 5	5	5	7	3	2	93	55	36	69	13	0.11	0.06	0.04	0.24	0.04	0 - 20	22	266	0.49
184 <i>Pleusymtes pulchella</i> (G.O. Sars, 1876)	20 - 25					2					3					0.01					20 - 25	2	3	0.01
185 <i>Protomedeia fasciata</i> Krøyer, 1842		30				1						2						0.01			30	1	2	0.01
186 <i>Rhachotropis inflata</i> (G.O. Sars, 1882)	20 - 25	15 - 30				2	5				3	27				0.01	0.07				15 - 30	7	30	0.08
187 <i>Rostriculodes borealis</i> (Boeck, 1871)		25 - 30	25 - 30	2.5 - 5	2.5 - 5	3	3	3	3		3	3	5	14		0.03	0.01	0.05	0.16		2.5 - 30	12	25	0.25
188 <i>Rozinante</i> cf. <i>fragilis</i> (Goes, 1886)				5					1					1					0.01		5	1	1	0.01
189 <i>Socarnes vahlii</i> (Krøyer, 1838)	20 - 30	5	20	2.5 - 5		4	1	1	2		7	3	1	7		0.06	0.33	0.06	0.12		2.5 - 30	8	18	0.57
190 <i>Syrrhoe crenulata</i> Goes, 1866	20 - 25	10 - 30				2	5				10	24				0.13	0.13				10 - 30	7	34	0.26
191 <i>Tryphosella schneideri</i> (Stephensen, 1921)	10	15	5 - 20			1	1	2			6	1	2			0.07	0.02	0.02			5 - 20	4	9	0.11
192 <i>Westwoodilla caecula</i> (Bate, 1856)		10 - 30				4						17							0.07		10 - 30	4	17	0.07

193 <i>Weyprechtia pinguis</i> (Krøyer, 1838)	15		0 - 5	2.5 - 5		1		7	4		7		28	18		1.15	0.50	0.79	0 - 15	12	53	2.44		
Class PYCNOGONIDA																								
194 <i>Nymphon gracile</i> Leach, 1814 ¹	5		2.5			1		1			2		1			0.04	0.04		2.5 - 5	2	3	0.08		
195 <i>Nymphon rubrum</i> Hodge, 1865 ¹	2.5 - 10	2.5 - 10				4	3				11	7				0.09	0.17		2.5 - 10	7	18	0.26		
196 <i>Phoxichilidium femoratum</i> (Rathke, 1799)	5 - 10	2.5 - 5	5			3	2	1			5	3	1			0.05	0.04	0.04	2.5 - 10	6	9	0.13		
197 <i>Pseudopallene circularis</i> (Goodsir, 1842)		5 - 15	5 - 30	2.5 - 10		3	7	4			15	22	25			0.21	0.14	0.35	2.5 - 30	14	62	0.70		
198 <i>Pseudopallene spinipes</i> (Fabricius, 1780) ¹			10 - 20					4					9				0.10		10 - 20	4	9	0.10		
Phylum MOLLUSCA																								
Class POLYPLACOPHORA																								
199 <i>Stenosemus albus albus</i> (Linnaeus, 1767)	15 - 30	15 - 25	15 - 25	2.5 - 10		7	3	3	4		34	3	6	8		0.58	0.47	0.49	0.24	2.5 - 30	17	51	1.78	
200 <i>Tonicella marmorea</i> (Fabricius, 1780)	5 - 30	0 - 30	5 - 30	2.5 - 10		11	10	11	4		279	227	114	11		10.21	21.25	6.04	1.17	0 - 30	36	631	38.67	
201 <i>Tonicella rubra</i> (Linnaeus, 1767)	10 - 30	5 - 25	1.3 - 25	5		9	5	9	2		173	80	152	3		1.73	1.21	1.49	0.02	1.3 - 30	25	408	4.45	
Class GASTROPODA																								
202 <i>Amphorina odhneri</i> (Derjugin et Gurjanova, 1926) ¹	2.5					1					2					0.04				2.5	1	2	0.04	
203 <i>Astyris rosacea</i> (Gould, 1840)		10	1.3	2.5		1	1	1			2	1	3			0.40	0.17	0.37		1.3 - 10	3	6	0.94	
204 <i>Boreotrophon clathratus</i> (Linnaeus, 1767)	10 - 30	5 - 25	5 - 30	2.5 - 5		5	4	7	3		16	25	18	8		0.90	2.21	0.86	0.69	2.5 - 30	19	67	4.66	
205 <i>Boreotrophon truncatus</i> (Linnaeus, 1767)		15				1					3						1.70			15	1	3	1.70	
206 <i>Buccinum cyaneum</i> Bruguiere, 1789-1792	5 - 25	2.5 - 20	15	2.5 - 5		7	6	1	2		11	48	2	7		13.18	16.18	21.60	0.44	2.5 - 25	16	68	51.41	
207 <i>Buccinum glaciale</i> Linnaeus, 1761	10 - 20	10 - 20	15	2.5 - 10		3	4	1	2		8	10	1	2		62.40	60.99	5.60	22.40	2.5 - 20	10	21	151.39	
208 <i>Clione limacina</i> (Phipps, 1774)		0				1					1						4.40			0	1	1	4.40	
209 <i>Coryphella salmonacea</i> (Couthouy, 1838)		2.5				1					2						0.16			2.5	1	2	0.16	
210 <i>Cryptonatica clausa</i> (Broderip et Sowerby, 1829)	30					1					1					0.63				30	1	1	0.63	
211 <i>Curtitoma trevellyana</i> (Turton, 1834)		25				1					3						0.42			25	1	3	0.42	
212 <i>Curtitoma violacea</i> (Mighels et Adams, 1842)		25				1					1						0.11			25	1	1	0.11	
213 <i>Cylichna alba</i> (Brown, 1827)			5					1					X					X		5	1	X	X	
214 <i>Dendronotus frondosus</i> (Ascanius, 1774)	2.5 - 10		2.5			3		1			7		1			0.10		0.48		2.5 - 10	4	8	0.58	
215 <i>Epheria crassior</i> (Montagu, 1803)	10					1					X							X		10	1	X	X	
216 <i>Erginus rubella</i> (Fabricius, 1780)	5 - 30	0 - 30	0 - 30	2.5 - 10		9	12	10	4		34	59	32	6		0.16	0.15	0.14	0.03	0 - 30	35	131	0.48	
217 <i>Lepeta coeca</i> (O.F. Müller, 1776)		25 - 30	20 - 30	2.5 - 10		3	3	3			14	5	4				0.31	0.29	0.18	2.5 - 30	9	23	0.78	
218 <i>Littorina saxatilis</i> (Olivi, 1792)		2.5				1					X						X			2.5	1	X	X	
219 <i>Margarites costalis</i> (Gould, 1841)			10					1					8					0.40		10	1	8	0.40	
220 <i>Margarites groenlandica</i> var. <i>groenlandica</i> (Gmelin, 1790)	5 - 30	2.5 - 25	2.5 - 30	2.5 - 10		9	9	11	5		80	124	79	53		1.70	1.83	1.57	0.85	2.5 - 30	34	336	5.95	
221 <i>Margarites helicina</i> (Phipps, 1774)	2.5 - 30	0 - 15	0 - 20	2.5 - 15	2.5 - 5	6	8	13	7	4	97	903	482	152	33	0.55	5.17	2.55	0.95	0.47	0 - 30	38	1667	9.68
222 <i>Moelleria costulata</i> (Möller, 1842)	30	10 - 30	10 - 30	2.5 - 10		1	6	7	5		1	26	20	18		0.01	0.04	0.04	0.04	2.5 - 30	19	65	0.13	
223 <i>Oenopota pingelii</i> (Möller, 1842)	30	15				1	1				1	1				0.06	0.10			15 - 30	2	2	0.16	
224 <i>Oenopota pyramidalis</i> (Strom, 1788)		20				1					2						0.18			20	1	2	0.18	
225 <i>Onoba castanea</i> (Möller, 1842)	10 - 25	2.5 - 15	2.5	5		4	2	1	1		6	4	1	1		0.02	0.03	0.01	0.05	2.5 - 25	8	12	0.10	
226 <i>Onoba jeffreysii</i> (Waller, 1864) ¹	10 - 30	10	2.5 - 30	2.5 - 5		2	1	6	3		2	2	23	36		0.01	0.02	0.03	0.12	2.5 - 30	12	63	0.18	
227 <i>Onoba karica</i> Golikov, 1986 ¹	5 - 30	2.5 - 15	5 - 20	5	2.5	4	4	5	1	1	87	58	88	4	1	0.26	0.12	0.13	0.04	0.01	2.5 - 30	15	238	0.55
228 <i>Palio dubia</i> (M. Sars, 1829) ¹			5					1					1					0.09		5	1	1	0.09	

264 <i>Myriotrochus rinkii</i> Steenstrup, 1851					5				2				24						3.36	5	2	24	3.36	
265 <i>Ocnus glacialis</i> (Ljungman, 1879)	5	2.5	2.5 - 20			1	2	3		1	2	5			0.04	0.24	0.11			2.5 - 20	6	8	0.40	
Class ECHINOIDEA																								
266 <i>Strongylocentrotus droebachiensis</i> (O.F. Müller, 1776)	10 - 30	5 - 25		15		9	4	1		51	9		3		412.09	272.46		86.36		5 - 30	14	63	770.91	
267 <i>Strongylocentrotus pallidus</i> (G.O. Sars, 1871)	5 - 30	5 - 20	5 - 20	5		5	5	5	1	27	19	13	2		130.85	145.50	131.32	35.16		5 - 30	16	61	442.83	
Class BRYOZOA																								
Order Cyclostomata																								
268 <i>Borgella tumulosa</i> Kluge, 1955 ¹	30		25			1		1		X		1			0.97		0.04			25 - 30	2	1	1.01	
269 <i>Crisia denticulata</i> (Lamarck, 1816)																				5	1	X	0.28	
270 <i>Crisia eburnea</i> (Linnaeus, 1758)				5					1				X				0.44			5	1	X	0.44	
<i>Crisia</i> spp.	5	5 - 10	2.5 - 30	2.5 - 15		1	3	6	5	X	X	X	X		0.02	0.01	5.53	2.01		2.5 - 30	15	X	7.57	
271 <i>Crisiella diversa</i> (Kluge, 1955)			2.5 - 25		0			2	1			X		X			0.30		0.01	0 - 25	3	X	0.31	
272 <i>Crisiella producta</i> (Smitt, 1865)			1.3 - 25		5			2	1			X		X			2.68		0.09	1.3 - 25	3	X	2.77	
<i>Crisiella</i> spp.	2.5 - 15	2.5 - 30	0 - 30	0 - 10	2.5	4	4	8	5	1	X	X	X	X	0.91	3.06	3.43	3.20	0.02	0 - 30	22	X	10.61	
273 <i>Desmeplagioecia</i> sp.				5					1				1				0.06			5	1	1	0.06	
274 <i>Diplosolen obelia</i> (Johnston, 1838)			25					1				7					0.18			25	1	7	0.18	
275 <i>Diplosolen</i> sp.n., aff.			25					1				2					0.10			25	1	2	0.10	
276 <i>Filicrisia geniculata</i> (Milne-Edwards, 1838)		2.5	5				1	1			X	X				0.27	0.16			2.5 - 5	2	X	0.43	
277 <i>Filicrisia smitti</i> (Kluge, 1946) ¹																				5	1	X	8.74	
278 <i>Lichenopora</i> sp.	2.5 - 30	2.5 - 30	2.5 - 30	2.5 - 15	2.5 - 5	11	14	14	7	3	99	139	129	75	18	0.32	0.62	0.91	0.66	0.26	2.5 - 30	49	460	2.77
279 <i>Lichenopora</i> sp.2		25					1					7					0.09			25	1	7	0.09	
280 <i>Oncousoecia canadensis</i> Osburn, 1933		25					1					4					0.11			25	1	4	0.11	
281 <i>Oncousoecia diastoporoides</i> (Norman, 1869)	20 - 30	25 - 30	5 - 25	5		4	3	4	1		100	82	14	1		1.43	1.23	0.21	0.01		5 - 30	12	197	2.89
282 <i>Oncousoecia polygonalis</i> (Kluge, 1915) ¹	20 - 30	25 - 30				3	3				8	2				0.11	0.05				20 - 30	6	10	0.17
283 <i>Tubulipora soluta</i> Kluge, 1946	25		10 - 30	5		1		4	1		2		6	1		0.05		0.07	0.05		5 - 30	6	9	0.17
<i>Tubulipora</i> spp.	5 - 30	2.5 - 30	5 - 30	2.5 - 15		10	7	12	7		100	48	174	17		0.58	0.36	0.80	0.19		2.5 - 30	36	339	1.92
284 <i>Tubulipora uniformis</i> Gostilovskaja, 1955 ¹				5					1				2					0.01			5	1	2	0.01
Order Ctenostomata																								
285 <i>Alcyonidium disciforme</i> Smitt, 1872				2.5 - 5					3					29				1.38		2.5 - 5	3	29	1.38	
286 <i>Alcyonidium gelatinosum</i> (Linnaeus, 1767)	15	2.5	2.5 - 30	2.5 - 10	2.5	1	1	4	2	1	X	X	X	X	0.05	0.14	3.02	1.53	5.20	2.5 - 30	9	X	9.95	
287 <i>Alcyonidium irregulare</i> Kluge, 1961 ¹			2.5					1					X				1.60			2.5	1	X	1.60	
288 <i>Alcyonidium mytili</i> Dalyell, 1847	20		10 - 20			1		2			2		2			0.62		0.28			5 - 20	3	4	0.89
289 <i>Bowerbankia imbricata</i> (Adams, 1800)		10 - 30		2.5			2		2			X		X			0.75		0.92	2.5 - 30	4	X	1.67	
290 <i>Flustrellidra corniculata</i> (Smitt, 1872)	2.5	2.5	0 - 2.5			1	2	3			X	X	X			0.11	0.18	0.53			0 - 2.5	6	X	0.82
Order Cheilostomata																								
291 <i>Amphiblestrum trifolium</i> (S. Wood, 1844)	30		20			1		1			2		1			0.08		0.05			20 - 30	2	3	0.13
292 <i>Arctonula arctica</i> (M. Sars, 1851)	10	5 - 15	10	5 - 10		1	2	1	2		6	2	1	3		0.27	0.20	0.02	0.09		5 - 15	6	12	0.58
293 <i>Bugulopsis peachii</i> (Busk, 1851)			2.5						1				X					0.02			2.5	1	X	0.02
294 <i>Callopora craticula</i> (Alder, 1857)	2.5 - 30	5 - 30	2.5 - 30	5 - 10		11	6	11	2		100	35	115	15		0.88	0.54	1.05	0.55		2.5 - 30	30	265	3.02
295 <i>Callopora lata</i> (Kluge, 1907)	5 - 30	5 - 30	2.5 - 30	2.5 - 10	5	11	6	13	4	1	30	45	266	13	2	0.33	0.80	2.59	0.20	0.03	2.5 - 30	35	356	3.95

296	<i>Callopora lineata</i> (Linnaeus, 1767)	2.5 - 20	2.5 - 15	2.5 - 25	2.5 - 10	2.5	5	6	5	5	1	18	12	14	32	1	0.05	0.04	0.06	0.15	0.01	2.5 - 25	22	77	0.31	
297	<i>Callopora smitti</i> Kluge, 1946	30		15 - 30			1		5			3		18			0.17		0.81			15 - 30	6	21	0.97	
	<i>Callopora</i> spp.	5 - 25	2.5 - 30	2.5 - 30	2.5 - 10	2.5 - 5	5	7	10	3	2	38	30	92	3	4	0.29	0.09	0.49	0.01	0.01	2.5 - 30	27	167	0.90	
298	<i>Callopora whiteavesi</i> (Norman, 1903) ¹	10 - 30	5 - 30	10 - 30	2.5 - 10	2.5	4	7	6	4	1	8	51	28	32	1	0.39	0.99	0.59	1.14	0.20	2.5 - 30	22	120	3.31	
299	<i>Cauloramphus cymbaeformis</i> (Hincks, 1877)	25					1					7					0.21					25	1	7	0.21	
300	<i>Cauloramphus intermedius</i> Kluge, 1961	2.5 - 30	0 - 15	2.5 - 30	2.5 - 10	2.5 - 5	9	6	12	7	3	29	139	127	30	3	0.13	1.07	0.46	0.14	0.03	0 - 30	37	328	1.84	
301	<i>Cauloramphus spiniferum</i> (Johnston, 1832)		5						1					3					0.14			5	1	3	0.14	
302	<i>Cellepora</i> sp.	30		30			1		1			1		1			0.80		0.20			30	2	2	1.00	
303	<i>Celleporina surcularis</i> (Packard, 1863)			30					1					1					12.80			30	1	1	12.80	
304	<i>Celleporina ventricosa</i> (Lorenz, 1886)	30					2					3					0.94					30	2	3	0.94	
305	<i>Cheiloporina sincera</i> (Smitt, 1868)	10		10 - 30	10		1		4	1		9		36	1		5.85		3.17	0.07		10 - 30	6	46	9.09	
306	<i>Codonellina</i> sp.n., aff.	25		10 - 30			1		2			3		2			0.64		0.10			10 - 30	3	5	0.74	
307	<i>Cribrilina annulata</i> (Fabricius, 1780)	5 - 25	2.5 - 30	2.5 - 30	2.5 - 15	2.5 - 5	4	9	12	8	3	39	113	36	69	16	1.29	1.24	0.31	0.83	0.30	2.5 - 30	36	273	3.96	
308	<i>Cylindroporella tubulosa</i> (Norman, 1868)	10 - 30	5 - 30	2.5 - 30	2.5 - 10		9	9	12	7		94	131	190	28		0.63	0.80	1.08	0.26		2.5 - 30	37	443	2.76	
309	<i>Cystisella saccata</i> subsp.n.			30					1					1					2.00			30	1	1	2.00	
310	<i>Dendrobeania fruticosa</i> (Packard, 1863)	10 - 15	5 - 20	10 - 30	2.5 - 10		2	3	7	4		X	X	X	X		0.01	0.08	7.57	7.40		2.5 - 30	16	X	15.07	
311	<i>Dendrobeania leviseni</i> (Kluge, 1929) ¹		10	20 - 25	5			1	4	1			X	X	X				0.61	19.60	20.84	5 - 25	6	X	41.06	
312	<i>Dendrobeania murrayana</i> (Johnston, 1847)	5 - 10	0 - 30	2.5 - 10	5		3	9	3	1		X	X	X	X		83.87	15.21	22.27	2.74		0 - 30	16	X	124.09	
313	<i>Dendrobeania pseudoleviseni</i> Kluge, 1952 ¹		5	5	5			1	1	2			X	X	X				0.05	56.80	15.11	5	4	X	71.96	
	<i>Dendrobeania pseudomurrayana</i> var. <i>fessa</i>	5 - 10	5 - 15	5	5		2	4	1	1		X	X	X	X											
314	(Kluge, 1955)																14.56	21.28	0.15	0.02		5 - 15	8	X	36.01	
315	<i>Doryporella</i> sp.n., aff.			25					1					2					0.54			25	1	2	0.54	
316	<i>Doryporella spathulifera</i> (Smitt, 1868)	15 - 30	15 - 30	10 - 30			3	3	9			16	5	36			0.66	0.27	0.53			10 - 30	15	57	1.46	
317	<i>Electra crustulenta arctica</i> Borg, 1931	2.5 - 30	0 - 30	1.3 - 30	2.5 - 10	2.5 - 5	6	12	10	6	3	6	126	63	81	18	0.01	0.16	0.28	2.12	0.36	0 - 30	37	294	2.94	
318	<i>Escharella indivisa</i> Levinsen, 1916 ¹				5					1					2					0.03		5	1	2	0.03	
319	<i>Escharella ventricosa</i> (Hassall, 1842)	25 - 30	30	20	2.5 - 10		3	1	1	3		23	2	1	6		0.20	0.02	0.02	0.35		2.5 - 30	8	32	0.60	
320	<i>Escharelloides</i> sp.n., aff.			30					1					5					1.84			30	1	5	1.84	
321	<i>Escharelloides spinulifera</i> (Hincks, 1889)			30					1					1					0.16			30	1	1	0.16	
322	<i>Escharoides jacksoni</i> (Waters, 1900)			30	5				1	1				1	1					0.01	0.04	5 - 30	2	2	0.05	
323	<i>Eucratea loricata</i> (Linnaeus, 1758)	2.5 - 20	2.5 - 30	0.5 - 20	0 - 15	2.5 - 5	8	8	8	8	3	X	X	X	X	X	148.54	104.92	90.55	16.96	2.63	0 - 30	35	X	363.60	
324	<i>Harmeria scutulata</i> (Busk, 1855)	5 - 15	2.5 - 30	1.3 - 10	2.5 - 15	2.5 - 5	3	8	6	8	4	61	76	43	340	48	3.74	0.96	0.97	5.17	1.08	1.3 - 30	29	568	11.91	
325	<i>Hippoponella hippopus</i> (Smitt, 1868)	20 - 30	5 - 25	25 - 30			4	2	2			5	3	2			0.15	0.09	0.21			5 - 30	8	10	0.46	
326	<i>Hippoponella parva</i> Androsova, 1958 ¹		25 - 30						3					54					1.99			25 - 30	3	54	1.99	
327	<i>Hippoporina borealis</i> (Waters, 1900)			25 - 30					2					2						0.16		25 - 30	2	2	0.16	
328	<i>Hippoporina harnsworthi</i> (Waters, 1900)			10 - 20	5				3	1				4	4				0.59	0.80		5 - 20	4	8	1.39	
329	<i>Hippoporina murdochi</i> (Kluge, 1961)	10	5	10 - 30			1	1	2			1	1	2			0.05	0.07	0.06			5 - 30	4	4	0.19	
330	<i>Hippoporina obesa</i> (Waters, 1900)	10	30				1	1				1	1				0.20	0.04				10 - 30	2	2	0.24	
331	<i>Hippoporina propinqua</i> (Smitt, 1868)	5 - 10					2					11					0.46					5 - 10	2	11	0.46	
332	<i>Hippoporina reticulatopunctata</i> (Hincks, 1877)	10 - 25	5 - 15	5 - 25	10		4	2	5	1		6	2	10	1		0.06	0.03	0.15	0.02		5 - 25	12	19	0.26	
333	<i>Hippoporina</i> sp.n., aff.	30					1					2					0.53					30	1	2	0.53	
334	<i>Hippoporina ussowi</i> (Kluge, 1908)	5 - 30	5 - 20	2.5 - 30	5		7	3	10	1		32	6	27	1		1.34	0.53	1.02	0.26		2.5 - 30	21	66	3.15	
335	<i>Hippothoa divaricata</i> var. <i>arctica</i> Kluge, 1906	25 - 30	15 - 30	15 - 30	10		3	5	5	1		3	52	23	1		0.02	0.40	0.53	0.01		10 - 30	14	79	0.97	
336	<i>Hippothoa expansa</i> Dawson, 1859		5 - 15						2					3					0.11			5 - 15	2	3	0.11	
337	<i>Hippothoa hyalina</i> (Linnaeus, 1767)	2.5 - 30	0 - 30	0 - 30	2.5 - 15	2.5 - 5	11	10	17	8	3	186	56	203	269	12	6.60	5.69	3.03	6.21	0.58	0 - 30	49	726	22.11	
338	<i>Microporella ciliata</i> (Pallas, 1766)	5 - 30	2.5 - 30	2.5 - 30	10		10	8	3	1		124	90	4	1		2.25	1.48	0.07	0.01		2.5 - 30	22	219	3.81	

383 <i>Tricellaria gracilis inermis</i> Kluge, 1961	10	5	10	5 - 10		1	1	1	2		X	X	X	X		0.01	0.01	0.03	0.02		5 - 10	5	X	0.06
384 <i>Tricellaria ternata</i> (Ellis et Solander, 1786)	2.5 - 20	2.5 - 30	1.3 - 30	0 - 15	5	8	8	14	8	2	X	X	X	X	X	219.17	88.46	33.71	20.13	0.07	0 - 30	40	X	361.54
385 <i>Umbonula patens</i> (Smitt, 1868)	10					1					3					0.08					10	1	3	0.08

Phylum CHORDATA

Class ASCIDIACEA

Order Aplousobranchia

386 <i>Didemnum roseum</i> M. Sars, 1851			10 - 25															0.85			10 - 25	3	5	0.85
387 <i>Synoicum</i> sp.1	5 - 10	5 - 10	5 - 25			4	2	5			31	28	30			273.50	88.60	40.80			5 - 25	11	89	402.90
388 <i>Synoicum</i> sp.2	5 - 10	5 - 15	5 - 25			2	2	2			7	14	2			3.20	8.40	3.00			5 - 25	6	23	14.60

Order Phlebobranchia

389 <i>Ascidia obliqua</i> Alder, 1863			5	2.5				1	1				1	1				6.00	4.00		2.5 - 5	2	2	10.00
390 <i>Cheliosoma</i> sp. juv.				2.5					1					1					2.00		2.5	1	1	2.00

Order Stolidobranchia

391 <i>Boltenia echinata</i> (Linnaeus, 1767)	10 - 20					2					2					12.40					10 - 20	2	2	12.40
392 <i>Botrylloides aureum</i> M. Sars, 1851			30					1					2					3.60			30	1	2	3.60
393 <i>Dendrodoa aggregata</i> (Rathke, 1806)	5 - 10	5	10 - 25			2	2	2			31	14	2			125.20	5.70	0.98			5 - 25	6	47	131.88
394 <i>Dendrodoa grossularia</i> (Van Beneden, 1846)				2.5 - 5					2					6					6.40		2.5 - 5	2	6	6.40
395 <i>Dendrodoa pulchella</i> (Verrill, 1871)	5 - 10	5				3	1				13	25				37.60	7.20				5 - 10	4	38	44.80
396 <i>Halocynthia aurantium</i> (Pallas, 1787) ¹	10					2					2					126.60					10	2	2	126.60
397 <i>Microcosmus</i> cf. <i>glacialis</i> M. Sars, 1859 ¹		2.5						1				1						0.12			2.5	1	1	0.12
398 <i>Molgula siphonalis</i> M. Sars, 1859		2.5 - 5						2				27						10.00			2.5 - 5	2	27	10.00
399 <i>Molgula</i> sp.1			2.5	2.5				1	1				14	2				9.60	1.60		2.5	2	16	11.20
400 <i>Molgula</i> sp.2			1.3					1					1					0.16			1.3	1	1	0.16
<i>Molgulidae</i> g. spp.	5-10	5	2.5			2	2	1			3	5	1			0.36	2.6	1.2			2.5 - 10	5	9	4.16
401 <i>Pyura</i> sp.			25					1					1					0.32			25	1	1	0.32
402 <i>Styela coriacea</i> (Alder and Hancock, 1848)		2.5		5				1	1			1		2				12.00	4.00		2.5 - 5	2	3	16.00
403 <i>Styela rustica</i> (Linnaeus, 1767)	15 - 25	25	5 - 25	2.5 - 10		2	1	5	4		2	2	7	8		3.60	136.00	5.03	40.40		2.5 - 25	12	19	185.03

Diverse	2.5 - 25	0 - 30	1.3 - 2.5	0 - 15	2.5 - 5	52	71	83	44	7	128	166	120	68	11	0.49	0.15	1.52	0.11	0.05	0 - 30	257	493	2.32
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Total	2.5 - 30	0 - 30	0 - 30	0 - 15	0 - 5	962	913	1193	512	114	48680	52077	41563	9418	1704	4225.98	2290.39	2511.09	1367.60	35.02	0 - 30	3697	153443	10438.79
Mean for all samples on transect	-	-	-	-	-	68.71	57.06	70.18	51.20	19.00	3477.14	3254.81	2444.88	941.80	284.00	301.86	143.15	147.71	136.76	5.84	-	56.88	2360.66	160.60

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Paper I

Paper II

Paper III

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