UNIVERSITY OF TROMSØ UiT

FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS
DEPARTMENT OF ARCTIC AND MARINE BIOLOGY

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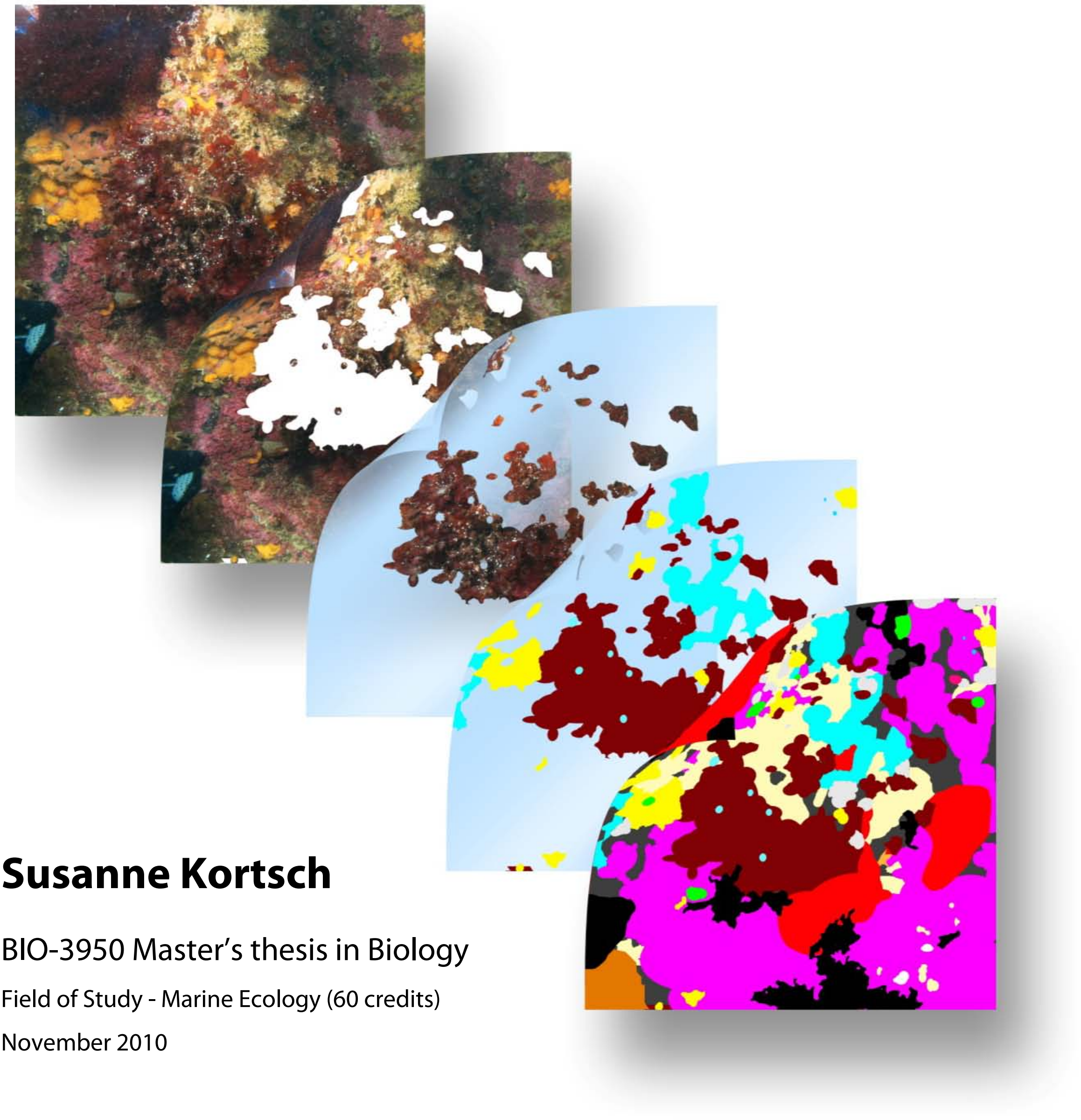
- Assessment of density and cover using image analysis



Susanne Kortsch

BIO-3950 Master's thesis in Biology

Field of Study - Marine Ecology (60 credits)

November 2010

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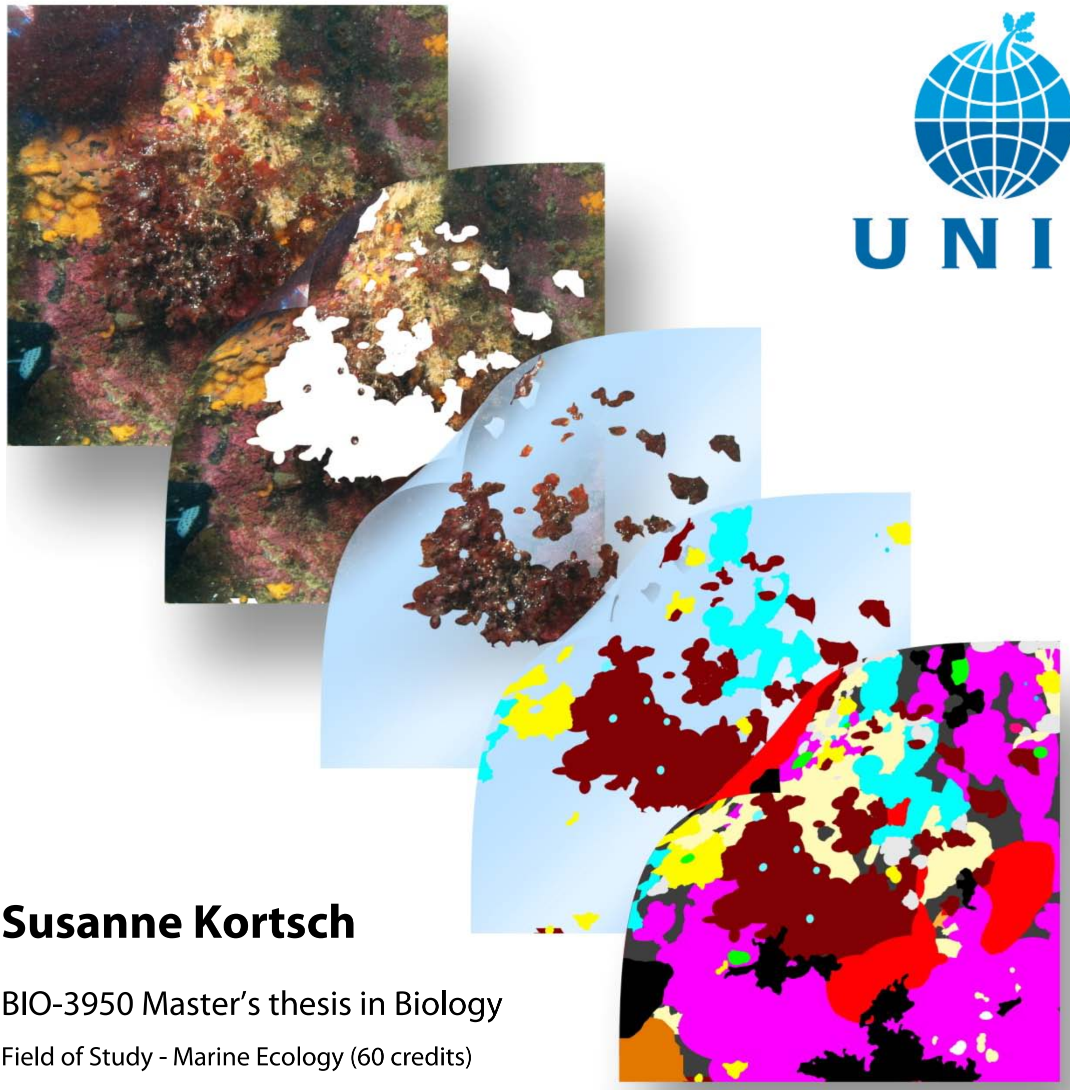

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“In nature’s infinite book of secrecy, a little can I read.”

William Shakespeare

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Abstract

Long-term patterns (1980-2008) in the structure of a macrobenthic sublittoral community on the rocky-bottom of a high Arctic fjord (Smeerenburgfjord) in northwest Svalbard were investigated using image analysis of underwater photographs from a permanently marked locality. Species composition revealed the locality to be characterized by calcareous algae, various brown- and red-algae, and several conspicuous sessile and colonial filter feeders. The most important biotic factors shaping the benthic community were competition for space and the low number of predatory species. Environmental factors regarded as having great impact on the community structure were the vertical orientation of the substrate and intermediate to strong water currents. Sea surface temperature (SST), West Spitsbergen Current (WSC) temperature and salinity, North Atlantic Oscillation (NAO) and sea ice cover (SIC) were tested as predictors for the variation in community structure between years. All together the environmental predictors accounted for 69% of the variation. Particularly, high correlations were found between the community structure, and the temperature gradients (SST and WSC) and SIC. High correlations were also found between the Shannon-Wiener Biodiversity (H') index and the SST (0.7) and SIC (-0.66). The most pronounced changes in community structure occurred after 1994. Among the species associated with these changes are: brown- and red-algae, *S. spirorbis* and Bryozoans. The most remarkable and persistent change observed was the expansion of leaf-like macroalgae, increasing from 1% cover in 1980 to 40% cover in 2008.

Keywords: Arctic, Macrobenthos, Time series, Biodiversity, Climate variability, Image analysis, Canonical Correspondence Analysis

1. Introduction

Natural communities are characterized by changes in species composition and abundances in response to biotic and abiotic factors at several temporal and spatial scales, making them dynamic. Biotic factors include interactions between species such as competition (e.g. for space) and predation. Abiotic factors include the physical and chemical properties of the environment. Such factors may have direct and/or indirect impact on species by invoking responses related to recruitment, growth, survival and mortality (Townsend et al. 2006). Long-term studies are necessary for understanding how spatial and temporal changes affect the structure of communities (Kröncke et al. 2001). If the observed changes are ordered and directional, some predictability can be achieved through data analysis (Lively et al. 1993). Additionally, long-term studies offer the possibility to separate human induced changes from natural variability by overcoming the stochastic noise which can mask a snapshot analysis (Chiappone and Sullivan 1994).

Many macrobenthic organisms (organisms > 1 mm) are sessile and long-lived. Due to these attributes they are regarded as good indicators of long-term changes (Underwood 1996; Kröncke et al. 2001). Within a hard-bottom macrobenthic community, resources (food supply via the planktonic community) and interaction among species and individuals (e.g. predation, grazing and competition for space) are the most important biotic factors (Paine and Vadas 1969). Space is considered to be one of the most limiting resources in hard-bottom, benthic communities (Dayton 1971; Paine and Vadas 1969), and competition for space is regarded as one of the main structuring biotic forces (Jackson 1977; Konar and Iken 2005; Bertness and Leonard 1997). The main abiotic factors structuring the community include hydrographical characteristics (e.g. salinity, temperature, and water currents), substrate characteristics (heterogeneity, angle of incline, exposure) and depth (Sahade et al. 1991; Glasby 2000). Previous studies show higher variation in species composition and diversity within heterogeneous habitats (Kuklinski et al. 2006; Bruno and Bertness 2001). Erect leaf-like macroalgae may function as ecosystem engineers by altering the primary substrate via their physical structures providing microhabitats, and energy (Jones et al. 1994). Additionally, leaf-like macroalgae may alter light attenuation and hydrodynamic flow over the primary substrate.

Local physical and chemical properties, partly dictated by large scale climate forcing (acting on several inter-annual and decadal timescales), can affect the composition of species (Beuchel et al. 2006; Kröncke et al. 2001). These physical and chemical parameters may influence species directly through tolerance levels or indirectly by mediating biotic interactions (Huston 1994). At present the world is experiencing a period of pronounced climate warming, suggested by many to be a consequence of human activities (IPCC 2007; NorACIA 2010). The greatest and most dramatic changes have been recorded within the Arctic where the average temperature has increased at twice the global average rate resulting in greater than normal retreat of glaciers, and reduction in sea ice (Comiso et al. 2008), shifts in patterns of snow-fall, and increased freshwater run-off (NorACIA 2010). These environmental changes may have direct and indirect impacts on the benthic biotopes, biodiversity and population dynamics of species through their effects on water column stratification, timing and species composition of pelagic productivity, light penetration, and inorganic sedimentation (Zajczkowski et al. 2010). Although the dramatic thinning and loss of Arctic sea ice during the last decade might be indisputable (Comiso et al. 2008), consequences for Arctic marine rocky-bottom benthic organisms are hardly explored with only a few long-term investigations existing (Beuchel et al. 2006; Beuchel and Gulliksen 2008).

A long-term ecological community study based on image analysis was initiated in Kongsfjord during August in 1980. Significant and persistent changes in rocky-bottom community structure from 1980 to 2003 were found. A considerable part of the observed inter-annual variability (45%) could be attributed to fluctuations in the North Atlantic Oscillation index (NAO). NAO is defined as the difference between the normalized sea level pressure between Iceland and the Azores (Hurrell 1995). Its dominant cyclical component spans ~7.9 years. Biodiversity was found to correlate negatively with NAO and temperature of the West Spitsbergen Current (WSC). Community changes were particularly abrupt between 1994 to 1996, where dense carpets of brown algae appeared, and the abundance of sea anemones declined (Beuchel et al. 2006). During this period the NAO underwent a modal shift from moderately positive to strongly negative values. Swings from one extreme phase of the NAO to another produce large changes in the mean wind speed, and direction over the Atlantic Ocean between 40°N and 60°N (Johannessen et al. 1999). Significant changes in oceans surface temperature, ocean currents (along with their related heat transport), and sea ice cover in the sub-Arctic and Arctic regions are all induced by this shift (Johannessen et al. 1999). Ecological effects from the NAO have been documented in several studies (Ambrose et al. 2006; Ottersen et al. 2001; Beuchel et al. 2006; Kröncke et al. 2001).

The present (monitoring) project based on image analysis, was initiated parallel with the analogous study in Kongsfjord. This study attempts to find patterns within benthic community structure with relation to biotic and abiotic factors. There are three main objectives to this study:

1) Present a quantitative description of a sublittoral macrobenthic community on a rocky bottom locality in Smeerenburgfjord, Svalbard.

2) Describe and discuss how the community has been changing during a 28-year period from 1980 to 2008 with regard to community structure, and diversity patterns.

3) Link the biological changes and observations to biotic and abiotic factors such as climate and hydrographical variability during the same period of time.

2. Materials and methods

2.1 Study site characteristics

The Svalbard archipelago situated between 76° to 81° N and 10° to 35°E is surrounded by four separate water bodies: the Arctic Ocean to the North, the Norwegian Sea to the south, the Barents Sea to the east, and the Greenland Sea to the west. Along Svalbard’s western coast the main hydrological influence is from the extension of the North Atlantic Current which carries relatively warm and salty water into the West Spitsbergen Current (WSC) (Svendsen et al. 2002). This makes the fjords on the western part of Svalbard rather subarctic than arctic (Hop et al. 2002). The volumes of Atlantic Water (AW) inflow to the fjords are controlled by local wind patterns and the bathymetry of the seafloor (Haugan 1999). Terrestrial influences come from the cold glacial freshwater run-off during spring and summer.

This study was conducted at a permanently marked monitoring station at Danskøya (79°41.33’N, 11°04.00’E), which is located on the northwest coast of the Svalbard archipelago in Smeerenburgfjord (Fig. 1). Smeerenburgfjord is a glacial fjord with a maximum depth of about ~220 m which experiences both seasonal sea ice cover (SIC) and mixed inputs from terrestrial and marine water masses.

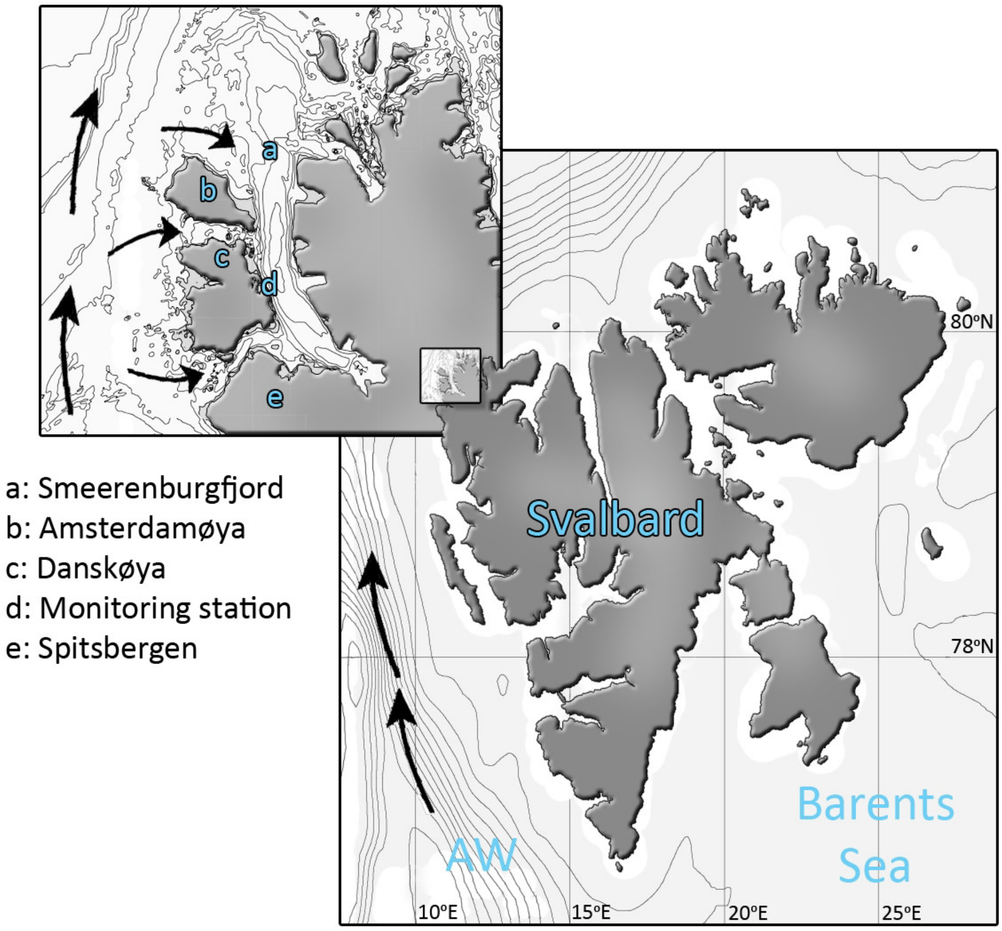


Figure 1. Map of the Svalbard archipelago and the study area at Danskøya in Smeerenburgfjord (79°41.33’N, 11°04.00’E), AW: Atlantic water.

The fjord is orientated in a North-South direction with steep mountains and glaciers running into the sea at its head. The western boundary is detached from Spitsbergen and comprised of the two islands. These islands, Amsterdamøya and Danskøya, are the northwestern most islands of the Archipelago. Topographically, this means the marine water masses can enter the fjord at three locations, at the northward pointing mouth (sill depth ~50 m) as well as the westward pointing sounds of Spitsbergen-Danskøya (sill depth ~20 m), and Danskøya-Amsterdamøya (sill depth ~10 m) (Fig. 1). That Smeerenburgfjord at the western boundary is comprised of two islands makes it, strictly, rather a sound than a fjord. However, for practical reasons and because the sound is known as Smeerenburgfjord, this term will be retained here.

No thorough, hydrographical investigation has yet been carried out in Smeerenburgfjord, but nine CTD-casts (three transects across the fjord spaced from the inner to the outer part) were collected on the 25 of September 2010 (Appendix XIV). These data show inflow of coastal water occurring across both these shallow sounds. The coastal water flows along the western side of the Smeerenburgfjord, which probably explains the strong current often experienced at the monitoring locality (Pers.comm. Bjørn Gulliksen). The eastern side of the fjord seems to consist of slightly lighter and less saline water (Appendix XIV). The lower salinity of this water is probably due to local influx of freshwater from rivers and melting glaciers in the inner part of Smeerenburgfjord, which due to the effects of the Coriolis force is concentrated on the eastside (Gilbert 1983). The experimental set-up at Danskøya is located on a vertical wall at a depth of 15 m. The wall is characterized by stony bedrock, covered with epibenthic macro-organisms. Since the wall is vertical, sediments from glacial run-off do not accumulate on the substrate.

2.2 Sampling design and set-up

This study spans a 28-year-period from 1980 to 2008. The collection method is based on a nondestructive photographic sampling technique, advantageous and suitable for performing long-term studies (Beuchel et al. 2010). In 1980 a permanent monitoring station was established in Smeerenburg at Danskøya. Since then, photographs have been taken annually between the middle of August and the beginning of September. From 1980 to 2003, the photographs were taken using a Hasselblad Super Wide Camera (SWC) with a Biogen 38 mm lens (including a correction lens to reduce “pillow distortion” of the pictures) in a Hasselblad underwater casing fitted with a Zeiss corrective glass port. The diver-operated camera setup was mounted on a (0.5 m x 0.5 m) metal frame. From 2003 and onwards the analogue Hasselblad camera was replaced by a digital Nikon D 100 6-mpx with a Nikkor 14 mm lens F/2.8 AF-D. The analogue photographs were scanned in high resolution (3-mpx). Two photos were taken of each quadrate with a slightly different angle (“stereo-pictures”), and the best from each pair was selected for image analysis.

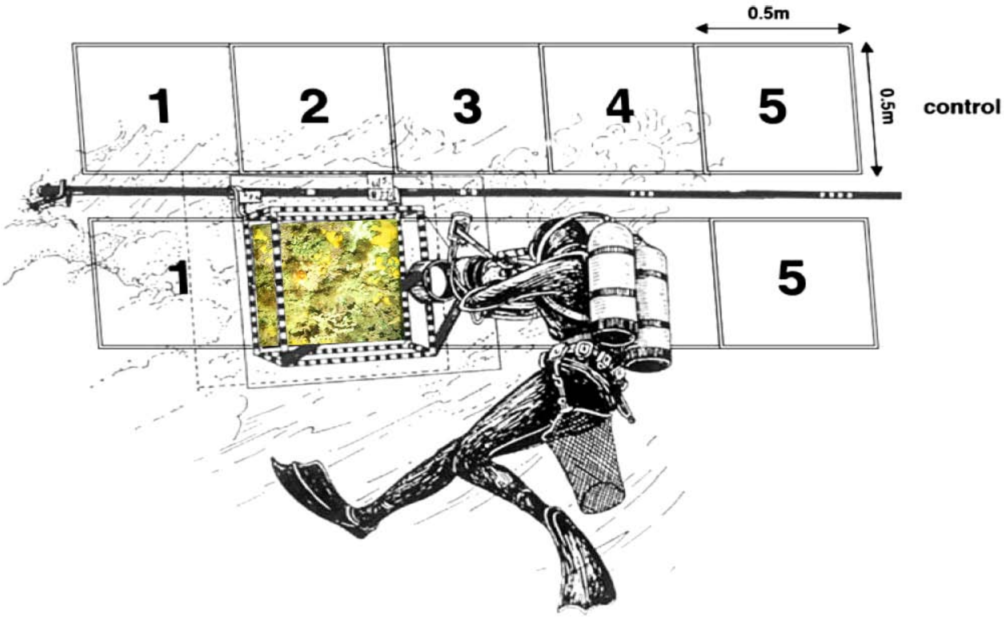


Figure 2. Sampling set-up for the permanent monitoring station at Danskøya, Smeerenburgfjord. The ten photographed areas are arranged in a 2x5 grid on a vertical wall at a depth of 15 m. Each square covers an area of 0.25 m^2. The diver-operated camera-rig is moved along a metal rod with notches, which assures the photographs to be taken exactly at the same position every year (redrawn from Lundälv, 1974).

In total, ten adjacent quadrates (each covering an area of 0.5 m x 0.5 m) were photographed, five quadrates served as control plots and the remaining five were manipulated when the study started in 1980 by removing all organisms, originally with the idea to follow recolonization and succession of organisms. In this study, however, only the control plots were used for analysis since the main purpose here is to relate the temporal changes in community structure to environmental parameters. Due to pragmatic reasons (time restriction), this study was limited to the analysis of photographs from every second year, a method considered reasonable given the longevity (more than 2 years) of benthic organisms. Since the study spans over a 28-year-period, it will capture overall trends in structural community changes at the locality.

2.3 Image analysis and processing

Digital image analysis was carried out using the program '*Adobe Photoshop® CS4 extended*' which now includes a scientific measuring function allowing area and count measurements of selected areas to be taken. This is an improvement over the method described by Beuchel et al. (2010). The measurement tool enables calibration of the pixels in the photograph to the original frame size in meter (0.5m x 0.5m). All the images were processed by adjusting color and contrast gradients in Photoshop depending on the quality of the photographs. Due to unequal lighting from camera strobes some particularly under- or overexposed areas needed extra thorough processing, in order to make the photographs easier to analyze. All selected areas (organisms) were measured in cm^2 and counted.

Organisms were indentified into the lowest taxon possible and grouped into colonial or solitary life forms (Table 3). Because macroalgae and sponges share a variety of characteristics with other colonial species such as asexual reproduction and indeterminate growth, they were categorized as colonial species in Table 3. Three groups were characterized as algal aggregations, consisting of algae and/or Hydrozoans and Bryozoans. They were compiled in 'aggregational' groups because these organisms sometimes live physically entangled and therefore are hard to separate in the photographs. Colonial taxa were calculated in percentage cover whilst solitary taxa were calculated both as percentage cover, and as counts per square meter.

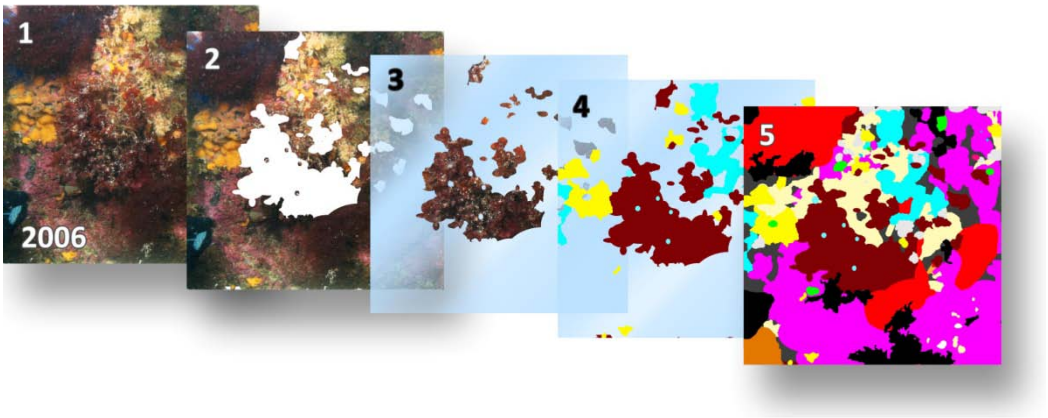


Figure 3. Illustration of the procedure in image analysis. Step 1: Image processing (unanalyzed photograph), Step 2 and 3: Taxa identification and taxa isolation, Step 4: color-coding of isolated taxa, Step 5: Analyzed photograph. The illustrated photograph was from 2006 (quadrate 5).

Practically, this means erect leaf like macroalgae block information below their thallus, in the same way as large motile organisms do. At the same time, the presence of macroalgae also constitutes a new substrate upon which other organisms can settle and thereby increase the total substratum area. To correct for this top-down error, the picture was divided into three layers (Table 1). 1) The first top layer is composed of the erect leaflike macroalgae. 2) The second intermediary layer is composed of the motile organisms, and 3) the third layer is made up of sessile solitary and colonial organisms living directly attached to the rock surface (Beuchel et al. 2010). In some cases the quality of underexposed parts in the photographs was quite poor and appeared as shaded areas, in other parts it was difficult to identify the organisms. These areas were denoted ´shaded areas` and ´unidentified areas`, both areas were quantified and subtracted from the total area. Because the percentage cover of the various organisms was calculated with respect to their presence in one of three layers, the total percent area (all layers compiled) turns out to be more than 100%.

Table 1. Calculation of the three layers

Layer	Organisms
1	Macroalgae (except calcareous algae) = Total area– (´shaded`- ´unidentified`)
2	Motile solitary organisms = Total area – (´shaded`-´unidentified`-´Layer 1`)
3	Calcareous algae & sessile solitary =Total area – (´shaded`-´unidentified`-´Layer 1 & 2`)

2.4 Environmental data

Environmental data sets were retrieved from several research sources. No long-term hydrographic data sets exist for Smeerenburgfjord, therefore (hydrographical) data sets collected near Smeerenburgfjord, were used as proxies. WSC data were taken from a transect (14 stations) at Sørkapp (76°N, 4°E - 22°E), and collected by the Institute of Marine Research in Tromsø (Pers.com. Sigrid Lind Johansen). Average WSC sea temperature (°C) and WSC salinity (psu) were collected annually between August and October, since 1977, for a 50-200 m transect right in the core of the WSC (Table 2). WSC annual, seasonal and 3 years means were calculated. The sea ice index data were obtained from the Norwegian Meteorological Institute as the monthly averaged SIC for the Svalbard region between 72°N-85°N and 0°E-40°E (Pers.com. Nick Hughes). SIC was defined and compiled of the estimates for fast ice, very close fast ice, and close fast ice. The annual mean, winter (Dec-Mar) and summer means (Jun-Sep) were calculated. Air temperature and precipitation data were retrieved from the eklima website administrated by the Norwegian Meteorological Institute (Table 2). The eklima data used were from the monitoring station nearest to the study site, which was near Ny Ålesund in Kongsfjord. Annual and seasonal average values for winter (Jan-Mar) and summer (Jun-Aug) were calculated. The North Atlantic Oscillation (NAO), Arctic oscillation (AO) indices and sea-surface temperatures (SST) data were obtained from different research websites (Table 2). SST was collected in the area 85° N and 20° E. In addition to seasonal, annual and three years means, the WSC temperature and NAO index were lag-calculated (1 year). Lag calculations were performed because the NAO is known to be strongly coupled to regional sea ice fluctuations, and the winter index was found to be lag-correlated (*r*~0.54) to the following summer and winter minimum SIC (Johannessen et al. 1999). Also the benthic community may have a lagged response to the changes in the environmental factors. All environmental parameters were correlated (product moment correlation) with species abundance data (Appendix III), the environmental parameters of ecological relevance and highest correlations with species data were used for Canonical Correspondence Analysis (CCA) (see section on multivariate analysis, 2.5.3).

Table 2. Websites of the environmental data sources, retrieved August 2010.

Data	Source
WSC	IMR, Marine Research Institute, Tromsø (Pers. comm. Sigrid Lind Johansen)
E-klima	http://sharki.oslo.dnmi.no
NAO	http://www.cgd.ucar.edu/cas/jhurrell/indices.html
AO	http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml
SST	http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.ersst.html
ICE COVER	Meteorological Institute, Tromsø (Pers. comm. Nick Hughes)

2.5 Statistical analysis

2.5.1 Descriptive community characteristics

Overall averages and standard deviation of density (solitary taxa) and percentage cover (colonial taxa) were calculated for all taxa for all years (Table 3). For the construction of the univariate plots, the organisms were put into five main categories; macroalgae, calcareous algae, colonial species, sessile and motile solitary organisms. Macroalgae include all algae except the calcareous algae, which were placed into its own group because of its predominance. The colonial group includes sessile sponges, Bryozoans, ascidians and Hydrozoans. The sessile and motile solitary organisms include all solitary taxa found in the two respective groups. The density of the main groups was calculated as the average percent cover of the study area for the three layers (Appendix IV). In addition, all solitary species were ordered in higher taxonomic levels, and portrayed as counts per square meter.

For all further calculations on diversity and multivariate data, the units applied were counts for solitary and percentage cover for colonial organisms; these two different units were applied in the same analysis. This is defendable because the values (percent cover and counts) are within the same range (Beuchel et al. 2006). Additionally, some very small organisms can occur in large numbers but cover relatively little area. The tube-dwelling polychaete, *Spirorbis. spirorbis* occurred in densities up to ~500 individuals per photograph as epifauna on red algae, but occupied little space. To avoid over-representation in the diversity indices, counts of *S. spirorbis* were downweighed by a factor 10. A comparison between the calculated (counts, percentage cover) and raw (area=cm^2) data for the Shannon-Wiener Biodiversity idex (H’) values is presented in Appendix IX.

2.5.2 Diversity indices

Diversity parameters were calculated to detect shifts in interannual diversity patterns. H’ based on natural logarithm (log-e), and both the Simpson index (1-D), and the Pielou index (J’) are highly inter-correlated (Appendix VIII). It would be superfluous to show all indices, therefore only the most commonly used, H’ index, is illustrated and discussed. The H’ index increases when diversity and evenness increase; still the Shannon index is more sensitive to species richness than to evenness (Magurran 1988). Diversity measures were calculated for all five photographs per year. 95% confidence intervals were generated by bootstrapping the five replicates with 10000 repetitions. *K*-dominance curves were established to detect shifts in dominance and evenness between years. The species were ranked in order of importance in terms of abundance and percentage cover on the x-axis (log scale) and with the percentage dominance on the y-axis (cumulative scale). The diversity measures were calculated in the Primer 6 statistical package (Clarke and Gorley 2006), the bootstrapping was performed in ‘R 2.10.1’ in the package ‘Boot’.

2.5.3 Multivariate analysis

In order to separate temporal trends in the benthic community from natural variation, a range of multivariate statistical techniques was applied. Non-parametric multi-dimensional-scaling (MDS) was carried out based on Bray-Curtis similarity measures (Appendix V) to reveal temporal changes in community structure (Kruskal 1964; Bray and Curtis 1957). MDS is an exploratory technique enabling visualization of patterns in the data by emphasizing structural variation in a low dimensional space. Analyses were performed using the Primer 6 statistical package (Clarke and Gorley 2006). Values were square-root transformed in order to downweigh the effect of the very abundant species (Field et al. 1982).

CCA was used to assess the strength of the relationships between species abundances and physical characteristics such as NAO, WSC temperature and salinity, and SST. The CCA is based on chi-square distances. The species values were square-root transformed in order to downweigh the effect of abundant species. The positions of species in the CCA triplot are determined by their correlation to the ordination axes and to the environmental gradients. The environmental gradients are designated by the arrows pointing in the direction of maximum change for the given gradient. The arrow length is proportional to its maximum rate of change (Braak and Verdonschot 1995). Monte Carlo permutation tests (199 permutations) were performed to see whether a significant statistical difference was present among years. The CCA was also performed on replicates for each year with time as a categorical variable (Appendix XII), but will not be discussed further since the replicate analyses showed similar significance level as the analyses based on averages for each year. All CCA estimations were performed in the statistical program ‘R 2.10.1’ using the package ‘Vegan’ (Oksanen 2010). Very rare species representing less than 0.1% were not included in the analysis.

3. Results

3.1 Site characteristics

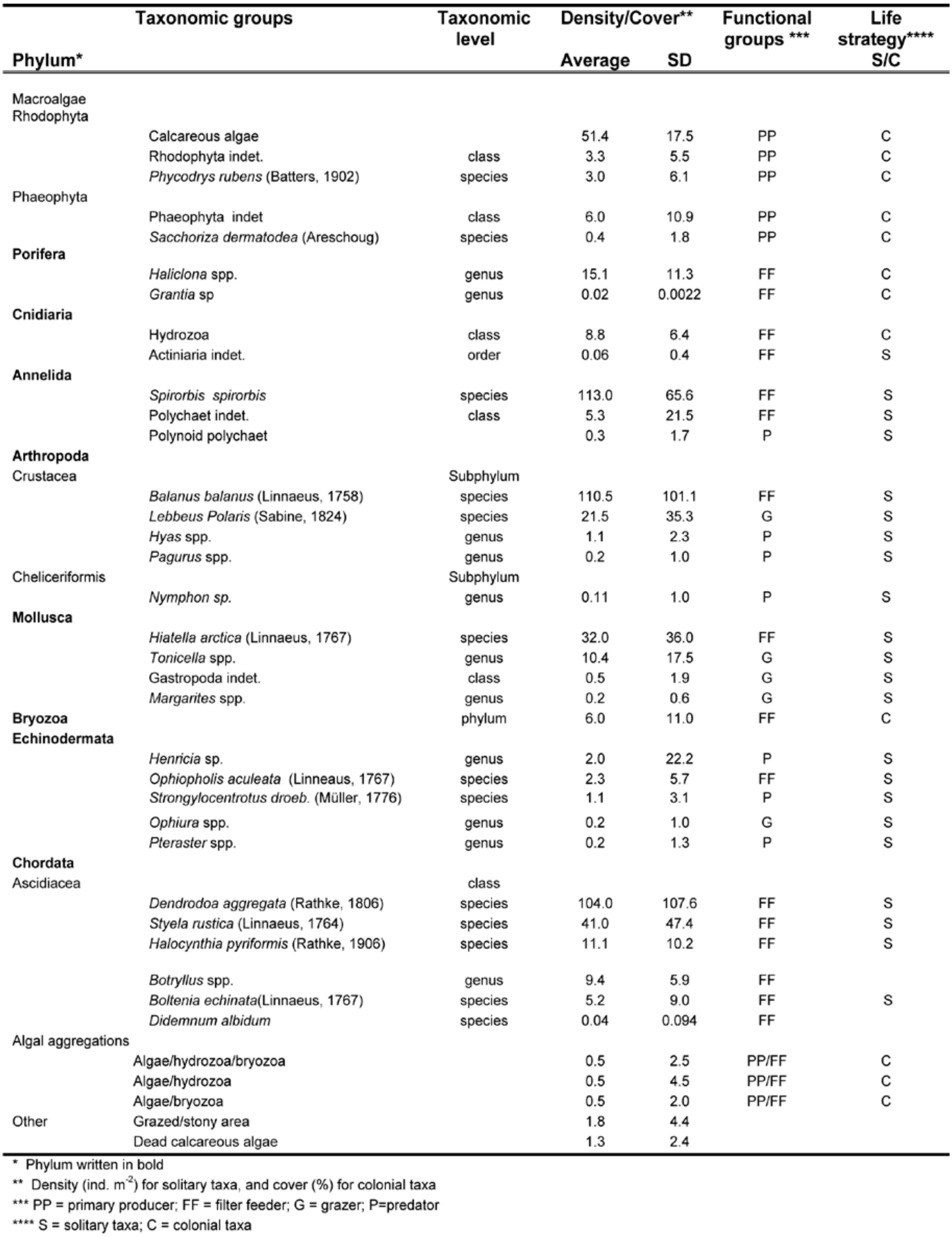
In total, 36 taxonomic groups were recognized in the photographs, of which 13 were identified to species and 9 to genus level (Table 3). The remaining (15) taxa were classified to higher taxonomic levels (e.g. phylum, class or order). Of all taxa recorded, 22 belong to solitary life-forms and 14 to colonial.

Regarding colonial life forms, the most predominant groups were macroalgae, sponges, ascidians, Bryozoans, and Hydrozoans. During the entire observation period, the calcareous macroalgae were abundant, averaging 51.4% with regard to percentage cover (Table 3). However, its coverage fluctuates between a maximum of 71.7% in 1984 and a minimum of 30.6% in 1994 (Fig. 4). Other macroalgal groups abundant at the locality are leaf-like brown-algae and red-algae. These become increasingly more abundant from 1994 and onwards, together covering a total of 42.7% of in 2008 (Fig. 6). The calcareous algae were not classified to lower taxonomic levels, yet from descriptions and distributions of macroalgae, the most dominant of them is suggested to be *Lithothamnion glaciale*. One of the brown algae comprised in the Phaeophyta group, is suggested to be *Desmerestia* sp.

Sponges, ascidians, bryozoans, and hydrozoans cover between 21.6% in 1982 and 65.5% in 2004 (Fig. 5). The plenitude of these colonial species is fluctuating between years and especially decades. However, the ascidia *Botryllus spp.* seems to fluctuate cyclically around a mean of 9% coverage. Hydrozoans are most abundant from 1980 to 1990 with peak coverage of 14% in 1986 and 1988; through the 1990s the coverage is lower, but more stable (~9%). The sponge *Haliclona spp.* is very abundant between 1992 and 2000. Bryozoans are barely present at the beginning of this study period in the 1980s; however, they become increasingly more present after 1996, covering a maximum of 32% in 2004 (Fig. 5). Apart from *Botryllus spp.*, all colonial taxa drop to a minimum coverage of about 2 % in 2008.

Solitary organisms were numerous (maximum 559 individuals m^{-2} in 1996) (Fig. 8), but occupied little space, with an average cover of 4.7% (Fig. 4). Together the colonial groups and calcareous algae cover 95.3% of the area on average (Fig. 4). Sessile solitary organisms cover between 1% in 2006 and 7.9% in 1980 of the area (Fig. 7). Motile species are the least represented organisms at the study locality, and cover between 0.1% (1980 and 2006) to 3.6% (2008) of the space (Fig. 7). Many of the predators are included in this group; the most numerous predators observed are *Henricia* sp. 3.8 ind. m^{-2} on average and *Strongylocentrotus droebachiensis* 1.1 ind. m^{-2} on average. The maximum recorded number for each is 5 individuals per square meter.

Table 3. The overall average (1980-2008) and standard deviation for the taxonomic groups identified in the photographs, Solitary taxa are measured in density (ind. m^{-2}) and the colonial taxa as cover (%).



	Taxonomic groups	Taxonomic level	Density/Cover**		Functional groups ***	Life strategy**** S/C
Phylum*			Average	SD		
Macroalgae						
Rhodophyta						
	Calcareous algae		51.4	17.5	PP	C
	Rhodophyta indet.	class	3.3	5.5	PP	C
	Phycodrys rubens (Batters, 1902)	species	3.0	6.1	PP	C
Phaeophyta						
	Phaeophyta indet	class	6.0	10.9	PP	C
	Sacchoriza dermatodea (Areschoug)	species	0.4	1.8	PP	C
Porifera						
	Haliclona spp.	genus	15.1	11.3	FF	C
	Grantia sp	genus	0.02	0.0022	FF	C
Cnidiaria						
	Hydrozoa	class	8.8	6.4	FF	C
	Actiniaria indet.	order	0.06	0.4	FF	S
Annelida						
	Spirorbis spirorbis	species	113.0	65.6	FF	S
	Polychaet indet.	class	5.3	21.5	FF	S
	Polynoid polychaet		0.3	1.7	P	S
Arthropoda						
Crustacea		Subphylum				
	Balanus balanus (Linnaeus, 1758)	species	110.5	101.1	FF	S
	Lebbeus Polaris (Sabine, 1824)	species	21.5	35.3	G	S
	Hyas spp.	genus	1.1	2.3	P	S
	Pagurus spp.	genus	0.2	1.0	P	S
Cheliceriformis		Subphylum				
	Nymphon sp.	genus	0.11	1.0	P	S
Mollusca						
	Hiatella arctica (Linnaeus, 1767)	species	32.0	36.0	FF	S
	Tonicella spp.	genus	10.4	17.5	G	S
	Gastropoda indet.	class	0.5	1.9	G	S
	Margarites spp.	genus	0.2	0.6	G	S
Bryozoa		phylum	6.0	11.0	FF	C
Echinodermata						
	Henricia sp.	genus	2.0	22.2	P	S
	Ophiopholis aculeata (Linneaus, 1767)	species	2.3	5.7	FF	S
	Strongylocentrotus droeb. (Müller, 1776)	species	1.1	3.1	P	S
	Ophiura spp.	genus	0.2	1.0	G	S
	Pteraster spp.	genus	0.2	1.3	P	S
Chordata						
Ascidiacea		class				
	Dendrodoa aggregata (Rathke, 1806)	species	104.0	107.6	FF	S
	Styela rustica (Linnaeus, 1764)	species	41.0	47.4	FF	S
	Halocynthia pyriformis (Rathke, 1906)	species	11.1	10.2	FF	S
	Botryllus spp.	genus	9.4	5.9	FF	
	Boltenia echinata(Linnaeus, 1767)	species	5.2	9.0	FF	S
	Didemnum albidum	species	0.04	0.094	FF	
Algal aggregations						
	Algae/hydrozoa/bryozoa		0.5	2.5	PP/FF	C
	Algae/hydrozoa		0.5	4.5	PP/FF	C
	Algae/bryozoa		0.5	2.0	PP/FF	C
Other	Grazed/stony area		1.8	4.4		
	Dead calcareous algae		1.3	2.4		

* Phylum written in bold

** Density (ind. m^{-2}) for solitary taxa, and cover (%) for colonial taxa

*** PP = primary producer; FF = filter feeder; G = grazer; P=predator

**** S = solitary taxa; C = colonial taxa

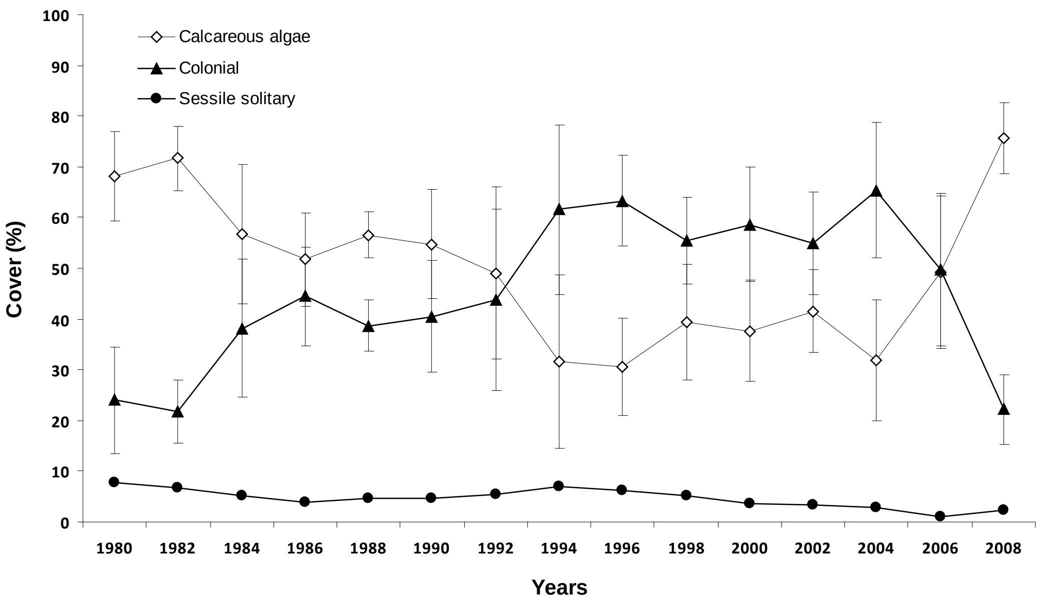


Figure 4. Relative percentages cover of calcareous algae, colonial taxa and solitary sessile taxa for every second year between 1980 and 2008. The groups 'colonial' and 'solitary sessile' are comprised of all species belonging to the respective group (appendix). All groups are calculated from layer 3, see text section 2.3 for explanation.

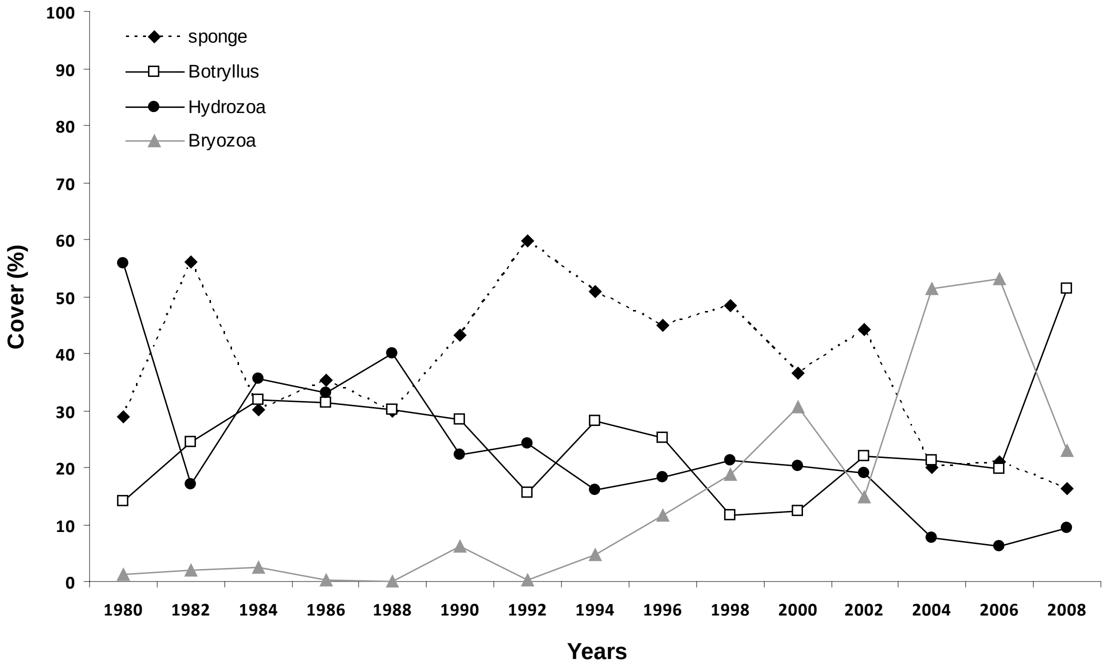


Figure 5. Percentage cover of the colonial species: *Haliclona spp.*, Hydrozoa, Bryozoa, and *Botryllus spp.* (Layer 3). The figure is a disintegration of the group colonial taxa from figure 1 into its components. (Standard deviations are not depicted for sake of simplicity).

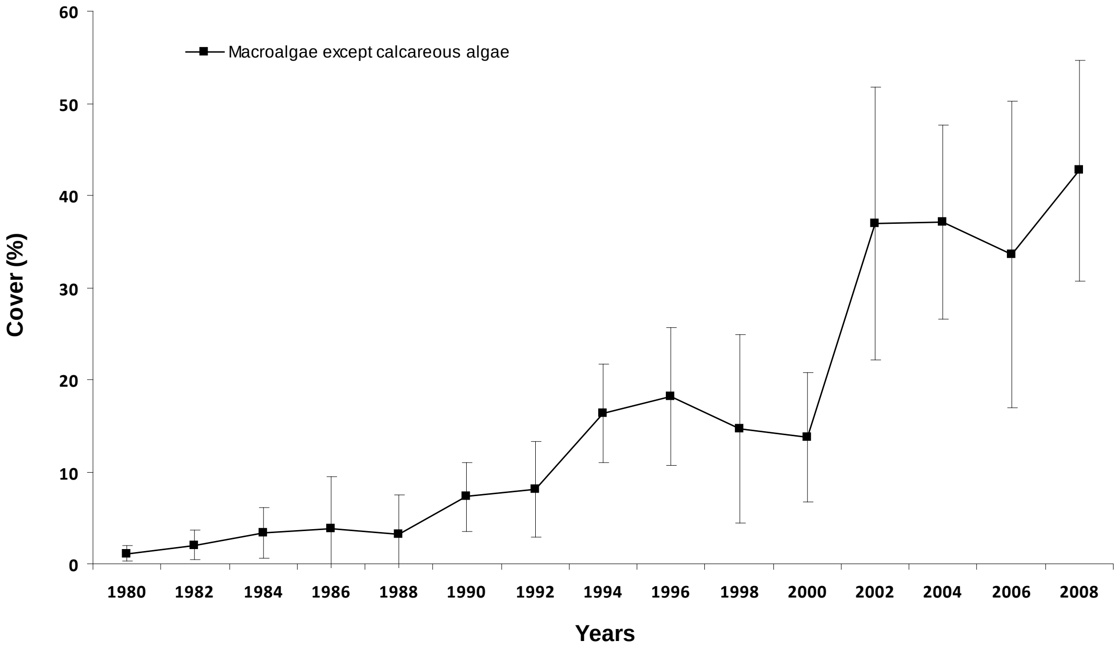


Figure 6. Percentage cover of macroalgae (except calcareous algae) and algal aggregations (Algae/Bryozoa/Hydrozoa) for every second year between 1980 and 2008. The macroalgae and algal aggregations are all calculated from layer 1, see section (2.3) in the text.

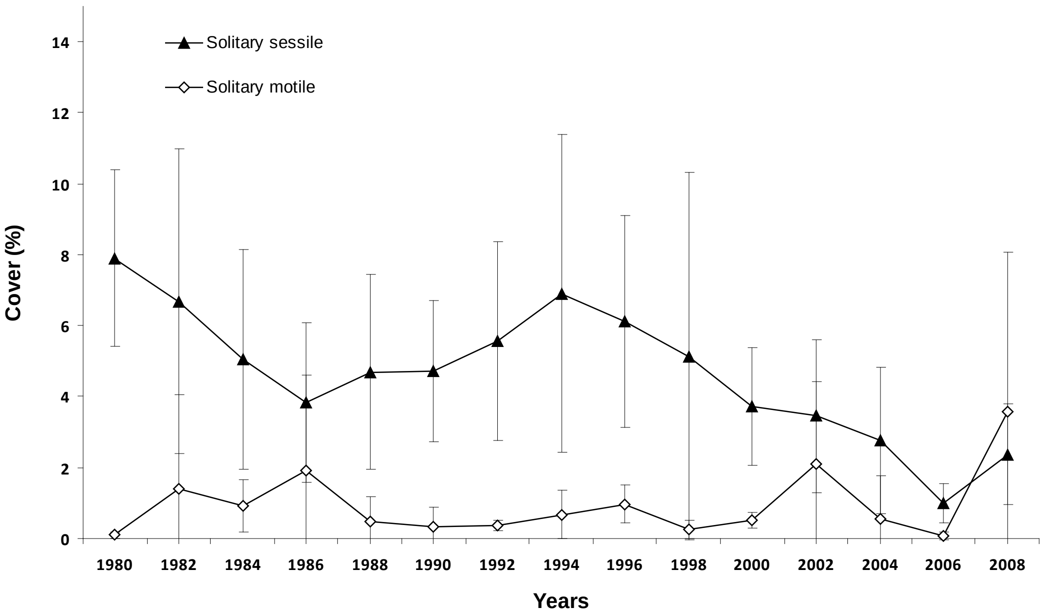


Figure 7. Percentage cover of solitary motile and sessile species. The motile are calculated from layer 2, and the solitary from layer 3, see text for explanation. The sessile solitary line is the same as in figure 4; it was depicted here because of higher resolution on the percentage y-axis and as a comparison to motile organisms.

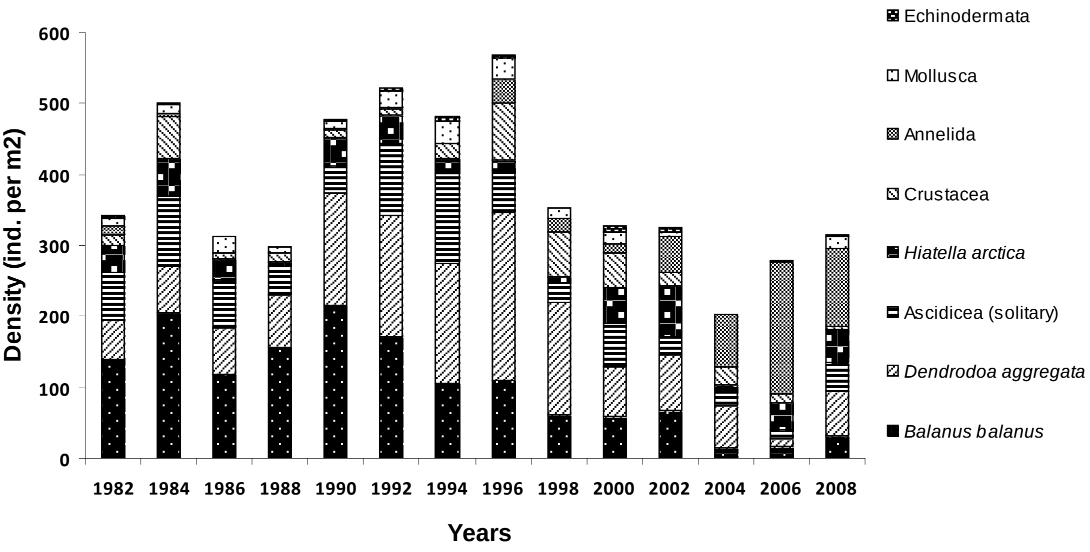


Figure 8. Total abundance (ind. m^{-2}) of solitary organisms grouped into higher taxa. *Dendrodoa aggregata, Balanus balanus, Hiatella arctica* were put into own categories because of their high densities. *Spirorbis spirorbis* comprised in the annelid group is downweighed by a factor 10.

Regarding the solitary life forms, the most common taxa are the filter-feeding crusteacean, *Balanus balanus,* and the ascidian, *Dendrodoa aggregata,* respectively 110 and 104 ind. m^{-2} (on average). Both reach maximum abundances of more than 200 ind. m^{-2} (Appendix I). Other ascidians reaching high numbers are *Styela rustica* (41 ind. m^{-2} on average) and *Halocynthia pyriformis* (11 ind. m^{-2} on average) (Table 3). The most common mollusks are the sessile filter feeding, *Hiatella arctica* (32 ind. m^{-2} on average), the motile grazing chiton, *Tonicella* spp. (10 ind. m^{-2} on average).

The comparative plot (Fig. 9) of functional groups (feeding strategy not trophic position) shows filter feeders dominating the solitary organisms (bars). Overall, there is a negative trend in the numbers of solitary filter feeders, apart from *S. spirorbis.* The highest accounts of solitary filter feeders were in the beginning of the 1980s and 1990s, and the lowest in the mid 2000 period. *S. spirorbis* is placed in its own group because of very high numbers at the end of the study period. Predatory species are scarce during the entire study period. Grazers are also represented in relatively low numbers except for the years 1984, and 1996-2000, this is due to high numbers of the crustacean, *Lebbeus polaris*. Some taxa are omnivorous (e.g. *S. droebachiensis*) consult Table 3, to see how they were classified here (grazer or predator). Colonial filter feeders are most common from 1994 to 2004, together covering ~50% during the entire period. In 2008 their abundance drops to the same percentage cover as in 1980s. Calcareous algae show an inverse relationship to colonial filter feeders with the highest representation in the 1980s and 2008. The most pronounced trend is recorded in the primary producers (all except calcareous algae) and *S. spirorbis*; from the start of the 1990s macroalgae show an ongoing positive trend with a noticeable increase in percentage cover from 2000 to 2002. *S. spirorbis* increased from 1996 and onwards becoming very abundant in 2006 and 2008 (~ 500 ind. m^{-2}).

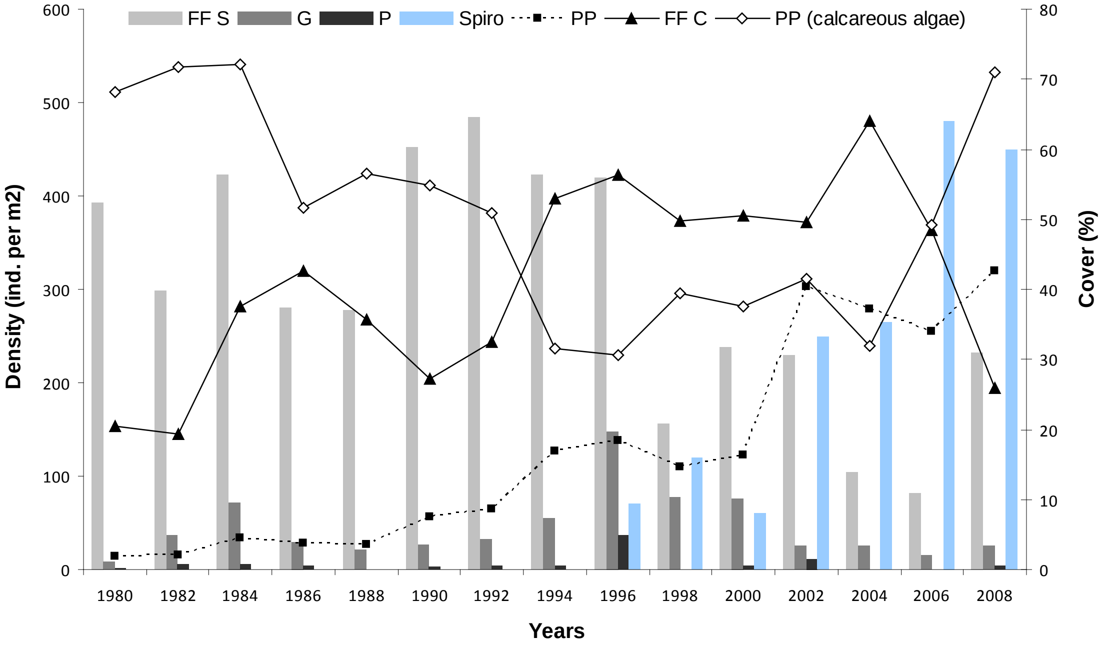


Figure 9. Comparative plot of the functional groups FF S= Filter feeders solitary, G= Grazer, P= Predator, PP= Primary producers except PP (calcareous algae) FF C= Filter feeding colonial. Spiro= *S. spirorbis* and calcareous algae were placed in their own groups because of high abundance. Note the different units on the y axis, solitary organisms are depicted as count data (bars), and the colonial organisms are depicted as percentage cover (lines).

3.2 Diversity patterns

Number of species (species richness) varies among years between 18-25 taxa, but no overall trend is apparent (Fig. 10). In contrast to species richness, H’ index shows an overall positive trend. The mean H’ values range from 1.7 to 2.2. Generally, the years from 1980 to 1998 were lower, with respect to biodiversity, compared to the period 2000-2008 characterized by the highest H’ value. The years with lowest H’ values are 1980, 1988 to 1990. In general, it seems the H’-values are higher towards the end of the study period which indicates the study area to become moderately more diverse from 2000 to 2008.

Just like the diversity indices, the *k*-dominance plot is an abstraction of the actual diversity of the community. The *k*-dominance plot presents the cumulative percentage dominance of species against their rank (log scale). The curves for the years 2000-2008 are all lower compared to the beginning of the study period (1980-1998), indicating relatively less dominance by single species, and a more even distribution of individuals among the middle-ranked species. As with the H’ values, it seems the community becomes more even towards the end of the study period, and hence more diverse. Furthermore, the curves within the 2000 period do not intersect with the remaining years, meaning the curves for 2000- 2008 are comparable to the other curves with respect to intrinsic diversity e.g. H’ diversity (Lambshead et al. 1983).

The Pearson’s product moment correlations (Table 4) between H’ and selected environmental parameters show that the diversity change in the study area is significantly correlated to SST annual mean (0.7) and SIC annual mean (-0.66). Positive correlations between WSC temperature and WSC salinity and H’ were found, but were not significant. No correlation was found between H’ and NAO 3 years mean.

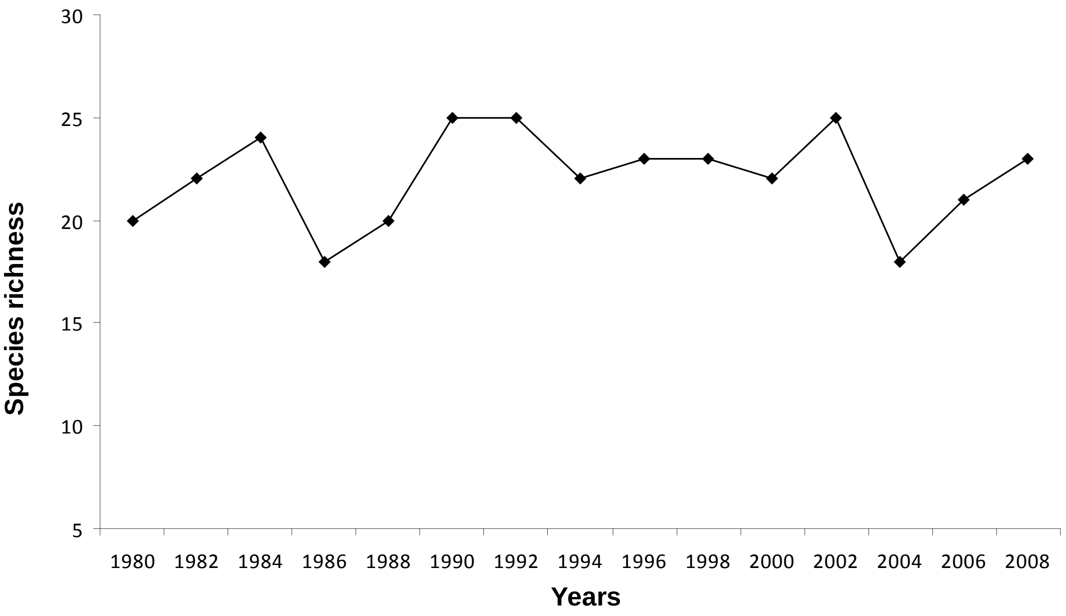


Figure 10. Species richness (number of species) for every second year (1980-2008).

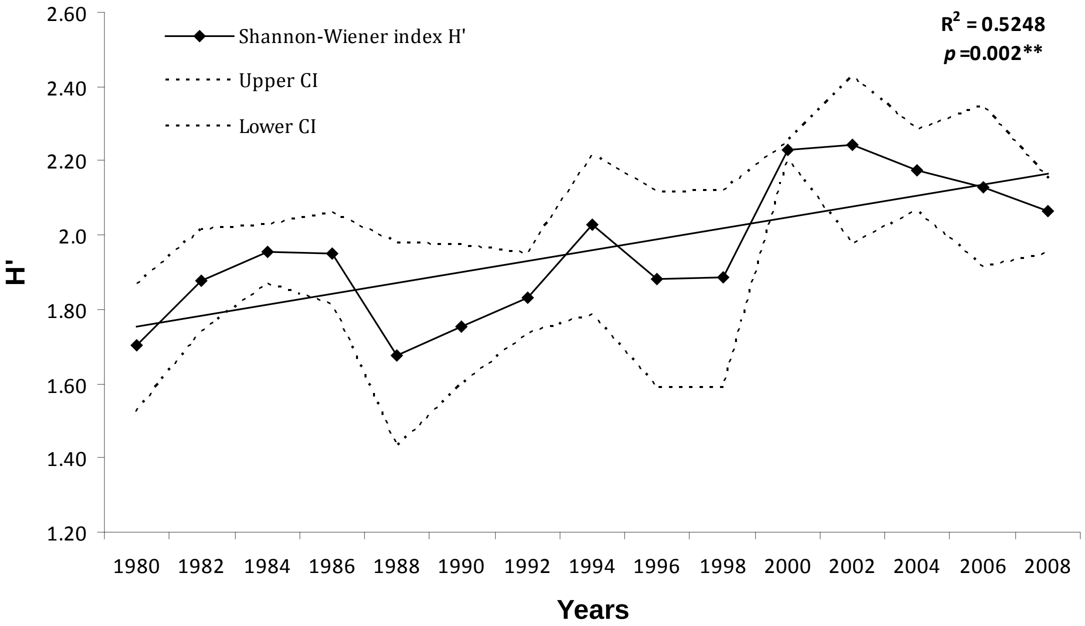


Figure 11. Shannon-Wiener index H' values for every second year (1980-2008) depicted with trendline and confidence intervals (CI). The CI values were generated by bootstrapping with 10000 repetitions. Significance level (= $p < 0.01$)**

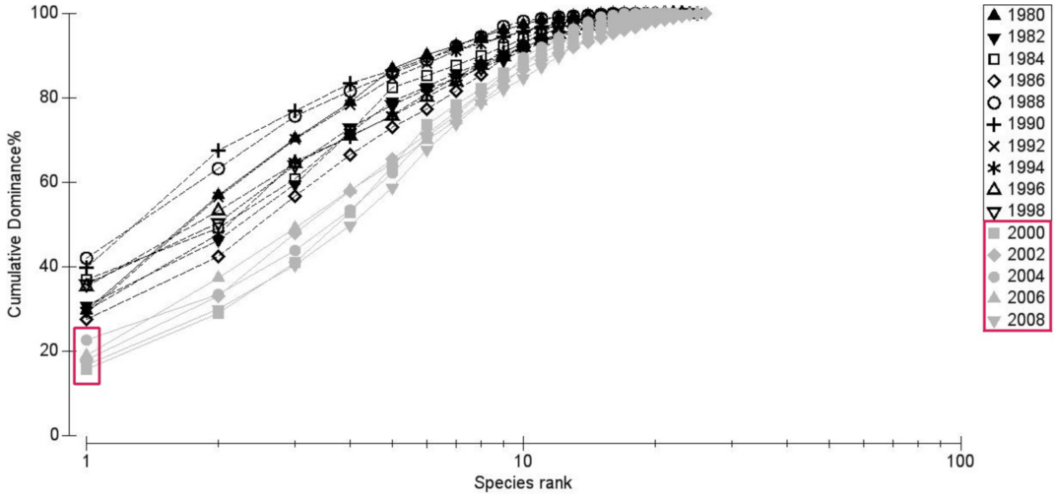


Figure 12. The *k*-dominance curve illustrates the cumultative percentage dominace of the species against their rank (log scale). Black lines are years between 1980 and 1998, grey lines are the years from 2000 to 2008. The 2000-2008 period is marked with a red sqaure.

Table 4. Significant correlations between environmental parameters and the diversity index H'

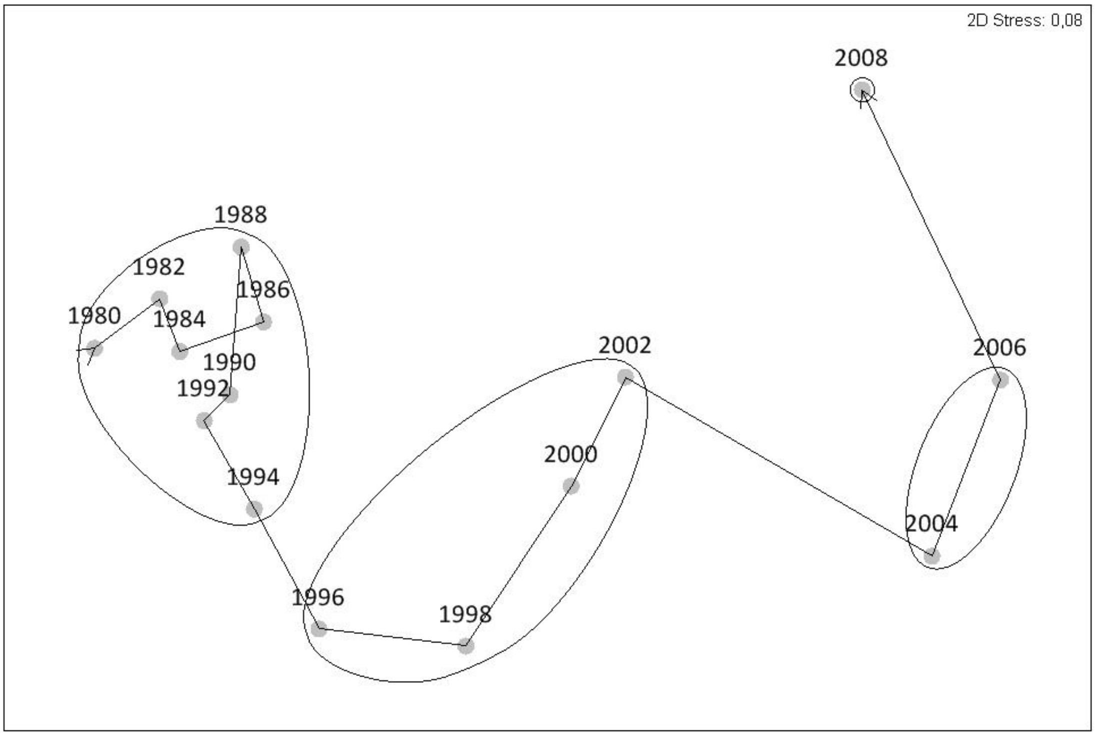
Shannon-Wiener (H')	Environmental parameter	σ
H'	SST M	0.7**
H'	ICE M	-0.66**
H'	WSC temp3M	0.5
H'	WSC sal3m	0.327
H'	NAO 3M	-0.018

Pearson correlation coefficient with significance level (= *p* <0.01)**

3.3 Community structure

The MDS plot based on benthos abundance and cover data clearly indicates a progression of the community structure throughout the entire study period (1980-2008). In general, consecutive years are closer together than years further apart in time. According to the 75% similarity level based on Bray-Curtis similarity index (Appendix V & VI), the study period is divided into four major groups; 1980 to 1994, 1996 to 2002, 2004 to 2006 and 2008. The years from 1980 to 1994 are tightly clustered indicating that these years are most similar with respect to community structure compared to the following years. From 1994 the benthic community appears to undergo major changes all the way up to 2008 as indicated by the length of the lines between the years (Fig. 13). From the univariate figure 9, it was derived that the community structure changed with respect to percentage cover of calcareous algae and colonial taxa. Calcareous algae was more abundant in the 1980s with colonial filter feeders becoming more so during the 1990s and 2000s with exception to 2008. From the middle of the 1990s and particularly from 2000 the primary producers expanded in abundance, while solitary sessile filter feeders simultaneously decreased.

The CCA triplot visualizes the association and correlation between species and years related to environmental variables (Fig. 14). The CCA constrained by environmental variables confirms the same trend as the MDS plot and the univariate figures. The benthic community structure at Danskøya is changing throughout the whole study period, but particularly from the mid 1990s and onwards. The Monte-Carlo permutation test (199 permutations) reveals a statistical significant (p=0.005**) relationship between the species and the environmental variables (Table 5). The first and second axes explain most of the variation in community structure related to environmental variables, 46% and 7% respectively. The years from 1980 to 1996 are located on the left side of the triplot. The years from 1998 to 2008 are located on the right side. This reveals a gradual and positively correlated change in community structure with the first ordination axis (Fig. 14). The time vector confirms the gradual change in community structure. This vector is closely aligned along the first ordination axis. Thus, the passing of time is most strongly and positively correlated with axis one.



Figur 13. Non-parametric multidimensional scaling (MDS) plot showing the change of the benthic community over a 28-year period as similarity between years based on Bray-Curtis. The data was square root transformed. Years located in proximity of each other are more similar in community structure than years far apart. Clusters of years with Bray-Curtis similarity levels at the 75% were encircled. The 75% levels were based on group-average linking in hierarchical cluster ordination (Appendix VI).

Together the environmental variables (predictors) account for 69% of the observed variation in community structure among years. The first ordination axis is positively correlated to the temperature and salinity gradients. The Annual average ice cover (ICEM) is negatively correlated to the first axis. ICEM is also negatively correlated to the temperature and salinity gradients. Annual average NAO (NAOM) is uncorrelated with the other environmental gradients, and seems to be slightly negatively correlated to the first ordination axis. Taxa most strongly correlating with the time vector along with the temperature and salinity gradients include: Phaeophyta, *P. rubens*, Bryozoa, and *S.* s*pirorbis*, and the aggregations between leaf-like macrolagae, Hydrozoa and Bryozoa. These taxa are changing along the environmental gradients. Since this correlation is positive, these taxa are increasing in abundance along the vectors. The red cluster of taxa in the CCA triplot where the axes meet, are taxa exhibiting less variation among years; therefore they do not stand out like the taxa most strongly correlated with the environmental variables.

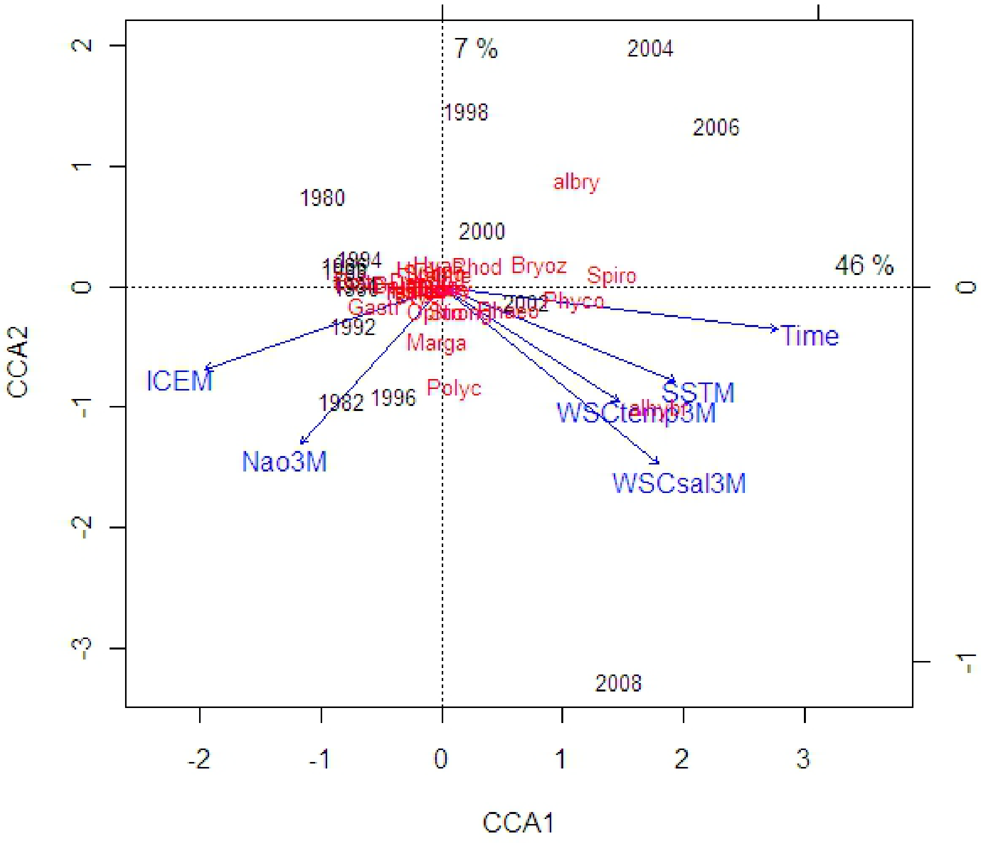


Figure 14. Canonical correspondence analysis (CCA) showing years (samples) and species related to time and the environmental variables: West Spitsbergen Current temperatures 3 years mean (WSCtemp3M), West Spitsbergen Current salinity 3 years mean WSCsal3M, Sea surface temperatures annual mean (SSTM), and NAO 3 years mean (NAO3M). The environmental variables are indicated by arrows. The variation accounted for by axis 1 (horizontal) and 2 (vertical) are 46% and 7%, respectively. Taxa associated with the time vector and the temperature gradients are abbreviated: Phaeo=Phaephyta, Marga= ***Margarites*** **spp., Polyc= Ploychaet indet, Bryoz=Bryozoa, Sipro=** ***Spirorbis spirorbis*****., Phyco=** ***Phycodrys rubens*****, alhybry=Algae/Hydrozoa/Bryozoa, Albry=Algae/Bryozoa.**

Table 5. Summary table for the CCA analysis and the Monte Carlo permutation test, ** indicates a significance level $p < 0.01$.

Analysis	Total Inertia (variance)	Inertia constrained axis	Inertia unconstrained axis	Eigenvalues		Significance level
				Axis 1	Axis 2	
CCA	0.3929	0.2717	0.1207	0.1811 (46%)	0.0296 (7%)	0.005**

4. Discussion

4.1 Community structure with respect to site and substrate characteristics

This study is aimed at describing the macrobenthic community structure with respect to biotic and abiotic factors in Smeerenburgfjord. All taxa recorded have been found previously within the coastal waters of the Svalbard archipelago (Hop et al. 2002; Gulliksen and Svensen 2004; Palerud et al. 2004). In both Smeerenburgfjord (51% cover) and Kongsfjord (63% cover), calcareous algae is on average the most dominant organism regarding percentage cover (Beuchel and Gulliksen 2008; Hop et al. 2002). Studies have shown calcareous algae to be present almost worldwide, and constituting a major space occupier within the high Arctic hard substrata, covering 60% of the primary substrate (Konar and Iken 2005; Johansen 1981). This is in accordance with the present study. Characterized by slow growth, its mere survival requires water movement along with little light (Johansen 1981). It often serves as substrates for other organisms and survives overgrowth (Konar and Iken 2005) which could explain how it regains dominance again at the sampling site, after years overgrown by other species, e.g. by sponges (1998) or Bryozoans (2004) (Appendix XV, photograph 1998-1 and photograph 2004-1).

Previous studies have shown how competition for space is one of the most structuring biotic factors in hard bottom communities (Jackson 1977; Konar and Iken 2005; Bertness and Leonard 1997). Thus, the inverse relationship between calcareous algae and the different sessile colonial filter feeders might be interpreted as a result of competition for space among these taxa.

Colonial taxa (including macroalgae) are the most dominant organisms at the study site with respect to coverage compared to solitary life forms occupying very little space despite their high density. This might be due to their extraordinary growth patterns and life history traits e.g. asexual versus sexual reproduction (Jackson 1977). Colonial taxa might be superior space competitors because of indeterminate growth. This allows them to occupy space laterally without requiring intervening stages of sexual reproduction, compared to solitary life forms (Jackson 1977). To compensate for this, solitary species tend to aggregate into assemblages (Yakovis et al. 2004). This was also observed in the present study, namely for *B. balanus*, *D. aggregata*, and *S. rustica*. Due to the indeterminate growth form of colonial taxa and to the aggregations among solitary sessile taxa, benthic community structure exhibits patchiness.

Several other aggregations among taxa were observed in this study. For instance during 1998 when sponges covered large areas, *D. aggregata* was also abundant (Appendix XV, photograph 1998-1). They were observed colonizing the spaces between the sponge structure, suggesting there is a positive relationship between the two (Appendix II). Sponges may serve as a refuge for *D. aggregata*, presumably protecting them from predators. Many invertebrate and fish species have been observed using the complex sponge structure in this manner (Krautter et al. 2001). Associations among macroalgae and various epifauna e.g. *S. spirorbis*, Hydrozoa and Bryozoa were also found.

Apart from macroalgae and colonial taxa, the study site is characterized by a high degree of filter feeders and few motile grazing and predatory taxa. Ascidians were the most diverse taxonomic group found in the area. Six different ascidians could be distinguished: four solitary and two colonial. This might, however, be due to methodological restrictions since classifying Hydrozoans and Bryozoans to species level is difficult from image analysis. Ascidians, on the other hand, are quite easy to distinguish because of their distinct and conspicuous features (morphology, colors, and characteristic siphons). With 273 species of Bryozoan and 127 species of Hydrozoan known to be residing in the waters around Svalbard, they are among the most diverse epibenthic taxa (Hop et al. 2002; Voronkov et al. 2010; Kuklinski et al. 2006). This means several more taxa could be expected at the sampling locality than were identified in this study.

Previous studies show that the nature of the substrate (its angle of inclination and degree of heterogeneity) has great importance in shaping the taxonomic and functional composition of species (Kuklinski et al. 2006; Wlodarska-Kowalczuk 2007). Water currents and sedimentation may also have an important structuring role in determining the community structure (Baynes and Szmant 1989). The substrate at the sampling site is characterized by being a rocky, vertical wall. Water currents are regarded as being relatively strong (Pers. comm. Bjørn Gulliksen).

The many sessile filter feeders indicate that these organisms thrive on rocky walls exposed to strong currents. In contrast, motile grazers and predators are scarce. It can be presumed it is too energetically costly for larger motile organisms to cling onto a wall under such conditions. It has, for instance, been observed that sea urchin, *S. droebachiensis*, prefers sheltered habitats compared to current-exposed coasts (Gulliksen and Svensen 2004; Sivertsen 1997). The success of filter feeders is amplified by few grazers and predators. Also the unhindered growth of leaf-like macroalgae might be attributed to a small sea urchin population at the study site. When present, sea urchins (*S. droebachiensis*) have great impact on the benthic communities by grazing down macrolalgae and other organisms (Hop et al. 2002; Paine and Vadas 1969). During 1999 the abundance of *S. droebachiensis* grew dramatically (max. 66 m^{-2}) within Kongsfjord. This coincided with an increase of brown algae. The subsequent reduction of brown algae from 80% to 13% (2000-2004) was attributed to the high density of *S. droebachiensis* (Ballentine 2010 unpubl.; Beuchel and Gulliksen 2008).

Almost no sediments were observed in the photographs due to the vertical orientation of the wall. The many filter feeders and primary producers at the study locality further confirm no sedimentation takes place. Several studies show how sedimentation has a negative effect on various benthic organisms through clogging of the filtering apparatus and blocking of photosynthesis due to turbid water (Irving and Connell 2002; Moore 1977). Due to this diversity is lowered at sites where pronounced sedimentation takes place e.g. in the vicinity of glaciers (Wlodarska-Kowalczuk et al. 2005; Kuklinski et al. 2006).

The many filter feeders, along with the frequent presence of the brittle star, *Ophiopholis aculeata*, are faunal indications of relatively strong currents at Danskøya. *O. aculeata* is often associated with hard substratum exposed to strong currents (Gulliksen and Svensen 2004). Also the increasing presence of macroalgae indicates that turbidity of the water column is low. This might be due to the position of the study site within the fjord. Its position near the Danskøya-Spitsbergen sound results in water currents originating to some degree from outside Smeerenburgfjord (Fig. 1). Parts of these currents are branches of the warmer and saltier WSC. The water entering is a mixture between WSC water and coastal water (Cottier et al. 2005) and therefore it is reduced in terrigenous material. The glacial melt water loaded with sediments that enters directly into the fjord from the surrounding glaciers is directed to the eastside of the fjord by the Coriolis. This is to the opposite side of the fjord to where the study site is situated, thereby reducing the effects of turbidity. All these factors combined (strong currents, the vertical nature of the substrate, and few predators/grazers) are favorable for the occurrence of filter feeders and primary producers.

4.2 Change in diversity patterns related to environmental parameters

The Shannon-Wiener Biodiversity found in Smeerenburg (H’= 1.7 to 2.2) was in the same range as in Kongsfjord (H’= 1.5 and 2.2) (Beuchel et al. 2006). The H’ values and *k*-dominance plot revealed that the community seemed to be more evenly distributed among the middle-ranked species in the 2000 period compared to the years with low H’ values in 1980s and 1990s. Years with low H’ values (e.g. 1980, 1988, and 1990) are characterized by a community structure dominated by few taxa: calcareous algae, *B. balanus*, and *D. aggregata*. The environmental plots (Appendix

XIII) reveal that these years had relatively low temperature, salinity, NAO and pronounced ice cover. This indicates that relatively colder years coincide with a community structure dominated by fewer species. A plausible explanation for these patterns could be that boreal taxa do not survive cold periods, but may reappear when temperature rise again (Kröncke et al. 2001). As temperature increased at the beginning of the 1990s more boreal taxa (e.g. various erect macroalgae and colonial filter feeders) were observed at the study site. Perhaps also the increased WSC flow during the beginning of the 1990s contributed to the occurrence of more boreal taxa at the study site (Karcher et al. 2003). Increased and faster WCS flow may have transported more benthic pelagic larvae faster to the northwest corner of Svalbard resulting in higher recruitment of e.g. colonial filter feeders.

In the Kongsfjord study, 45% of the variation in the diversity patterns was attributed to the NAO (Beuchel et al. 2006). No strong correlations between NAO and the H' values could be found in Smeerenburgfjord (Table 4). However, similarities between the localities were observed in temporal community development based on species abundance similarities (MDS): both studies exhibit little variation from 1980 until 1994 followed by increased annual (every second year for Smeerenburgfjord) changes until the end of the observation period in 2008. From 1994 to 1996 the NAO shifted from moderately positive to strongly negative mode (Hurrell 1995), coinciding with an increase in diversity in Kongsfjord. Brown algae increased dramatically from < 5% to 80% accompanied by a decline in sea anemones (Beuchel et al. 2006). Along with brown algae, several other faunal taxa increased. The increase in macroalgae is in accordance with what was found in the present study. In Smeerenburgfjord macroalgae increased as well from the middle of 1990s, but more slowly than in Kongsfjord. In contrast to Kongsfjord, hardly any sea anemones were found. However, it seemed the increase in macroalgae was followed by a decline in sessile filter feeders. This indicates that the two sites are controlled by similar environmental factors, but with different biotic responses. In 2000, an abrupt increase in macroalgae was recorded in Smeerenburgfjord coinciding with a rapid decline in SIC from 1996 to 2000 and an increase in SST and WSC salinity. In 2008, the cover of colonial species (e.g. *Botryllus spp.*, Hydrozoa, and sponge) decreased whereas calcareous algae became more abundant again resembling the years in the early 1980s (Fig 4). These change in community structure in 2008 coincide with increased summer SIC (Appendix XIII). Fluctuations in SIC seem to have considerable impact on the community structure at Danskøya. Also the diversity patterns in Smeerenburgfjord were significantly correlated to SST ($r = 0.7$) and SIC ($r = -0.66$). Alterations in SST and SIC are partly dictated by changes in large scale climatic fluctuations such as the NAO (Kattsov et al. ; Johannessen et al. 1999). Thus, the NAO operating on a larger climatic scale has its local manifestations in Smeerenburgfjord mediated through environmental factors such as SST, WSC temperature and salinity and SIC. These environmental factors have strong influence on the composition of species.

4. 3 Changes in community structure related to macroalgae

The most consistent change in species composition and structure was the increase of erect, leaf-like macroalgae, particularly in the 2000 period. This is illustrated with the univariate plot (Fig. 6) and the CCA (Fig. 14). Macroalgae and other taxa (*S. spirorbis*, Bryozoa, aggregations between Algae/Bryozoa/Hydrozoa) were positively correlated to the principal ordination axis and to the time vector along with the environmental factors, WSC temperature and salinity and SST. The SIC gradient was negatively correlated to the principal ordination axis. This indicates a positive relationship between these taxa and the environmental gradients, and a negative relationship with SIC. According to the CCA, together, the environmental factors account for 69% of the variation in community structure between years. Temperature and light (intensity and timing) are among the most important factors controlling recruitment, growth reproduction and survival of macroalgae (Gómez et al. 2009). Hence, increasing temperature and salinity gradients and reducing SIC are plausible explanations for the increasing success of primary production by benthic macroalgae.

The presence of *S. spirorbis* is highly correlated ($r = 0.9$) to the presence of *P. rubens* (Appendix II). *S. spirorbis*, along with many Hydrozoans and Bryozoans, lives in close association with the macroalgae as epifauna. Macrolagae may alter the primary substrate due to their their relatively large biomass and erect physical structure (thallus), allowing them to have some ecosystem engineering effects on associated flora and invertebrate fauna (Jones et al. 1994). This may lead to changes in the community structure and species composition. Via their physical structures they may alter the substrate in terms of homogeneity, light penetration, provision of habitats (substrate) and energy. Species living as epifauna or epiflora may increase whereas species competing for space with algae may decrease. An investigation conducted on taxa associated with kelp forests revealed how 208 species lived in close association with algae. The epifauna yielding the highest numbers were: Bryozoa, polychaeta and Hydrozoa (Wlodarska-Kowalczuk et al. 2009). Of the macroalgae collected in Hornsund (South-west Svalbard), the highest number of species associated with any macroalgae was that of *P. rubens*, on average 17 species of epifauna were identified per individual algae (Wlodarska-Kowalczuk et al. 2009). *P. rubens* is the macroalgae which increased most considerably at Danskøya. Not nearly as many species living in association with *P. rubens* were found in this study. However, this may be a consequence of sampling restrictions since many small species hiding in the canopy of algae may not be captured in the photographs.

Parallel with the expansion of macroalgae at the study site, solitary filter feeders decreased in numbers, especially *B. balanus* and solitary ascidians (Fig. 8). One of the ascidians, *Boltenia echinata,* was last recorded in the photographs from 1998. In an experimental study it was found that algae acted as a controlling factor on the growth of the barnacles (Barnes 1955). Yet, it was less evident why growth was restricted. It has been documented how the growth and productivity of benthic filter feeders is a function of current speed (Leonard et al. 1998; Sanford et al. 1994). Thus, marine macroalgae may via their physical structures, alter the hydrodynamic characters of the benthic realm and may therefore change growth of sessile benthic filter feeders. This, on the other hand, may influence the sessile filter feeders differently depending how they catch their prey items (actively or passively), and whether they are favored by slow or high water flow (Gili and Coma 1998). However, it may be more likely that macroalgae may change the settlement and recruitment success of benthic species by occupying the substrate space making it harder for sessile taxa to settle near kin members and aggregate. Many solitary sessile taxa need to settle in the vicinity of kin members in order to thrive and reproduce (Gili and Coma 1998). Barnacles e.g. are dependent on settling near members of their kin since they reproduce by penetrating their reproductive organ into the neighboring barnacle (Anderson 1994).

Global temperatures are predicted to increase, especially in the Arctic (IPCC 2007). As temperature partly controls survivorship of macroalgae, the biogeographic distribution of boreal macroalgal species is expected to expand further north, in particular for temperate (mid Europe) and polar regions where some of the algal species live near their physiological tolerance limit (Müller et al. 2009). Thus, the expansion of *P. rubens* in Smeerenburgfjord during the last 20 years (as observed in this study) along with other macrolagal taxa (e.g. *Sacchoriza dematodea* and other unidentified brown- and red-algae) may be interpreted as biogeographic range expansion due to warming. It has to be taken into account that this study is done only at one sampling site in the fjord. Nevertheless, growth in the biomass of macroalgae already have been observed in other parts of the Svalbard archipelago e.g. in Hornsund (south Svalbard) and in Isfjord (Weslawski et al. 2010; Sakshaug et al. 2009). Further expansion of more boreal marine species is expected in the Arctic due to warming (Müller et al. 2009; Cheung et al. 2009). Perhaps the unique recordings from the permanent monitoring stations at Danskøya (in Smeerenburgfjord) and at Kvadehauken (in Kongsfjord) may help to elucidate some of the biological changes expected to occur in the future.

4.4 Methodical constraints

Like most sampling techniques, photographic image analysis has its strengths and weaknesses. The non-invasive and non-destructive nature of the technique is unique, suitable and advantageous for long-term studies such as the one presented here. Image-analysis offers the opportunity to monitor changes in an assemblage of species (community) over time in order to study succession and recolonization, *per se*, or in relation to climate variability (Beuchel and Gulliksen 2008). Because many benthic species are long-lived and sessile, it also offers the study of life history traits and auto-ecology of selected species. Finally, the photographs are archived and can be reexamined whenever necessary, thus being used in different projects in the future. The fast acquisition in the field also reduces the costs incurred.

The most pronounced constraint of the technique is quantitative inaccuracy due to varying image quality (induced by e.g. strong currents, wave-action, and low visibility) and the two-dimensional representation of a three-dimensional space. Photographs of low quality are most common before digital photography (before 2003) when it was not possible to adjust the photographs *in situ*. However, the processing of the photographs in "Photoshop" and the division of the photograph into layers should help to reduce some of these limitations. The difficulty to recognize certain taxa to species level (e.g. Bryozoans, Hydrozoa, algae) and to identify small and cryptic taxa may result in underestimation of species, thus in an underestimation of diversity as well. However, a study comparing suction sampling to photographic analysis found large epibenthic specimens (e.g. *Tonicella* spp. and *B. balanus*) in similar abundances between photographs and suction sampling (Jørgensen and Gulliksen 2001), indicating how image analysis is reliable with respect to large and conspicuous organisms. Thus, photographic analysis may be successfully used to define macro-benthic assemblages (Jørgensen and Gulliksen 2001; Dayton et al. 1974).

The samples (photographs) of the present study are not independent replicates due to autocorrelation in time and space. Therefore, the results may be biased: consecutive years will logically be more alike than years further apart in time. The temporal bias may statistically have resulted in higher correlations in the CCA than would have been the case if estimates were independent. Temporal autocorrelation was not accounted for when calculating the *p*-values. The spatial autocorrelation was not accounted for because average values were used in the MDS and the CCA. However, the long and continuous sampling of the site is unique and may counterbalance the lack of independence between photographs. Furthermore, Beuchel et al. (2006) found pronounced and reliable shifts in community structure in Kongsfjord during the same time period as the present study. The analogy in the sampling design between these two localities makes it highly relevant to compare the species composition between the two sites statistically, strengthening the results and the statistical out-put further. Additionally, the differences between the two sites in substrate orientation (vertical versus horizontal) may shed light on some of the controlling factors for the community structure, regarding the significance of the substrate inclination.

5. Conclusion

In this master thesis, I have attempted to:

1) Give a quantitative description of the temporal community structure of a high Arctic fjord on the basis of image analysis

2) Discuss how the community has been changing during a 28 year period (1980-2008) with respect to species composition and diversity patterns

3) Relate the changes in community structure to biotic and abiotic factors

The most pronounced and continuous trend in abundance change among all taxa was the increase of erect, leaf-like macroalgae. It is regarded that macroalgae exert ecosystem engineering effects by altering the primary substrate, thus impacting the entire structure and species composition of the community. The community structure underwent considerable changes after 1994 through to the end of study period in 2008. The environmental parameters SST, WSC temperature and salinity, NAO and SIC were used as predictors for the variation in community structure. It was found that the most significant environmental parameters (WSC salinity and temperature, SST, and SIC) accounted for 69% of the variation between years. The correlations between biodiversity estimates (H’) and environmental parameters showed significant relationships between H’ and SST and SIC. On this account, this study suggests that the environmental factors exerting most impact on community structure at the sampling site at Danskøya are: SST and SIC. Additional abiotic factors influencing the community structure are: the vertical orientation of the substrate, intermediate to strong currents. The most important biotic factors shaping the community structure are: competition for space (among sessile species), and little predation due to few grazers and predators.

Acknowledgments

This dissertation was part of a fulfillment in a master Degree in the field of Marine Ecology at the University of Tromsø (UiT) and at the University centre on Svalbard (UNIS). I thank my supervisors, Bjørn Gulliksen and Ole Jørgen Lønne, for giving me the chance to gain insight into the secret world of the undersea creatures in the high Arctic. I also would like to thank them for support during the writing process. Special thanks goes to Bjørn Gulliksen for support during the species identification process. Special thanks goes also to Frank Beuchel for teaching me the methods in 'Photoshop' necessary for image analysis, and for his support during the entire process. I would like to thank Raul Primicerio for an inspiring course on multivariate statistics and for support on the multivariate techniques. Finally, I would like to thank Paul Renaud, Sibylle Liso, and Carl Ballentine, Johan Aarstein for reviewing the thesis and correcting my English. And lots of love goes to Johan Aarstein for his support in difficult moments.

6. References

Ambrose WG, Carroll ML, Greenacre M, Thorrold SR, McMahon KW (2006) Variation in Serripes groenlandicus (Bivalvia) growth in a Norwegian high-Arctic fjord: evidence for local- and large-scale climatic forcing. Global Change Biology 12 (9):1595-1607.

Anderson DT (1994) Barnacles: Structure, function, devlopment and evolution. Chapman & Hall, London

Ballentine C (2010 unpubl.) Changes within the sublittoral benthic faunal composition of Kongsfjorden, a high Arctic fjord. Sams, Scottish Marine Institute Oban

Barnes H (1955) The growth rate of Balanus balanoides (L.). Oikos:109-113

Baynes T, Szmant A (1989) Effect of current on the sessile benthic community structure of an artificial reef. Bulletin of Marine Science 44 (2):545-566

Bertness M, Leonard G (1997) The role of positive interactions in communities: lessons from intertidal habitats. Ecology 78:1976-1989

Beuchel F, Gulliksen B (2008) Temporal patterns of benthic community development in an Arctic fjord (Kongsfjorden, Svalbard): results of a 24-year manipulation study. Polar Biology 31 (8):913-924

Beuchel F, Gulliksen B, Carroll M (2006) Long-term patterns of rocky bottom macrobenthic community structure in an Arctic fjord (Kongsfjorden, Svalbard) in relation to climate variability (1980-2003). Journal of Marine Systems 63 (1-2):35-48

Beuchel F, Primicerio R, Lønne O, Gulliksen B, Birkely S (2010) Counting and measuring epibenthic organisms from digital photographs: A semiautomated approach. Limnolology and Oceanography: Methods 8:229-240

Bray J, Curtis J (1957) An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27 (4):325-349

Bruno J, Bertness M (2001) Habitat modification and facilitation in benthic marine communities. In: Marine Community Ecology. Sinauer Associates

Braak C, Verdonschot P (1995) Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences-Research Across Boundaries 57 (3):255-289

Cheung W, Lam V, Sarmiento J, Kearney K, Watson R, Pauly D (2009) Projecting global marine biodiversity impacts under climate change scenarios. Fish and Fisheries 10 (3):235-251

Chiappone M, Sullivan K (1994) Ecological structure and dynamics of nearshore hard-bottom communities in the Florida Keys. Bulletin of Marine Science 54 (3):747-756

Clarke K, Gorley R (2006) Primer v6: manual/tutorial Primer - E. Ltd Plymouth

Comiso J, Parkinson C, Gersten R, Stock L (2008) Accelerated decline in the Arctic sea ice cover. Geophysical Research Letters 35 (1):1703

Cottier F, Tverberg V, Inall M, Svendsen H, Nilsen F, Griffiths C (2005), Water mass modification in an Arctic fjord through cross-shelf exchange: The seasonal hydrography of Kongsfjorden, Svalbard. Journal of Geophysical Research 110: pc12005

Dayton P (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41 (4):351-389

Dayton P, Robilliard G, Paine R, Dayton L (1974) Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecological Monographs 44 (1):105-128

Field J, Clarke K, Warwick R (1982) A practical strategy for analysing multispecies distribution patterns. Marine Ecology Progress Series 8:37-52

Gilbert R (1983) Sedimentary processes of Canadian arctic fjords. Sedimentary Geology 36 (2-4):147-175

Gili J, Coma R (1998) Benthic suspension feeders: their paramount role in littoral marine food webs. Trends in Ecology & Evolution 13 (8):316-321

Glasby T (2000) Surface composition and orientation interact to affect subtidal epibiota. Journal of Experimental Marine Biology and Ecology 248 (2):177-190

Gómez I, Wulff A, Roleda M, Huovinen P, Karsten U, Quartino M, Dunton K, Wiencke C (2009) Light and temperature demands of marine benthic macroalgae and seaweeds in polar regions. Botanica Marina 52 (6):593-608

Gulliksen B, Svensen E (2004) Svalbard and life in polar oceans. Kom forlag a/s, Kristiansund

Haugan P (1999) Structure and heat content of the West Spitsbergen Current. Polar Research 18 (2):183-188

Hop H, Pearson T, Hegseth E, Kovacs K, Wiencke C, Kwasniewski S, Eiane K, Mehlum F, Gulliksen B, Wlodarska-Kowalczuk M (2002) The marine ecosystem of Kongsfjorden, Svalbard. Polar Research 21 (1):167-208

Hurrell J (1995) Decadal trends in the North-Atlantic Oscillation: regional temperatures and precipitation. Science 269 (5224):676-679

Huston MA (1994) Biological Diversity. Cambridge University Press, Cambridge

IPCC (2007). IPCC Fourth Assesment Report: Climate Change 2007. Cambridge University Press, United Kingdom

Irving A, Connell S (2002) Sedimentation and light penetration interact to maintain heterogeneity of subtidal habitats: algal versus invertebrate dominated assemblages. Marine Ecology Progress Series 245:83-91

Jackson J (1977) Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. The American Naturalist 111:743

Johannessen O, Shalina E, Miles M (1999) Satellite evidence for an Arctic sea ice cover in transformation. Science 286 (5446):1937

Johansen HW (1981) Coralline algae, a first synthesis. CRC Press, Florida

Jones C, Lawton J, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373-386

Jørgensen L, Gulliksen B (2001) Rocky bottom fauna in arctic Kongsfjord (Svalbard) studied by means of suction sampling and photography. Polar Biology 24 (2):113-121

Karcher M, Gerdes R, Kauker F, Köberle C (2003) Arctic warming: Evolution and spreading of the 1990s warm event in the Nordic seas and the Arctic Ocean. Journal og Geophyical Research 108 (C2):3034

Kattsov V, Källén E, Cattle H, Christensen J, Drange H, Hanssen-Bauer I, Jóhannesen T, Karol I, Raeisaenen J, Svensson G (2005) Future climate change: modeling and scenarios for the Arctic Region. In: Arctic Climate Impact Assessment (ACIA). Cambridge University Press, Cambrigde, United Kingdom, 1042 pp.

Konar B, Iken K (2005) Competitive dominance among sessile marine organisms in a high Arctic boulder community. Polar Biology 29 (1):61-64

Krautter M, Conway K, Barrie J, Neuweiler M (2001) Discovery of a “living dinosaur”: Globally unique modern hexactinellid sponge reefs off British Columbia, Canada. Facies 44 (1):265-282

Kruskal J (1964) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29 (1):1-27

Kröncke I, Zeiss B, Rensing C (2001) Long-term variability in macrofauna species composition off the island of Norderney (East Frisia, Germany) in relation to changes in climatic and environmental conditions. Marine Biodiversity 31 (1):65-82

Kuklinski P, Gulliksen B, Lønne O, Weslawski J (2006) Substratum as a structuring influence on assemblages of Arctic bryozoans. Polar Biology 29 (8):652-661

Lambshead P, Platt H, Shaw K (1983) The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. Journal of Natural History 17 (6):859-874

Leonard G, Levine J, Schmidt P, Bertness M (1998) Flow-driven variation in intertidal community structure in a Maine estuary. Ecology 79 (4):1395-1411

Lively C, Raimondi P, Delph L (1993) Intertidal community structure: space-time interactions in the northern Gulf of California. Ecology 74 (1):162-173

Magurran AE (1988) Ecological Diversity and Its Measurement. Princeton University Press, Princeton

Moore P (1977) Inorganic particulate suspensions in the sea and their effects on marine animals. Oceanography and Marine Biology: an Annual Review 15:225-363

Müller R, Laepple T, Bartsch I, Wiencke C (2009) Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters. Botanica Marina 52 (6):617-638

NorACIA (2010) Klimaendringer i norsk arktis. Rapportserie 136. Norsk Polarinstitut, Tromsø (Norwegian)

Oksanen Y (2010) Multivariate Analysis of Ecological Communities in R: vegan tutorial. Accessed 25.5.2010 2010

Ottersen G, Planque B, Belgrano A, Post E, Reid P, Stenseth N (2001) Ecological effects of the North Atlantic oscillation. Oecologia 128 (1):1-14

Paine R, Vadas R (1969) The effects of grazing by sea urchins, Strongylocentrotus spp., on benthic algal populations. Limnology and Oceanography 14 (5):710-719

Palerud R, Gulliksen B, Brattegard T, Sneli J-A, Vader W (2004) The marine macroorganisms in Svalbard waters A catalogue of the terrestial and marine animals of Svalbard, Skrifter 201, Norwegian Polar Institute, Tromsø

Sahade R, Stellfeldt A, Tatián M, Laudien J (1991) Macro-epibenthic communities and diversity of Arctic Kongsforden, Svalbard, in relation to depth and substrate. Berichte zur Polar- und Meeresforschung 2003:103-111

Sakshaug E, Johnsen G, Kovacs K (2009) Ecosystem Barents Sea,Tapir Academic Press, Tronheim

Sanford E, Bermudez D, Bertness M, Gaines S (1994) Flow, food supply and acorn barnacle population dynamics. Marine Ecology Progress Series 104:49-49

Sivertsen K (1997) Geographic and environmental factors affecting the distribution of kelp beds and barren grounds and changes in biota associated with kelp reduction at sites along the Norwegian coast. Canadian Journal of Fisheries and Aquatic Sciences 54 (12):2872-2887

Svendsen H, Beszczynska Møller A, Hagen J, Lefauconnier B, Tverberg V, Gerland S, Ørbøk J, Bischof K, Papucci C, Zajaczkowski M (2002) The physical environment of Kongsfjorden–Krossfjorden, an Arctic fjord system in Svalbard. Polar Research 21 (1):133-166

Townsend CR, Begon M, Harper JL (2006) Essentials of Ecology. Second edn. Blackwell Publishing, Yakovis E, Artemieva A, Mikhail F (2004), Spatial patterns indicates and influence of barnacle and ascidian aggregations on the surrounding benthic assemblage. Journal of Experimental Marine Biology and Ecology 309: 155-172

Underwood A (1996) Detection, interpretation, prediction and management of environmental disturbances: some roles for experimental marine ecology. Journal of Experimental Marine Biology and Ecology 200 (1-2):1-27

Voronkov A, Stepanjants S, Hop H (2010) Hydrozoan diversity on hard bottom in Kongsfjorden, Svalbard. Journal of the Marine Biological Association of the United Kingdom 90 (7):1337-1352

Weslawski J, Wiktor J, Kotwicki L (2010) Increase in biodiversity in the arctic rocky littoral, Sorkappland, Svalbard, after 20 years of climate warming. Marine Biodiversity 40 (2):123-130

Wlodarska-Kowalczuk M (2007) Molluscs in Kongsfjorden (Spitsbergen, Svalbard): a species list and patterns of distribution and diversity. Polar Research 26 (1):48-63

Wlodarska-Kowalczuk M, Pearson T, Kendall M (2005) Benthic response to chronic natural physical disturbance by glacial sedimentation in an Arctic fiord. Marine Ecology Progress Series 330:31-41

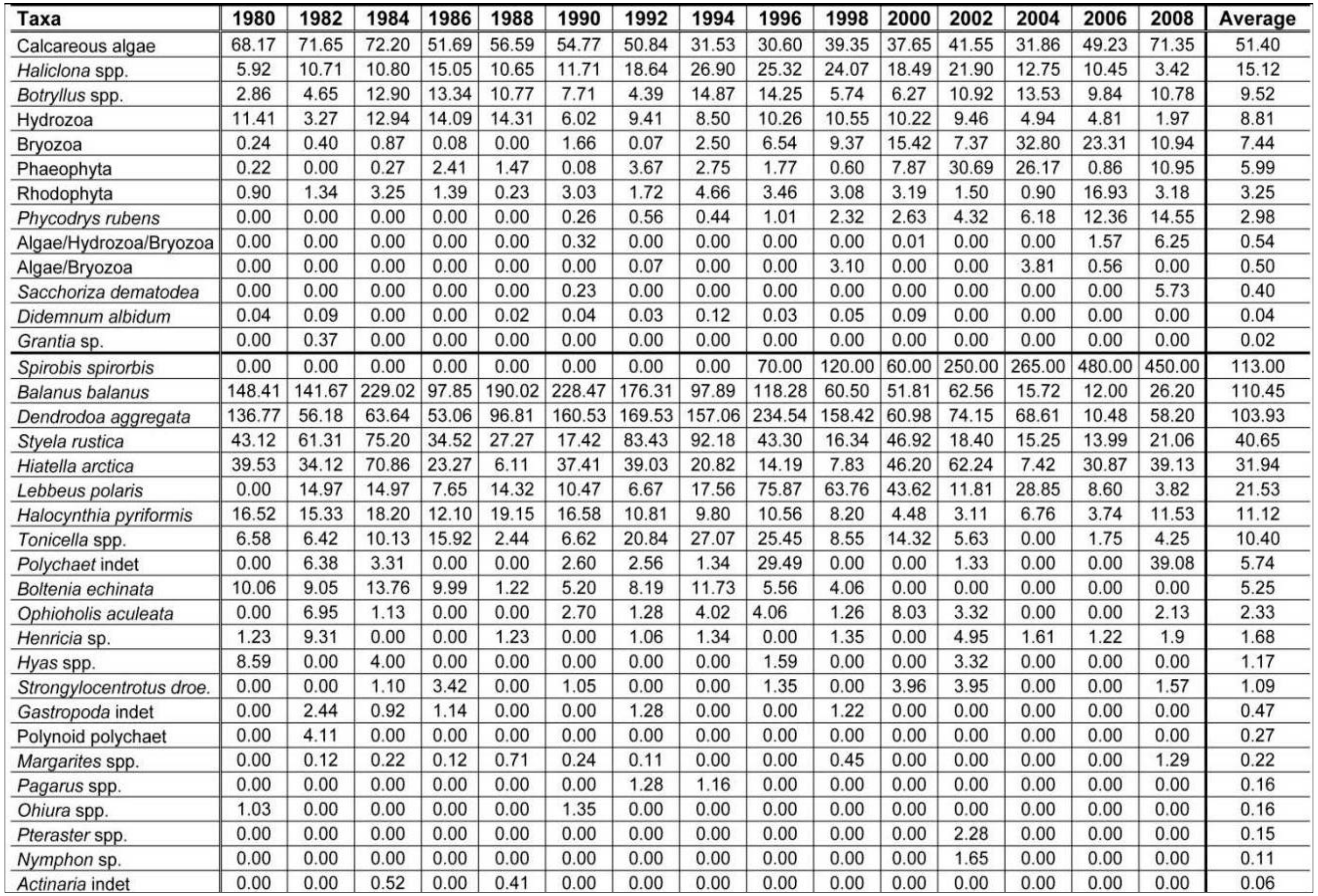
Wlodarska-Kowalczuk M, Kuklinski P, Ronowicz M, Legezynska J, Gromisz S (2009) Assessing species richness of macrofauna associated with macroalgae in Arctic kelp forests (Hornsund, Svalbard). Polar Biology 32 (6):897-905

Zajczkowski M, Nygård H, Hegseth E, Berge J (2010) Vertical flux of particulate matter in an Arctic fjord: the case of lack of the sea-ice cover in Adventfjorden 2006–2007. Polar Biology 33 (2):223-239

7. Appendices

Appendix I:

Taxa list (average values)



Taxa	1980	1982	1984	1986	1988	1990	1992	1994	1996	1998	2000	2002	2004	2006	2008	Average
Calcareous algae	68.17	71.65	72.20	51.69	56.59	54.77	50.84	31.53	30.60	39.35	37.65	41.55	31.86	49.23	71.35	51.40
Haliclona spp.	5.92	10.71	10.80	15.05	10.65	11.71	18.64	26.90	25.32	24.07	18.49	21.90	12.75	10.45	3.42	15.12
Botryllus spp.	2.86	4.65	12.90	13.34	10.77	7.71	4.39	14.87	14.25	5.74	6.27	10.92	13.53	9.84	10.78	9.52
Hydrozoa	11.41	3.27	12.94	14.09	14.31	6.02	9.41	8.50	10.26	10.55	10.22	9.46	4.94	4.81	1.97	8.81
Bryozoa	0.24	0.40	0.87	0.08	0.00	1.66	0.07	2.50	6.54	9.37	15.42	7.37	32.80	23.31	10.94	7.44
Phaeophyta	0.22	0.00	0.27	2.41	1.47	0.08	3.67	2.75	1.77	0.60	7.87	30.69	26.17	0.86	10.95	5.99
Rhodophyta	0.90	1.34	3.25	1.39	0.23	3.03	1.72	4.66	3.46	3.08	3.19	1.50	0.90	16.93	3.18	3.25
Phycodrys rubens	0.00	0.00	0.00	0.00	0.00	0.26	0.56	0.44	1.01	2.32	2.63	4.32	6.18	12.36	14.55	2.98
Algae/Hydrozoa/Bryozoa	0.00	0.00	0.00	0.00	0.00	0.32	0.00	0.00	0.00	0.00	0.01	0.00	0.00	1.57	6.25	0.54
Algae/Bryozoa	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	3.10	0.00	0.00	3.81	0.56	0.00	0.50
Sacchoriza dematodea	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.73	0.40
Didemnum albidum	0.04	0.09	0.00	0.00	0.02	0.04	0.03	0.12	0.03	0.05	0.09	0.00	0.00	0.00	0.00	0.04
Grantia sp.	0.00	0.37	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Spirobis spirorbis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	70.00	120.00	60.00	250.00	265.00	480.00	450.00	113.00
Balanus balanus	148.41	141.67	229.02	97.85	190.02	228.47	176.31	97.89	118.28	60.50	51.81	62.56	15.72	12.00	26.20	110.45
Dendrodoa aggregata	136.77	56.18	63.64	53.06	96.81	160.53	169.53	157.06	234.54	158.42	60.98	74.15	68.61	10.48	58.20	103.93
Styela rustica	43.12	61.31	75.20	34.52	27.27	17.42	83.43	92.18	43.30	16.34	46.92	18.40	15.25	13.99	21.06	40.65
Hiatella arctica	39.53	34.12	70.86	23.27	6.11	37.41	39.03	20.82	14.19	7.83	46.20	62.24	7.42	30.87	39.13	31.94
Lebbeus polaris	0.00	14.97	14.97	7.65	14.32	10.47	6.67	17.56	75.87	63.76	43.62	11.81	28.85	8.60	3.82	21.53
Halocynthia pyriformis	16.52	15.33	18.20	12.10	19.15	16.58	10.81	9.80	10.56	8.20	4.48	3.11	6.76	3.74	11.53	11.12
Tonicella spp.	6.58	6.42	10.13	15.92	2.44	6.62	20.84	27.07	25.45	8.55	14.32	5.63	0.00	1.75	4.25	10.40
Polychaet indet	0.00	6.38	3.31	0.00	0.00	2.60	2.56	1.34	29.49	0.00	0.00	1.33	0.00	0.00	39.08	5.74
Boltenia echinata	10.06	9.05	13.76	9.99	1.22	5.20	8.19	11.73	5.56	4.06	0.00	0.00	0.00	0.00	0.00	5.25
Ophioholis aculeata	0.00	6.95	1.13	0.00	0.00	2.70	1.28	4.02	4.06	1.26	8.03	3.32	0.00	0.00	2.13	2.33
Henricia sp.	1.23	9.31	0.00	0.00	1.23	0.00	1.06	1.34	0.00	1.35	0.00	4.95	1.61	1.22	1.9	1.68
Hyas spp.	8.59	0.00	4.00	0.00	0.00	0.00	0.00	0.00	1.59	0.00	0.00	3.32	0.00	0.00	0.00	1.17
Strongylocentrotus droe.	0.00	0.00	1.10	3.42	0.00	1.05	0.00	0.00	1.35	0.00	3.96	3.95	0.00	0.00	1.57	1.09
Gastropoda indet	0.00	2.44	0.92	1.14	0.00	0.00	1.28	0.00	0.00	1.22	0.00	0.00	0.00	0.00	0.00	0.47
Polynoid polychaet	0.00	4.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27
Margarites spp.	0.00	0.12	0.22	0.12	0.71	0.24	0.11	0.00	0.00	0.45	0.00	0.00	0.00	0.00	1.29	0.22
Pagarus spp.	0.00	0.00	0.00	0.00	0.00	0.00	1.28	1.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16
Ohiura spp.	1.03	0.00	0.00	0.00	0.00	1.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16
Pteraster spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.28	0.00	0.00	0.00	0.15
Nymphon sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.65	0.00	0.00	0.00	0.11
Actinaria indet	0.00	0.00	0.52	0.00	0.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06

Appendix II:

Correlation between species, values marked with grey are correlations >0.5.

Corr.	Balan	Dend	Litho	Styel	Hiate	Lebb	Spong	Spiro	Tonic	Haloc	Botry	Hydro	Bryoz	Polyc	Phaeo	Bolte	Rhod	Phyco	alhyd	Ophio	Marga	Strong	Hyas	alhyb	albry	Gastr
Balan	1,00																									
Dendr	0,35	1,00																								
Litho	0,44	-0,38	1,00																							
Styel	0,33	0,31	-0,09	1,00																						
Hiate	0,11	-0,28	0,39	0,30	1,00																					
Lebbe	-0,06	0,37	-0,42	0,01	-0,27	1,00																				
Spong	-0,10	0,59	-0,80	0,45	-0,21	0,53	1,00																			
Spiro	-0,72	-0,55	-0,02	-0,49	0,13	-0,23	-0,33	1,00																		
Tonic	0,20	0,68	-0,45	0,70	-0,10	0,36	0,72	-0,49	1,00																	
Haloc	0,80	0,15	0,66	0,03	-0,10	-0,18	-0,46	-0,50	0,00	1,00																
Botry	-0,20	-0,04	-0,38	0,09	-0,24	0,23	0,25	0,15	0,27	-0,04	1,00															
Hydro	0,42	0,22	-0,10	0,26	-0,13	0,27	0,30	-0,58	0,32	0,29	0,10	1,00														
Bryoz	-0,81	-0,38	-0,45	-0,46	-0,18	0,14	-0,05	0,72	-0,38	-0,69	0,22	-0,47	1,00													
Polyc	-0,18	0,25	0,12	-0,09	0,02	0,22	-0,11	0,18	0,18	0,07	0,26	-0,37	0,00	1,00												
Phaeo	-0,53	-0,27	-0,35	-0,04	0,25	-0,13	0,10	0,31	-0,27	-0,60	0,28	-0,23	0,53	0,01	1,00											
Bolte	0,61	0,35	0,22	0,61	-0,02	0,00	0,16	-0,59	0,57	0,59	0,07	0,42	-0,65	-0,18	-0,52	1,00										
Rhod	-0,38	-0,27	-0,11	-0,24	0,09	0,01	-0,03	0,75	-0,08	-0,34	0,11	-0,32	0,42	-0,02	-0,21	-0,21	1,00									
Phyco	-0,75	-0,47	0,04	-0,44	0,17	-0,20	-0,36	0,93	-0,44	-0,45	0,15	-0,65	0,66	0,42	0,36	-0,63	0,56	1,00								
alhyd	0,01	0,78	-0,51	0,18	-0,43	0,54	0,64	-0,20	0,67	-0,02	0,36	0,02	-0,14	0,45	-0,27	0,19	0,11	-0,15	1,00							
Ophio	-0,10	0,12	-0,28	0,37	0,32	0,37	0,40	-0,23	0,38	-0,38	-0,12	-0,13	0,00	0,15	0,09	-0,17	-0,08	-0,12	0,19	1,00						
Marga	-0,09	-0,16	0,46	-0,30	-0,04	-0,17	-0,46	0,21	-0,33	0,29	0,02	-0,23	-0,10	0,56	-0,06	-0,26	-0,14	0,46	-0,05	-0,19	1,00					
Strong	-0,16	-0,22	-0,13	0,09	0,51	0,10	0,13	-0,06	0,17	-0,23	0,17	0,22	0,00	0,10	0,34	-0,15	-0,15	0,05	-0,23	0,51	-0,01	1,00				
Hyas	0,22	-0,08	0,12	0,29	0,52	0,33	0,13	-0,09	0,01	0,03	0,33	0,29	-0,16	0,04	0,30	0,14	-0,08	-0,12	-0,05	0,05	-0,13	0,26	1,00			
alhybr	-0,40	-0,27	0,37	-0,27	0,21	-0,28	-0,50	0,59	-0,28	0,00	0,09	-0,57	0,20	0,69	0,10	-0,36	0,23	0,81	-0,06	-0,08	0,81	0,09	-0,16	1,00		
albry	-0,50	-0,05	-0,42	-0,43	-0,55	0,26	0,13	0,23	-0,33	-0,38	0,05	-0,18	0,67	-0,21	0,35	-0,30	-0,03	0,19	-0,01	-0,29	-0,04	-0,32	-0,19	-0,12	1,00	
Gastr	0,30	-0,10	0,37	0,17	-0,02	0,08	0,01	-0,34	0,07	0,23	-0,32	0,05	-0,38	-0,16	-0,34	0,45	-0,21	-0,36	-0,18	-0,04	-0,02	-0,11	0,03	-0,23	0,05	1,00

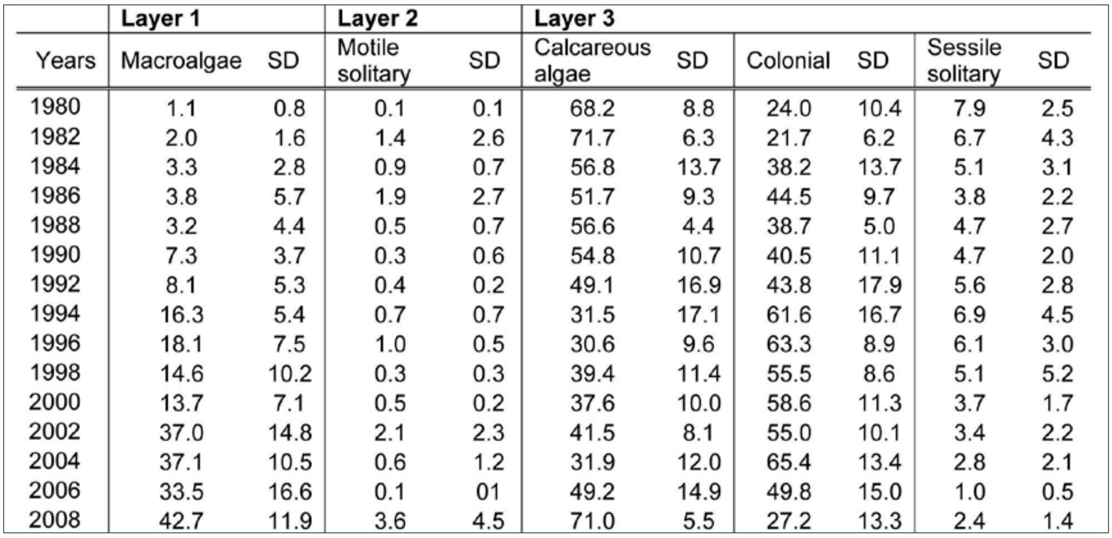
Appendix III:

Correlations between environmental variables and species, grey values indicate correlations > 0.5

Parameters	Bala	Dend	Litho	Styel	Hiate	Lebbe	Spong	Spiro	Tonic	Haloc	Botry	Hydro	Bryoz	Polyc	Phaeo	Bolte	Rhod	Phyco	alhyd	Ophio	Marga	Strong	Hyas	alhybr	albry	Gastr
TempM	-0.25	-0.23	-0.04	-0.03	0.54	0.16	-0.07	0.56	-0.12	-0.36	0.11	-0.44	0.49	0.12	0.26	-0.22	0.56	0.51	-0.11	0.16	-0.14	0.18	0.39	0.26	0.04	-0.18
TempW	-0.10	-0.14	0.11	-0.04	0.51	0.07	-0.25	0.49	-0.07	-0.16	0.05	-0.50	0.33	0.37	0.04	-0.29	0.55	0.51	0.00	0.29	0.00	0.13	0.21	0.42	-0.29	-0.38
TempS	-0.30	-0.38	-0.08	-0.46	0.05	-0.26	-0.17	0.57	-0.54	-0.24	0.17	0.05	0.41	-0.34	0.40	-0.32	0.34	0.41	-0.36	-0.67	0.01	-0.06	0.21	0.06	0.40	-0.24
NaoW	0.35	-0.04	0.24	0.37	0.35	-0.42	-0.11	-0.25	-0.01	0.20	-0.32	-0.09	-0.29	-0.32	-0.05	0.17	-0.23	-0.14	-0.31	0.20	0.21	0.10	-0.13	0.09	-0.20	0.07
Nao3M	0.50	0.31	0.00	0.60	0.28	-0.07	0.16	-0.35	0.48	0.24	0.13	-0.15	-0.33	0.10	-0.12	0.33	-0.13	-0.25	0.20	0.39	-0.04	0.11	0.08	0.00	-0.46	-0.03
Nao1lag	0.32	0.33	0.03	0.15	0.00	0.36	0.07	-0.15	0.34	0.29	0.24	-0.33	-0.11	0.47	-0.33	0.15	0.09	-0.04	0.48	0.36	0.16	-0.03	0.06	0.20	-0.23	0.01
Nao3lag	0.09	0.41	-0.28	0.33	0.00	0.34	0.58	-0.18	0.56	-0.11	0.15	0.43	-0.26	0.06	-0.12	0.30	0.02	-0.15	0.33	-0.08	0.00	0.18	0.24	-0.11	-0.02	0.29
AOW	0.26	0.06	0.07	0.16	0.48	-0.30	0.04	-0.08	0.02	-0.01	-0.15	-0.35	-0.22	0.06	0.16	-0.19	-0.10	0.02	-0.06	0.41	0.18	0.31	0.01	0.19	-0.38	-0.07
AOS	0.09	0.43	-0.41	0.59	0.03	0.18	0.61	-0.08	0.69	-0.12	0.39	0.25	-0.23	0.00	-0.19	0.35	0.36	-0.16	0.63	0.20	-0.34	-0.08	0.22	-0.21	-0.39	-0.32
AO3MW	0.22	0.45	-0.28	0.31	0.13	-0.03	0.33	-0.14	0.31	-0.05	0.13	-0.31	-0.05	0.12	0.18	0.01	-0.10	-0.04	0.33	0.22	0.05	-0.01	0.03	0.07	-0.03	-0.18
WSCtempM	-0.11	0.04	-0.04	0.05	0.29	-0.15	-0.10	0.49	-0.11	-0.22	-0.10	-0.55	0.38	-0.03	0.08	-0.11	0.55	0.42	0.03	-0.06	-0.13	-0.35	0.04	0.22	0.11	-0.32
WSCtemp3M	-0.38	0.09	-0.27	0.05	0.20	0.06	0.23	0.52	0.32	-0.45	0.26	-0.51	0.38	0.36	0.17	-0.07	0.54	0.55	0.28	0.09	-0.02	-0.04	0.05	0.39	0.03	-0.11
WSCtemp1lag	-0.34	0.16	-0.41	0.24	0.14	0.27	0.39	0.42	0.43	-0.48	0.37	-0.27	0.34	0.37	0.17	-0.08	0.49	0.43	0.36	0.12	-0.09	0.11	0.18	0.25	0.01	-0.11
WSCtemp3lag	-0.64	0.11	-0.56	0.02	-0.36	0.25	0.47	0.33	0.30	-0.45	0.55	-0.04	0.34	0.31	0.24	-0.19	0.20	0.44	0.47	0.00	0.32	0.09	-0.11	0.36	0.34	-0.24
WSCsal	-0.29	-0.44	0.35	-0.33	0.41	-0.39	-0.62	0.69	-0.53	-0.09	-0.17	-0.58	0.45	0.04	0.16	-0.21	0.51	0.62	-0.40	-0.26	0.00	-0.15	0.00	0.44	0.07	-0.26
WSC3M	-0.40	-0.66	0.43	-0.15	0.33	-0.35	-0.53	0.71	-0.39	-0.16	0.07	-0.67	0.36	0.30	0.16	-0.21	0.45	0.71	-0.38	-0.13	0.27	-0.04	0.02	0.62	-0.05	0.19
SSTM	-0.53	-0.08	-0.36	0.02	0.24	0.33	0.17	0.48	0.15	-0.50	0.47	-0.22	0.57	0.42	0.46	-0.31	0.30	0.59	0.11	0.19	0.11	0.44	0.29	0.42	0.17	-0.35
SSTW	-0.49	-0.06	-0.23	0.30	0.16	0.27	0.18	0.38	0.37	-0.42	0.41	-0.13	0.36	0.46	0.25	0.01	0.28	0.45	0.15	0.12	-0.02	0.26	0.22	0.33	0.01	-0.05
SSTS	-0.56	-0.18	-0.38	-0.40	0.23	0.41	0.22	0.50	-0.11	-0.57	0.28	-0.11	0.51	0.25	0.38	-0.58	0.39	0.53	0.08	0.27	0.09	0.58	0.27	0.28	0.18	-0.31
ICEM	0.33	0.38	0.14	0.16	-0.46	-0.04	0.11	-0.63	0.24	0.43	-0.18	0.35	-0.59	0.08	-0.31	0.32	-0.63	-0.52	0.23	-0.09	0.19	-0.25	-0.31	-0.23	-0.16	0.31
ICEW	0.49	0.48	-0.06	0.23	-0.54	0.31	0.32	-0.76	0.37	0.46	0.08	0.49	-0.48	-0.04	-0.29	0.48	-0.59	-0.78	0.39	-0.09	-0.20	-0.33	0.01	-0.62	-0.02	0.29
ICES	0.28	0.29	0.36	-0.04	-0.32	-0.12	-0.13	-0.44	0.09	0.46	-0.45	0.07	-0.56	0.23	-0.50	0.19	-0.45	-0.25	0.16	-0.04	0.47	-0.23	-0.51	0.10	-0.02	0.41
PrecM	0.10	0.21	-0.11	0.15	0.48	0.05	0.08	0.00	0.21	0.02	0.42	0.14	-0.07	0.40	0.40	-0.06	0.10	0.13	0.10	0.01	0.01	0.53	-0.52	-0.21	0.41	-0.54
Prec1lag	0.05	0.23	-0.15	0.61	0.12	-0.37	0.35	-0.15	0.31	-0.13	0.00	-0.10	-0.29	-0.12	0.13	0.16	-0.13	-0.07	0.19	0.17	0.11	-0.15	-0.09	0.06	-0.18	-0.08

Appendix IV:

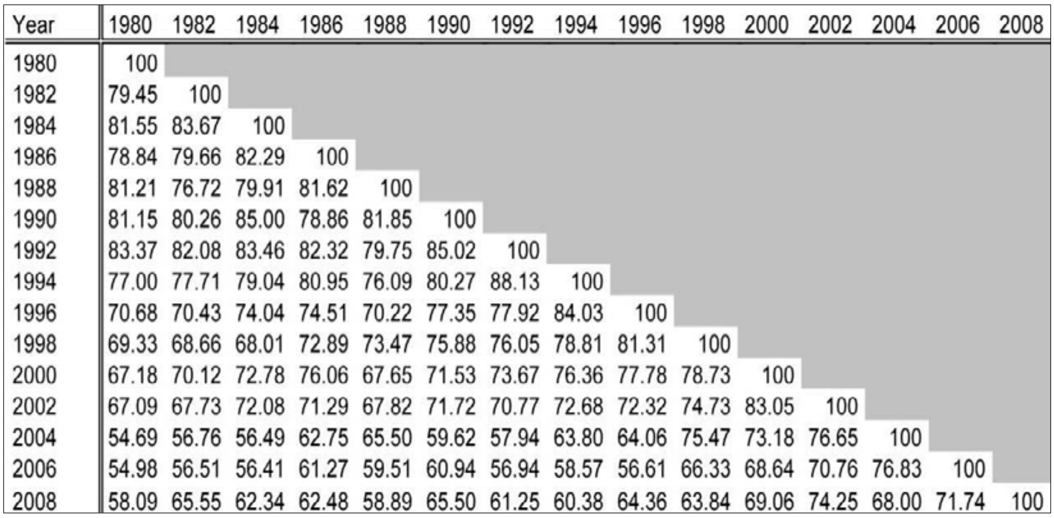
Calculations of major groups in the different layers as described in section 2.3.



	Layer 1		Layer 2		Layer 3					
Years	Macroalgae	SD	Motile solitary	SD	Calcareous algae	SD	Colonial	SD	Sessile solitary	SD
1980	1.1	0.8	0.1	0.1	68.2	8.8	24.0	10.4	7.9	2.5
1982	2.0	1.6	1.4	2.6	71.7	6.3	21.7	6.2	6.7	4.3
1984	3.3	2.8	0.9	0.7	56.8	13.7	38.2	13.7	5.1	3.1
1986	3.8	5.7	1.9	2.7	51.7	9.3	44.5	9.7	3.8	2.2
1988	3.2	4.4	0.5	0.7	56.6	4.4	38.7	5.0	4.7	2.7
1990	7.3	3.7	0.3	0.6	54.8	10.7	40.5	11.1	4.7	2.0
1992	8.1	5.3	0.4	0.2	49.1	16.9	43.8	17.9	5.6	2.8
1994	16.3	5.4	0.7	0.7	31.5	17.1	61.6	16.7	6.9	4.5
1996	18.1	7.5	1.0	0.5	30.6	9.6	63.3	8.9	6.1	3.0
1998	14.6	10.2	0.3	0.3	39.4	11.4	55.5	8.6	5.1	5.2
2000	13.7	7.1	0.5	0.2	37.6	10.0	58.6	11.3	3.7	1.7
2002	37.0	14.8	2.1	2.3	41.5	8.1	55.0	10.1	3.4	2.2
2004	37.1	10.5	0.6	1.2	31.9	12.0	65.4	13.4	2.8	2.1
2006	33.5	16.6	0.1	01	49.2	14.9	49.8	15.0	1.0	0.5
2008	42.7	11.9	3.6	4.5	71.0	5.5	27.2	13.3	2.4	1.4

Appendix V:

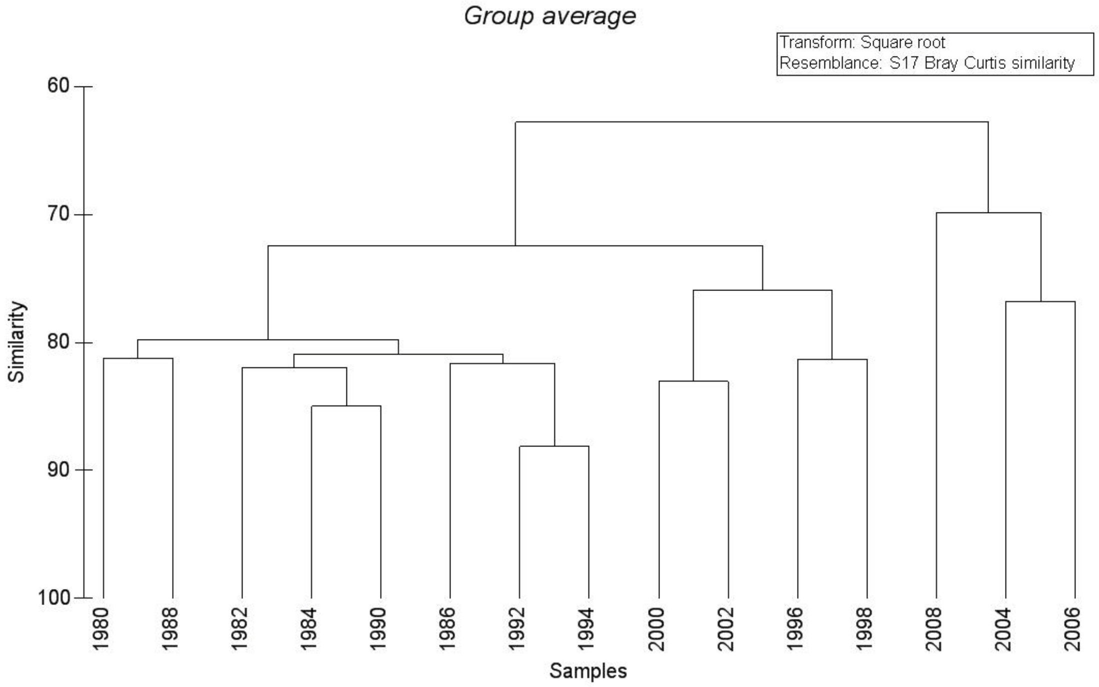
Bray-Curtis similarity matrix



Year	1980	1982	1984	1986	1988	1990	1992	1994	1996	1998	2000	2002	2004	2006	2008
1980	100														
1982	79.45	100													
1984	81.55	83.67	100												
1986	78.84	79.66	82.29	100											
1988	81.21	76.72	79.91	81.62	100										
1990	81.15	80.26	85.00	78.86	81.85	100									
1992	83.37	82.08	83.46	82.32	79.75	85.02	100								
1994	77.00	77.71	79.04	80.95	76.09	80.27	88.13	100							
1996	70.68	70.43	74.04	74.51	70.22	77.35	77.92	84.03	100						
1998	69.33	68.66	68.01	72.89	73.47	75.88	76.05	78.81	81.31	100					
2000	67.18	70.12	72.78	76.06	67.65	71.53	73.67	76.36	77.78	78.73	100				
2002	67.09	67.73	72.08	71.29	67.82	71.72	70.77	72.68	72.32	74.73	83.05	100			
2004	54.69	56.76	56.49	62.75	65.50	59.62	57.94	63.80	64.06	75.47	73.18	76.65	100		
2006	54.98	56.51	56.41	61.27	59.51	60.94	56.94	58.57	56.61	66.33	68.64	70.76	76.83	100	
2008	58.09	65.55	62.34	62.48	58.89	65.50	61.25	60.38	64.36	63.84	69.06	74.25	68.00	71.74	100

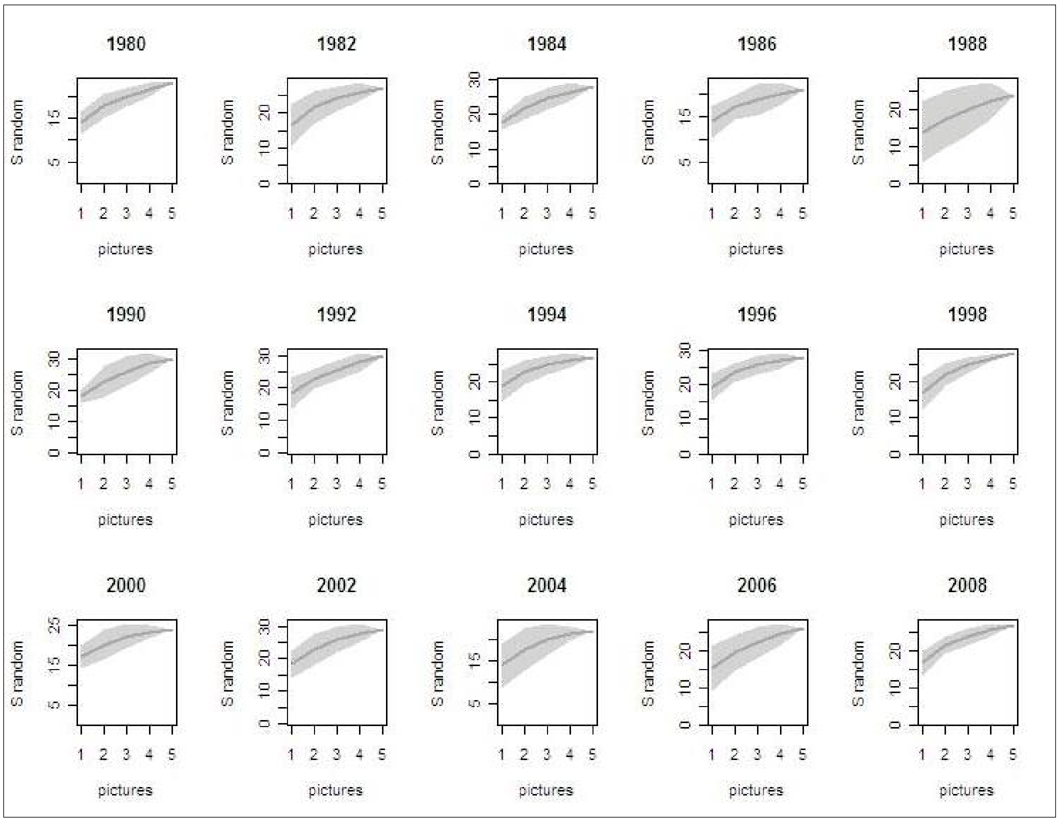
Appendix VI:

Hierarchical ordination clustering using group-average linking based on Bray-Curtis similarities (square root transformed data).



Appendix VII:

Species accumulation curves (Number of species (S) as a function of number of samples (pictures analyzed)). The plots were generated with pictures selected randomly 50 times.



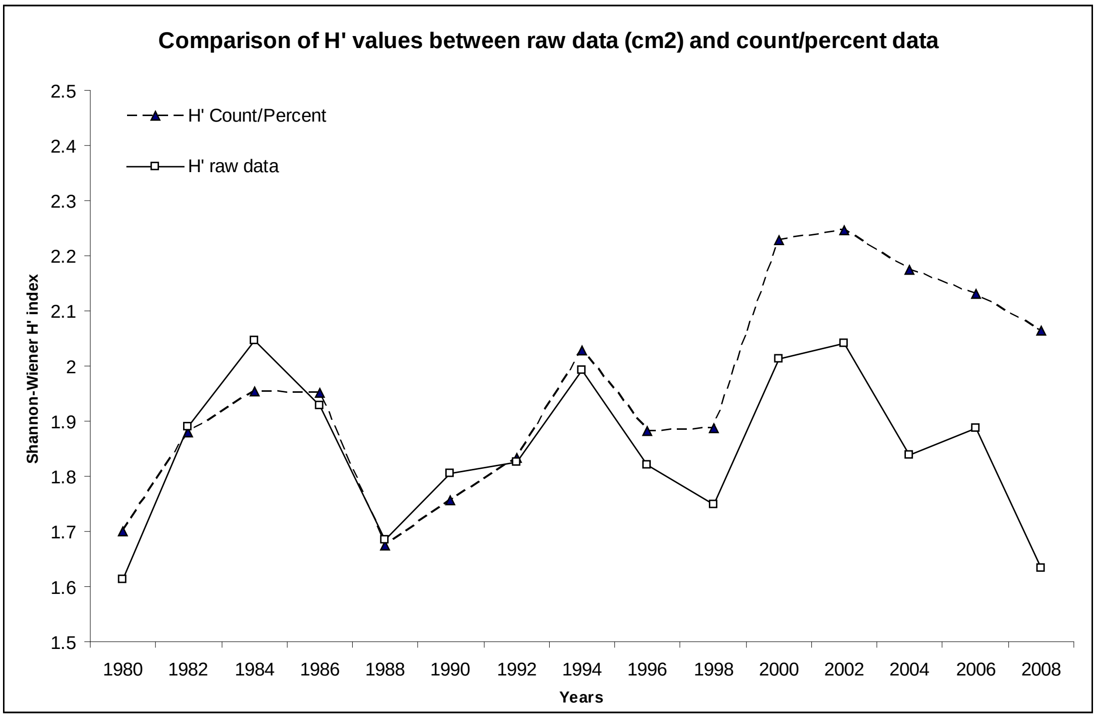
Appendix VIII:

Correlations between diversity indices

Pearson’s product moment correlations	
Shannon-Wiener index (H’) - Pielou’s evenness index (J’)	**0.83**
Shannon-Wiener index (H’) - Simpson index (1-D)	**0.93**
Pielou’s evenness index (J') - Simpson index (1-D)	**0.90**

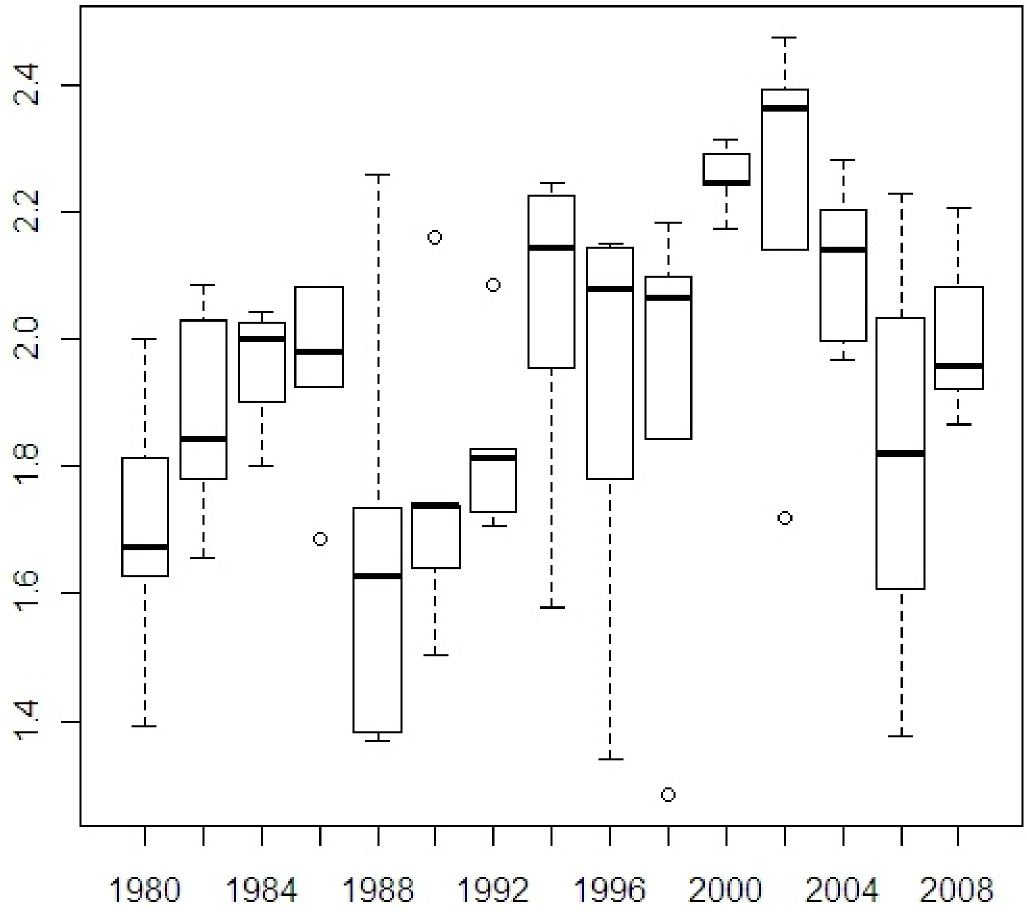
Appendix IX:

Comparison of Shannon-Wiener H’ (counts and percentage) and Shannon-Wiener H’ raw data (cm^2).



Appendix X:

Boxplot showing variation among H’ values within years. Years on the x-axis and H’ values on the Y axis.



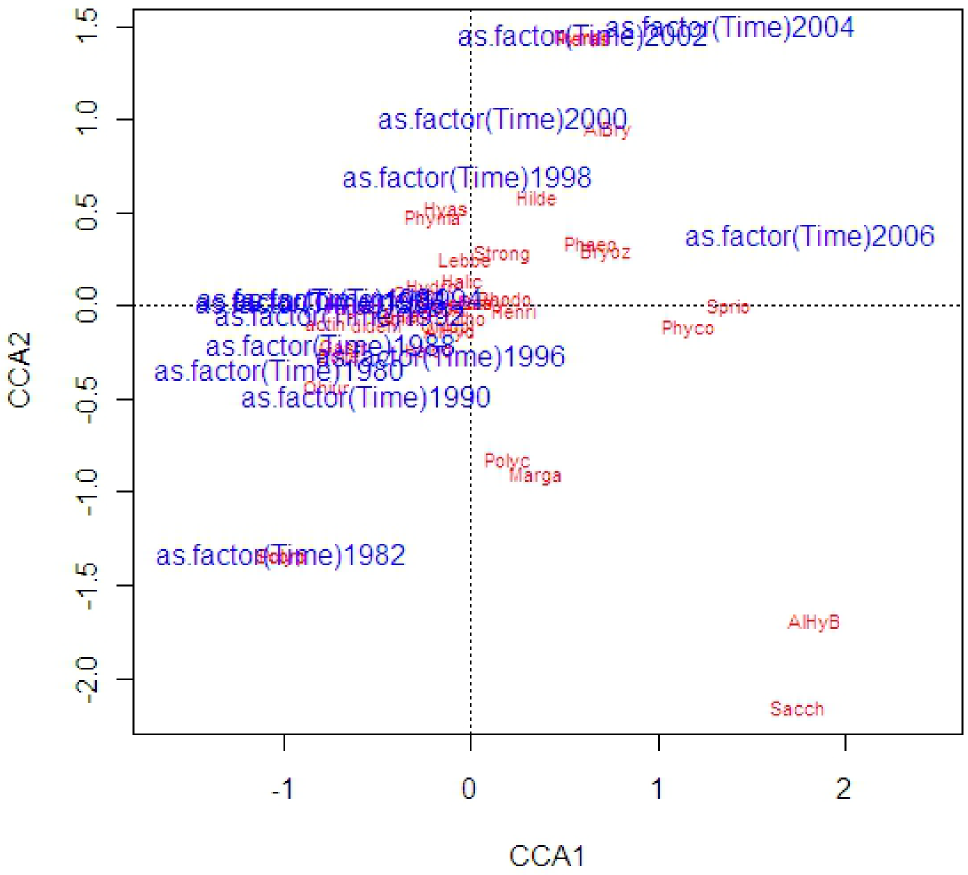
Appendix XI:

R output for CCA (Fig 14).

```
Call: cca(X = sqrt(species), Y = env)

              Inertia Rank

Total          0.3924

Constrained    0.2717    6

Unconstrained  0.1207    8

Inertia is mean squared contingency coefficient

Eigenvalues for constrained axes:

    CCA1     CCA2     CCA3     CCA4     CCA5     CCA6

0.181195 0.029694 0.024172 0.018360 0.012078 0.006162

Eigenvalues for unconstrained axes:

     CA1      CA2      CA3      CA4      CA5      CA6      CA7      CA8

0.032179 0.026920 0.023066 0.013808 0.011374 0.006546 0.003992 0.002813

> plot(species.cca)# summary of CCA result

> anova(species.cca)

Permutation test for cca under reduced model

Model: cca(X = sqrt(species), Y = env)

         Df  Chisq      F N.Perm Pr(>F)

Model     6 0.2717 3.0010    199  0.005 **

Residual  8 0.1207

---Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’
```

Appendix XII:

CCA biplot with replicates and ‘time’ as a categorical variable



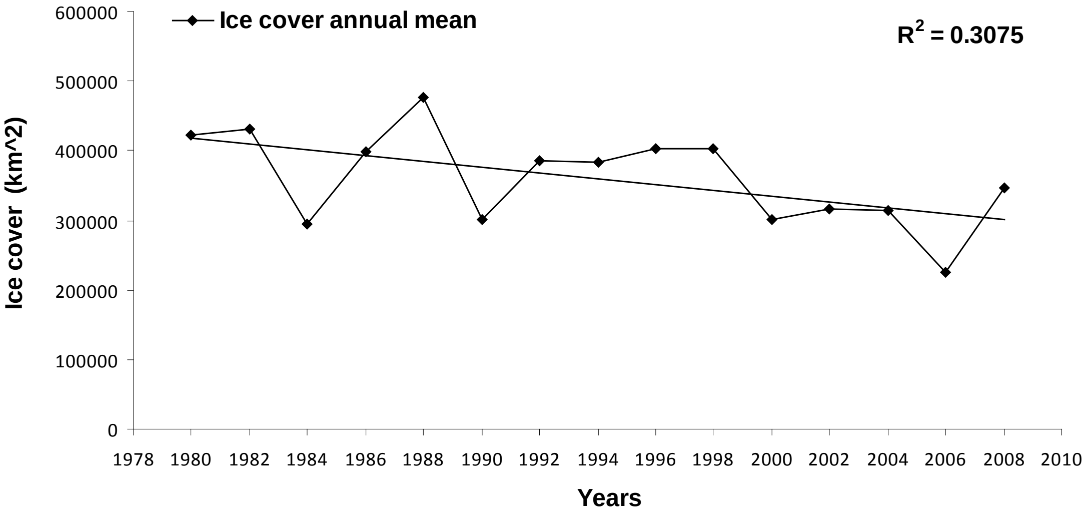
CCA Output in R with ‘Time’ as a categorical variable

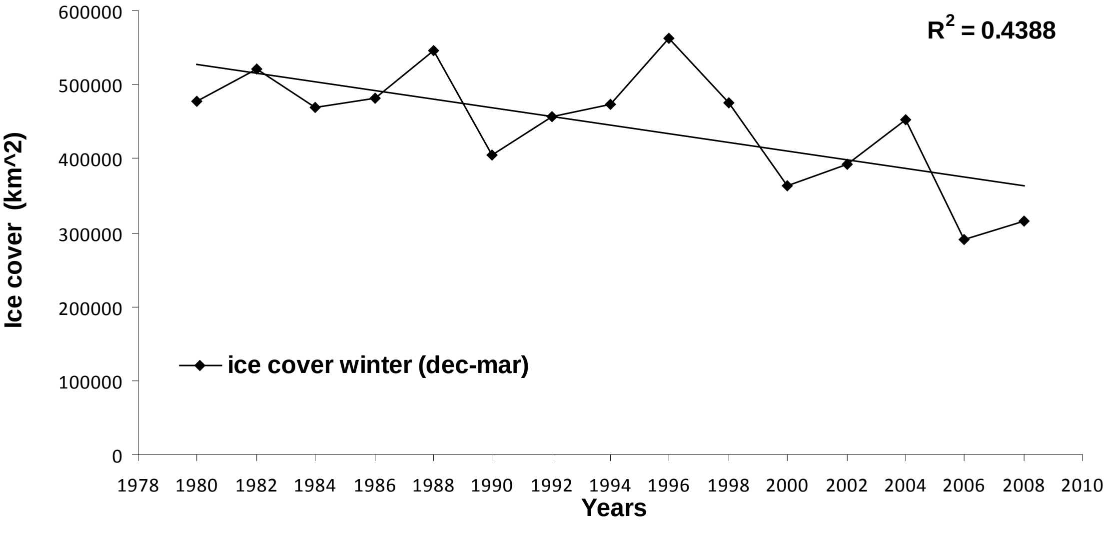
```
Call: cca(formula = log(species + 1) ~ as.factor(Time))

            Inertia Rank

Total         1.4355

Constrained    0.5119   14
```

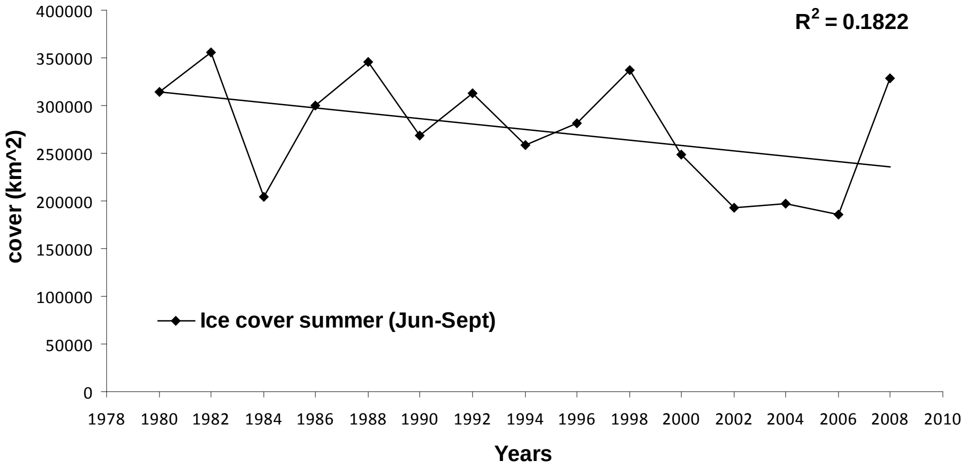
```
Unconstrained  0.9236   39

Eigenvalues for constrained axes:

    CCA1     CCA2     CCA3     CCA4     CCA5     CCA6     CCA7     CCA8

0.185535 0.069179 0.051079 0.044693 0.037891 0.027579 0.025079 0.019221

    CCA9    CCA10    CCA11    CCA12    CCA13    CCA14

0.016636 0.010448 0.009964 0.006215 0.005689 0.002669

Eigenvalues for unconstrained axes:

    CA1     CA2     CA3     CA4     CA5     CA6     CA7     CA8

0.10500 0.08357 0.08196 0.05997 0.05526 0.05300 0.04922 0.04461

(Showed only 8 of all 39 unconstrained eigenvalues)

> plot(species.cca)

> anova(species.cca)

Permutation test for cca under reduced model

Model: cca(formula = log(species + 1) ~ as.factor(Time))

         Df  Chisq      F N.Perm Pr(>F)

Model    14 0.5119 2.3751    199  0.005
```

Appendix XIII:

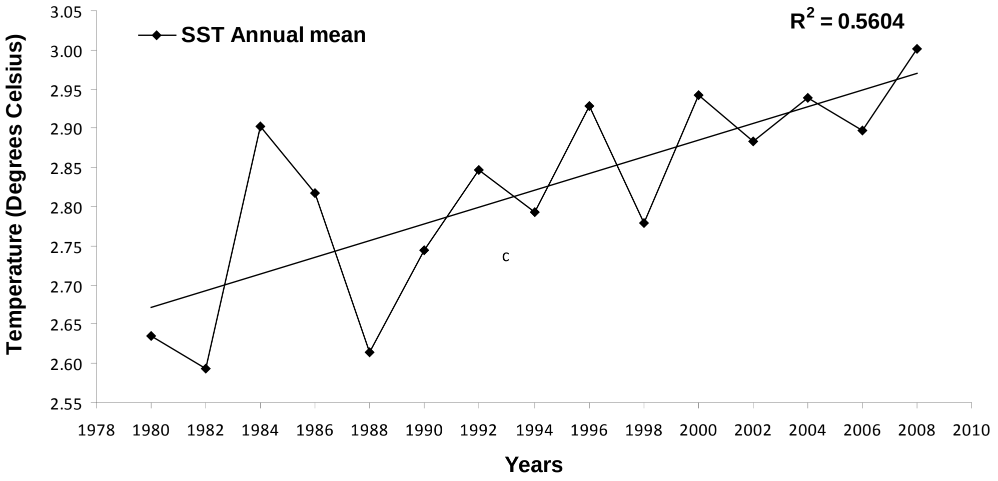
Univariate plots of selected environmental parameters (WSC, SST, SIC, and NAO) for the study period (1980-2008).



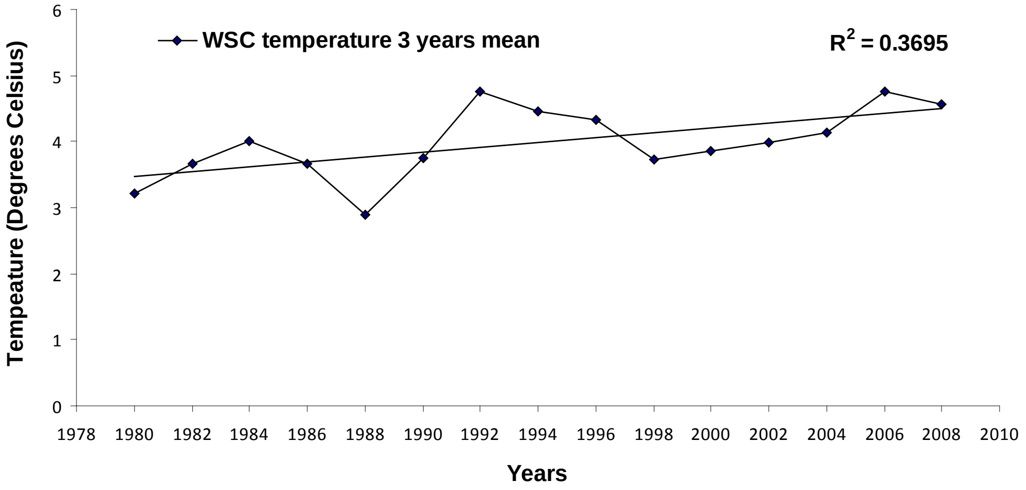




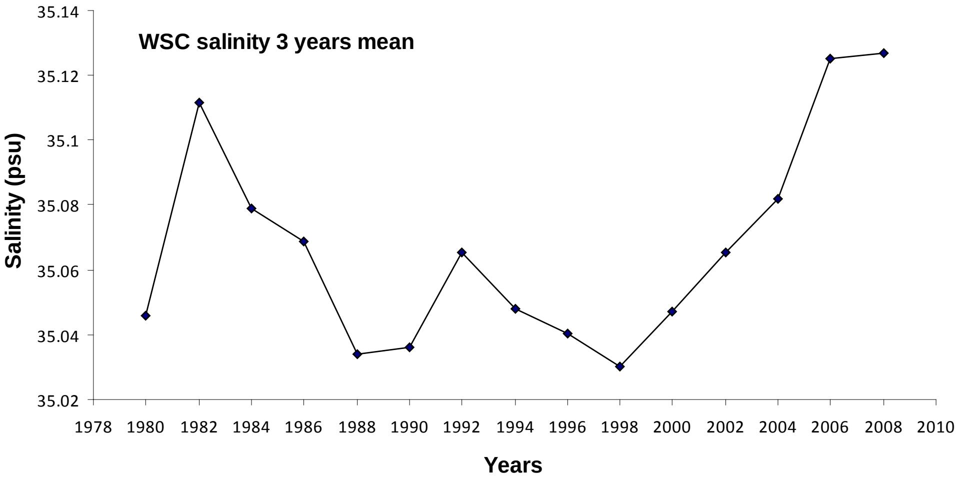
R^2 = 0.1822
cover (km^2)
400000
350000
300000
250000
200000
150000
100000
50000
0
Ice cover summer (Jun-Sept)
1978 1980 1982 1984 1986 1988 1990 1992 1994 1996 1998 2000 2002 2004 2006 2008 2010
Years

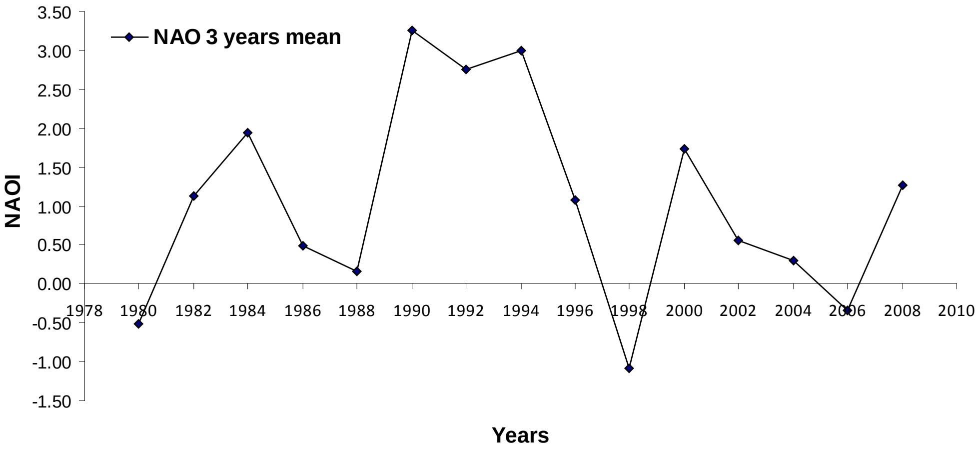


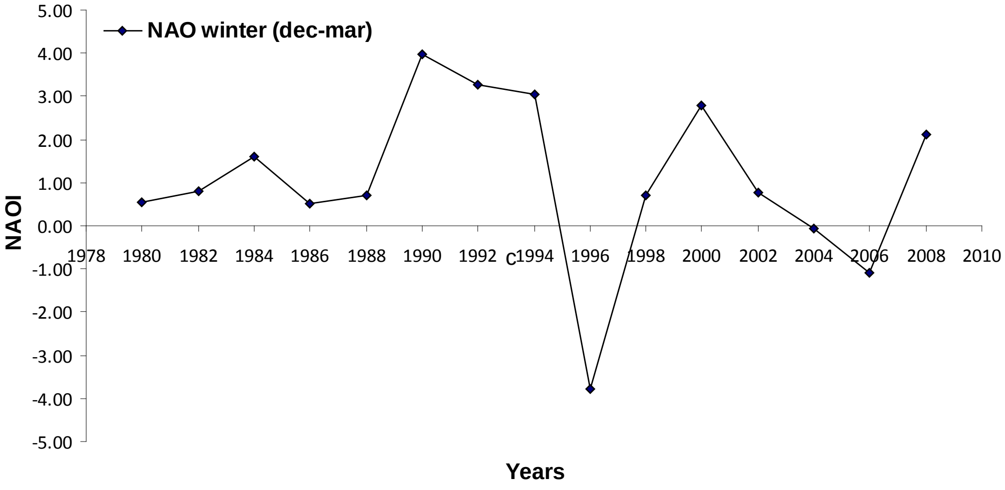
SST Annual mean
R^2 = 0.5604
Temperature (Degrees Celsius)
3.05
3.00
2.95
2.90
2.85
2.80
2.75
2.70
2.65
2.60
2.55
c
1978 1980 1982 1984 1986 1988 1990 1992 1994 1996 1998 2000 2002 2004 2006 2008 2010
Years



WSC temperature 3 years mean
R^2 = 0.3695
Tempeature (Degrees Celsius)
6
5
4
3
2
1
0
1978 1980 1982 1984 1986 1988 1990 1992 1994 1996 1998 2000 2002 2004 2006 2008 2010
Years


WSC salinity 3 years mean
Salinity (psu)
35.14
35.12
35.1
35.08
35.06
35.04
35.02
1978 1980 1982 1984 1986 1988 1990 1992 1994 1996 1998 2000 2002 2004 2006 2008 2010
Years

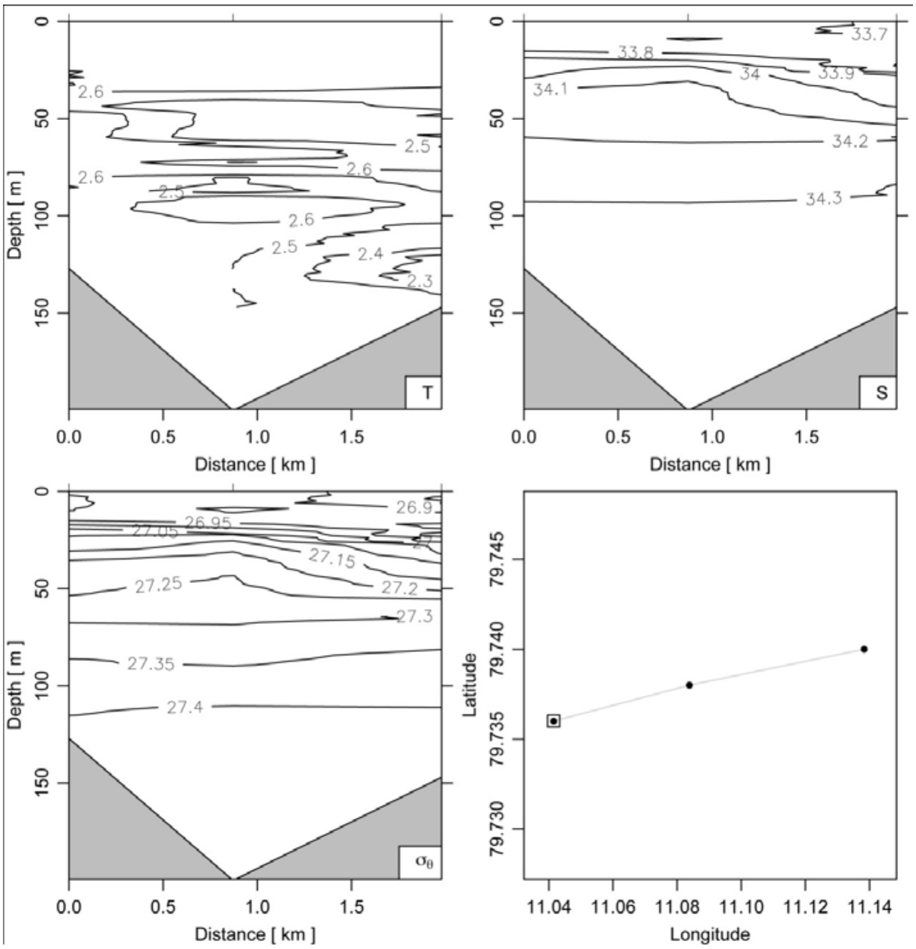

NAO 3 years mean
NAOI
3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.00
-0.50
-1.00
-1.50
1978 1980 1982 1984 1986 1988 1990 1992 1994 1996 1998 2000 2002 2004 2006 2008 2010
Years


NAO winter (dec-mar)
NAOI
5.00
4.00
3.00
2.00
1.00
0.00
-1.00
-2.00
-3.00
-4.00
-5.00
1978 1980 1982 1984 1986 1988 1990 1992 c 1994 1996 1998 2000 2002 2004 2006 2008 2010
Years

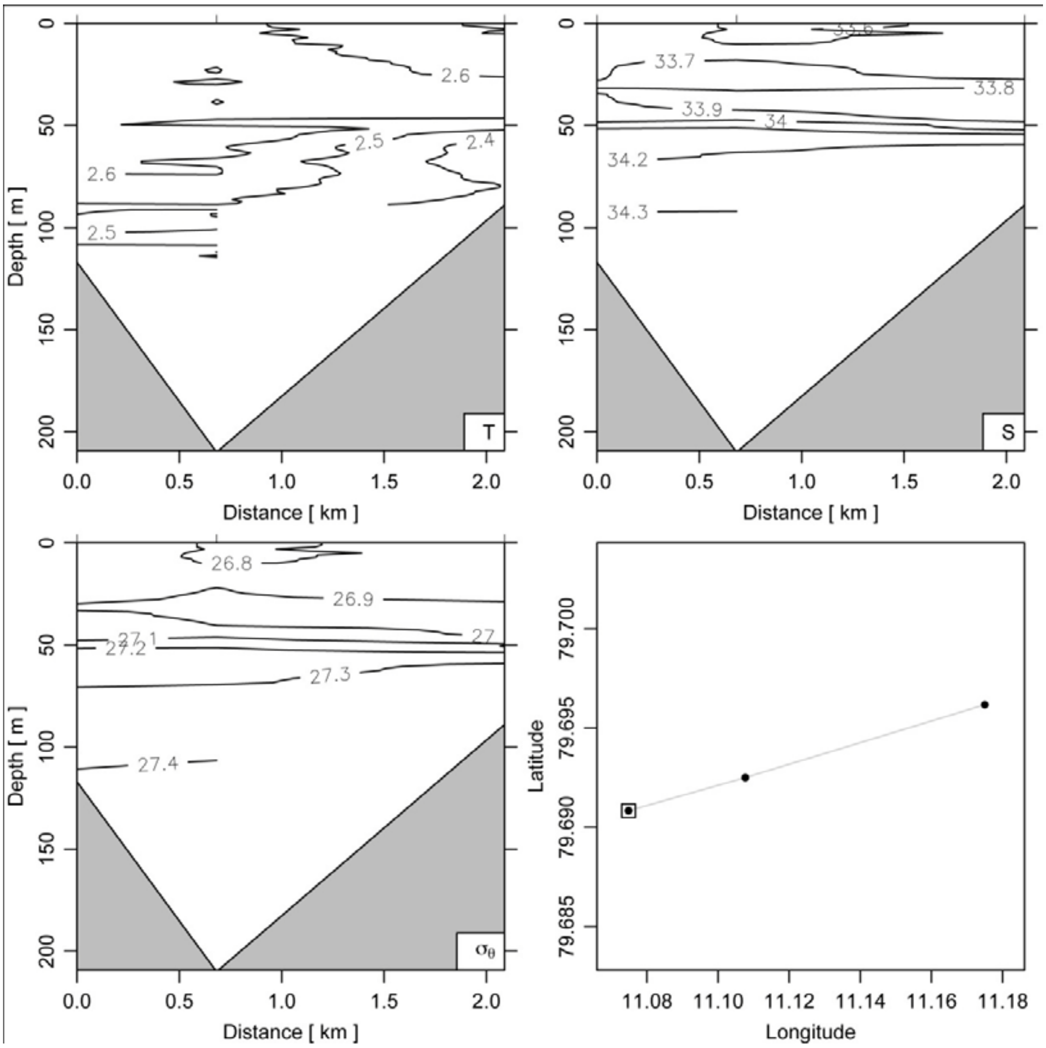
Appendix XIV:

CTD data from Smeerenburgfjord, 3 transects

North:

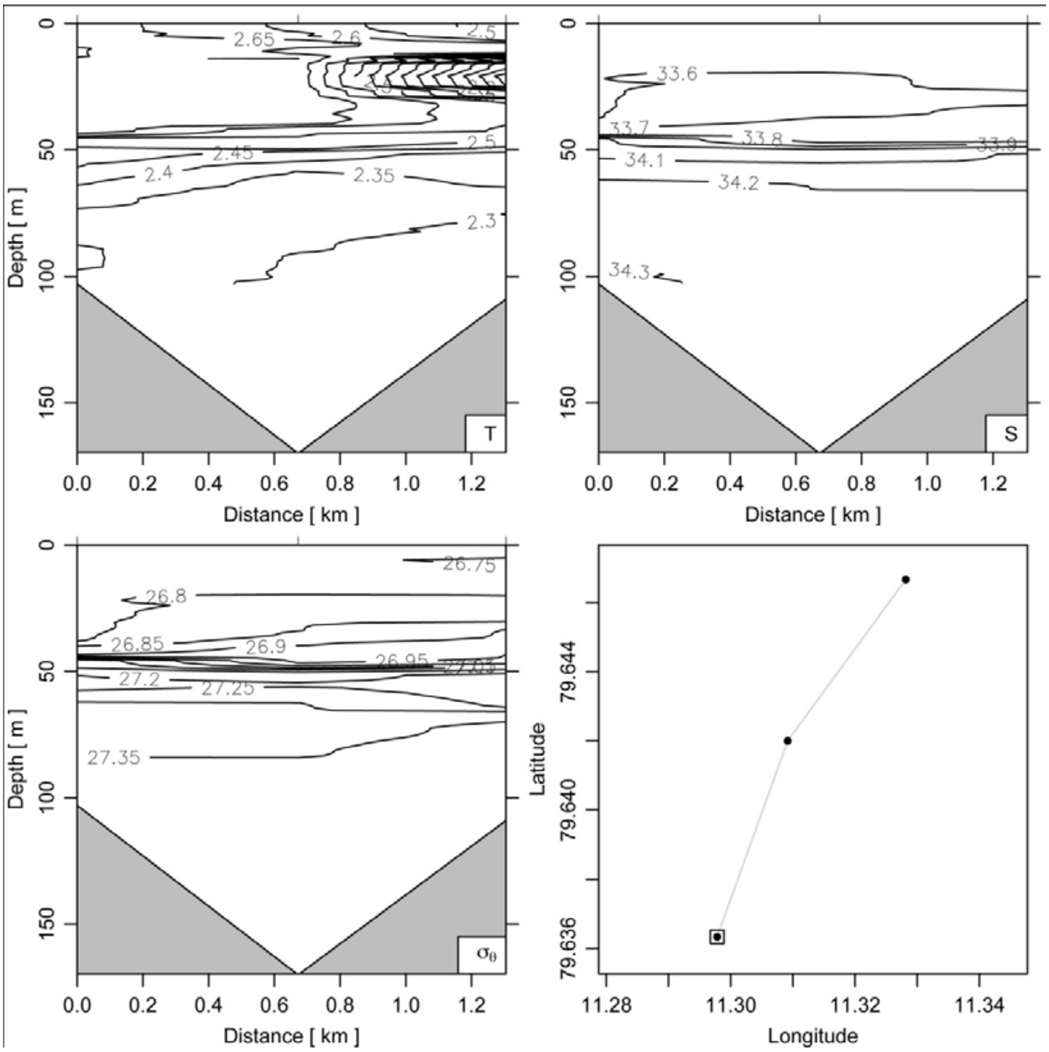


Middle:


2.6
2.5
2.4
2.6
2.5
T
Depth [m]
Distance [km]
33.6
33.7
33.8
33.9
34
34.2
34.3
S
26.8
26.9
27
27.1
27.2
27.3
27.4
σ_θ
0
50
100
150
200
0.0
0.5
1.0
1.5
2.0
Latitude
Longitude
79.700
79.695
79.690
79.685
11.08
11.10
11.12
11.14
11.16
11.18


NORTH
MIDDLE
Monitoring Station
SOUTH

South:


T
S
σθ
Depth [m]
Distance [km]
Latitude
Longitude
2.65
2.6
2.5
2.45
2.4
2.35
2.3
33.6
33.7
33.8
33.9
34.1
34.2
34.3
26.75
26.8
26.85
26.9
26.95
27.05
27.2
27.25
27.35
0
50
100
150
0.0
0.2
0.4
0.6
0.8
1.0
1.2
79.636
79.640
79.644
11.28
11.30
11.32
11.34


NORTH
MIDDLE
Monitoring Station
SOUTH

Appendix XV:

Selected photographs from years in 1980, 1990 and 2000.