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Recolonization and succession of a subtidal hard-bottom epibenthic community in Smeerenburgfjorden, NW Svalbard.

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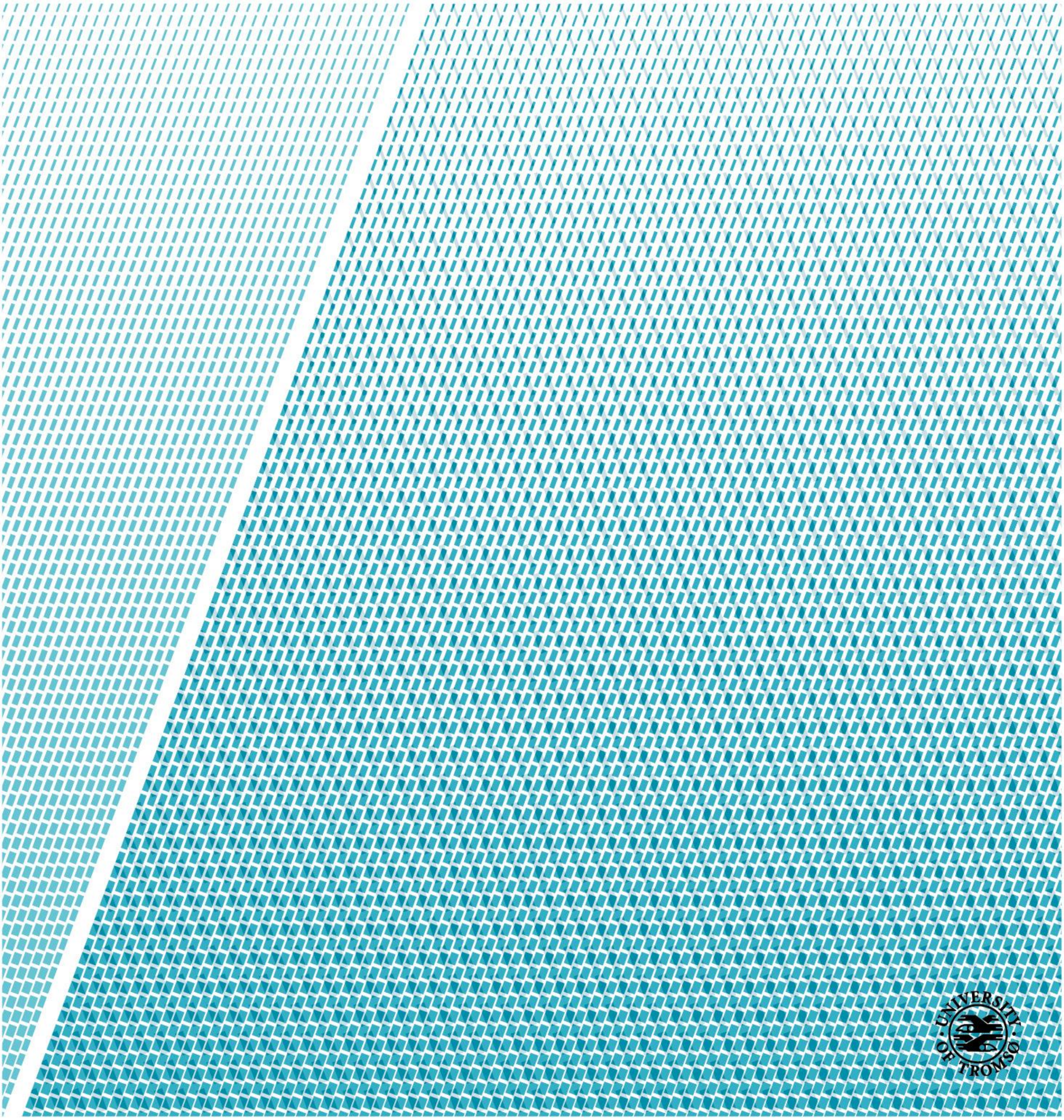

Abstract

Rapid changes to the physical environment of Arctic marine systems in recent years impact the structure and function of benthic ecosystems. Exploring the resilience of these systems to perturbations requires a solid understanding of key ecological processes and must be conducted over appropriate time scales due to the slow growth and recruitment of many Arctic benthic organisms. This study addresses the successional pattern of a hard-bottom benthic community in Smeerenburgfjorden (NW Svalbard) after a perturbation and the functional traits involved in the different stages of recolonization. Spanning nearly four decades, the time series was initiated in 1980 by clearing the substrate free of organisms on a vertical rock wall at 15 meters depth, and the site was subsequently photographed annually by scuba divers. The structure of the ecosystem was investigated by estimating the abundance (solitary taxa) and percentage cover (colonial taxa and macroalgae) of the benthic organisms from the images, whereas the ecological functioning of the system was examined via functional traits analysis based on literature sources. Single taxa showed different return rates and fluctuating abundance and cover throughout the time series. Hydrozoans and mobile mollusk grazers *Tonicella* spp. and *Margarites* spp. appeared in the early recolonization stage, whereas late-successional taxa included ascidians, sponges, barnacles, and the bivalve *Hiatella arctica*. A climate-driven foliose macroalgae takeover was observed in the year 2000, in conjunction with a reorganization in the invertebrate community structure. Recovery rate at community level following the clearing confirms previous observations of slow recolonization in polar benthic systems. It took ten years for the cleared substrate to be covered by living organisms comparable to the control area, and the convergence of the community compositions of cleared and control transects took more than two decades. The community-weighted mean traits displayed a decrease in body size and longevity in response to the clearance manipulation, and a small increase in mobility and grazing and predatory feeding habits. This study provides insights into the succession and recolonization of Arctic hard-bottom benthic communities after a perturbation and their implications for ecosystem functioning, important knowledge at a time of rapid change and increasing borealization of high-latitude ecosystems.

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1 Introduction

Polar marine ecosystems are facing changes to their physical environment at an unprecedented rate due to anthropogenic climate change. Temperatures in the Arctic are increasing at up to three times the global average, resulting in rapidly retreating sea ice and increased freshwater discharge from thawing glaciers, which leads to altered light regimes in the water column (Kortsch et al., 2012, Krause-Jensen and Duarte, 2014, Wassmann et al., 2011). On the Westcoast of Svalbard, also altered ocean currents advect warm salty water northwards (Renaud et al., 2015), and all of these factors have major implications for marine communities. These include for example a poleward shift in the biogeographic range of cold-temperate species (Frainer et al., 2017, Grebmeier et al., 2006, Krause-Jensen and Duarte, 2014), a prolonged productive season (Paar et al., 2016), and altered ecological interactions (Molis et al., in press). Drastic changes in benthic community structure caused by climate change have already been documented in the Arctic (Bartsch et al., 2016, Jueterbock et al., 2013, Kortsch et al., 2012, Wassmann et al., 2011).

Benthos, i.e. the community living in or on the seabed, comprise over 90% of the Arctic marine fauna (Renaud et al., 2015), and are often characterized by high biomass in areas of high pelagic production due to the generally tight benthic-pelagic coupling (Cochrane et al., 2009, Iken et al., 2010). Arctic coastal hard-bottom habitats are dominated by encrusting coralline and canopy-forming macroalgae, and as ecosystem engineers, the algae stimulate biodiversity, provide habitat, shelter, and food to higher trophic levels (Krause-Jensen and Duarte, 2014). These systems host a diverse suite of invertebrates (Gulliksen and Svensen, 2004), including sponges, ascidians, bryozoans, cnidarians, as well as several taxa of crustaceans, molluscs, polychaetes, and echinoderms (Beuchel and Gulliksen, 2008, Palerud et al., 2004, Voronkov et al., 2016), but more extensive knowledge on the structure and dynamics of hard-bottom habitats is yet to be established (Voronkov et al., 2016).

Studies assessing temporal variability in community structure must be undertaken at appropriate time-scales, particularly considering the high longevity and slow growth of many resident invertebrates (Beuchel et al., 2006). Here, long-term time-series are an essential but often underfunded tool. The few existing long-term studies indicate recent drastic reorganization in the structure of Arctic benthos (Bartsch et al., 2016, Beuchel and Gulliksen, 2008, Kortsch et al., 2012, Weslawski et al., 2010), further stressing the need for such baseline studies. Kortsch *et al.* (2012) found a sudden shift in community structure characterized by an eightfold and fivefold increase in macroalgal cover in Smeerenburgfjorden and Kongsfjorden, respectively. This regime shift, here defined as a sudden shift between alternate states of a community (Deyoung et al., 2008), was associated with simultaneous changes in benthic invertebrate community structure and was linked to altered light regime caused by increasing temperatures and associated number of ice-free days (Kortsch et al., 2012). Other long-term studies have found an increase in kelp biomass and a shift in the distribution of kelp to shallower depths on hard-bottom in Kongsfjorden, probably associated with reduced disturbance from ice-scouring, an extended ice-free period, and increased turbidity (Bartsch et al., 2016). This upwards trend of macroalgae was paralleled by a tenfold increase in biomass and production of macrozoobenthos in the upper sublittoral (Paar et al., 2016). This finding is in line with results from a study in Hornsund and Sørkappland, Svalbard, which also found an upwards shift in macroalgae and associated benthos in the intertidal, as well as a retreat of cold-water arctic species (Weslawski et al., 2010). These recent observations highlight the need for timeseries studies on both structure and function of Arctic benthos that span over several decades (Wassmann et al., 2011).

Succession is the observed change in a community over time following a perturbation that creates available substrata (Connell and Slatyer, 1977) and can be classified as either primary or secondary, depending on whether the substrate was previously inhabited. *Primary succession* is the process following a disturbance that made a previously uninhabitable area available for colonization, and a *secondary succession* is one where the area becomes available because the disturbance has eradicated the previous inhabitants (Connell and Slatyer, 1977). Near-shore polar benthic communities are thought to be among the most disturbed marine environments globally, with wave action, currents, periodic salinity fluctuations and close to freezing temperatures, and most importantly the influence of ice constantly putting pressure on these systems (Barnes, 1999). Succession of Arctic hard-bottom ecosystems is nevertheless poorly understood (Meyer et al., 2017), and recolonization appears to occur at much slower rates here compared to those of lower latitudes (Molis et al., in press). These habitats are anticipated to expand in the future when retreating glaciers and reduced ice-scour provide new areas for colonization (Krause-Jensen and Duarte, 2014, Paar et al., 2016), so it is crucial to gain insights into the dynamics of succession.

Three different models are often used to describe the sequence of succession by early and late colonizers: the facilitation, inhibition, and tolerance models (Connell and Slatyer, 1977). In the facilitation model, early colonizers modify the environment in a way that facilitates colonization by later-succession species. In contrast, the inhibition model states that late colonists are inhibited by early colonists until space/resources have been released. According to the tolerance model, the modifications of the pioneers neither facilitate nor inhibit colonization of later colonists. Instead, the tolerance model assumes that late-succession species either simply arrived later or were present but grew more slowly, and that the sequence in which species appear is determined by their life-history characteristics (Connell and Slatyer, 1977).

Successful recruitment is the first step in colonization of newly exposed substrata and early colonists are often characterized by fast-growing poor competitors whereas slow-growing strong competitors dominate in later stages (Meyer et al., 2017). These two types of organisms can also be termed r-strategists or opportunists and k-strategists, respectively (Jablonski and Lutz, 1983). This categorization suggests that recovery time of a system following a perturbation inherently depends on several functional traits of organisms (Beuchel and Gulliksen, 2008, Molis et al., in press). A functional trait is defined in Degen et al. (2018) as a “component of an organism’s phenotype that influence *ecosystem processes* and its response to environmental factors”. Fast-growing organisms with planktonic life stages may for example promote colonization more readily than slow-growing organisms with a full benthic life cycle (Meyer et al., 2017, Renaud et al., 2015). Adult traits like mobility and feeding habit are also important since mobile taxa often migrate to disturbed areas to graze on newly established recruits (Beuchel and Gulliksen, 2008). In general, recruitment and recolonization appear to occur at very slow rates in the Arctic (Beuchel and Gulliksen, 2008, Konar, 2007, Molis et al., in press) and must preferably be studied over timescales exceeding the longest living occupants in the community.

The main aim of this thesis is to investigate the secondary succession and ecosystem function of the benthic community in Smeerenburgfjorden, a shallow rocky fjord-like passage in Svalbard, over a 37-year period. The long-term data from the manipulation study, initiated in 1980 by clearing a near-shore vertical wall free of organisms, were obtained from non-invasive, photographic samples taken annually at the same site. I combined taxonomic and functional traits approaches to address the implications of changes in community structure for the functioning of the ecosystem, given the strong link between ecosystem processes and functional traits (Hussin et al., 2012, Krumhansl et al., 2016). The thesis addresses the following questions about Arctic benthos;

1) What is the successional pattern in a cleared rocky epibenthic community, and when is the state of the control community reached?

2) Which functional traits are involved in the different stages of recolonization and succession of the community following a perturbation?

2 Methods

2.1 Site description

Smeerenburgfjorden is a glacial fjord located in the northwestern Svalbard archipelago (Figure 1). This part of Svalbard is influenced by the West Spitsbergen Current, which advects warm saline water northwards as an extension of the North Atlantic Current (Svendsen et al., 2002). The time series site is located at 79°41.33'N, 11°04.00'E, approximately 50 meters from the coast off Danskøya in the outer part of Smeerenburgfjorden (Figure 1). The fjord has three openings which in fact makes it a sound but given the name, the term fjord will be used in this thesis. Smeerenburgfjorden has an inflow of coastal water in the western part, often creating strong currents at the monitoring site. The fjord has three shallow sills at approximately 10 m, 20 m, and 50 m, and a maximum depth of approximately 220m at its deepest (Kortsch, 2010). Ice cover in winter and glacial run-off in summer influence light regime and sedimentation in the water column.

No long-term hydrographic monitoring has been conducted in Smeerenburgfjorden. Satellite-derived data on sea-surface temperature and number of ice-free days obtained from the NW Svalbard region showed an increase of 0.5°C from 1980-2010 and 3.3 days per year over the same period (Kortsch et al., 2012).

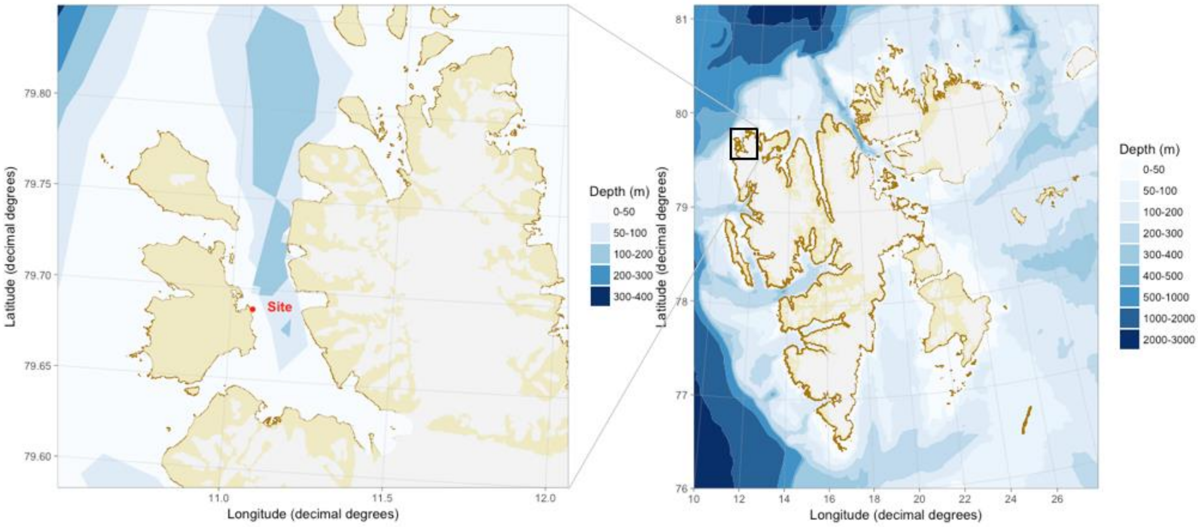


Figure 1. Map of Smeerenburgfjorden and the Svalbard archipelago.

The underwater monitoring station is positioned on a vertical rock wall at 15 meters depth (+/-0.5m due to changes in tide). Above the sampling station is a plateau at 6-8 meters, followed by a vertical drop to another plateau ~17 meters, after which the bottom drops to 40-50 meters. A belt of macroalgae was present on the 6-8 meters plateau with decreasing density with depth at the time of sampling in June

2017 (pers. dive obs.). The top three meters of the water column had a high content of particles at the time of sampling in June 2017, though the underlying water masses where less turbid.

2.2 Experimental design and photographic sampling

The experimental design was specified in 1980, by establishing a permanent underwater station with two rows of five adjacent 50cm x 50cm quadrats. In addition, an identical design was also applied in Kongsfjorden (Beuchel and Gulliksen, 2008), Isfjorden, and on mainland Norway (MD reports on Svalbard and mainland), which allow broader generalization of results if compared.

The monitoring site is marked with bolts drilled in to the bedrock. A metal rod is attached to each bolt where a camera fitted on a 50cm x 50cm metal frame fits, ensuring the exact same areas are sampled each year by moving the camera rig along a fixed set of quadrats. The five lower quadrats where scraped clear of organisms with various tools, and the five upper quadrats were left untouched to serve as controls (Figure 2). The five manipulated plots were photographed by SCUBA divers before and after the clearing of substrate manipulation, and all plots were subsequently photographed every year in August/September. Exceptions to this systematic sampling procedure were in 2014 and 2016 in which no sampling was undertaken, and in 2017 where the images were taken in June instead of autumn.

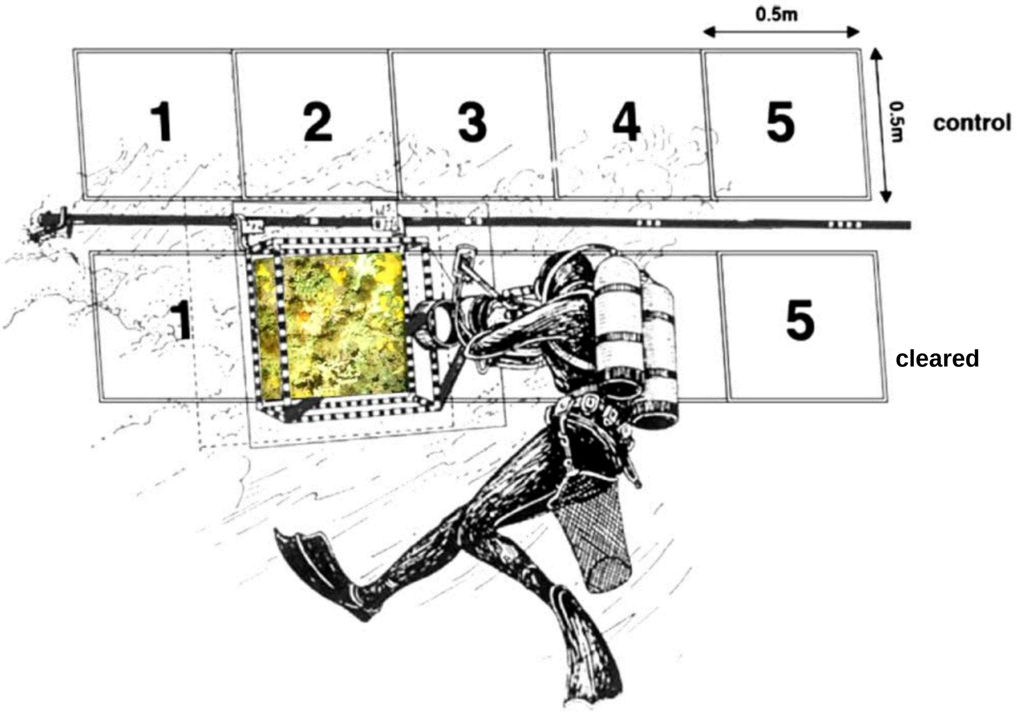


Figure 2. Experimental and sampling design redrawn from Lundälv (1971) in Beuchel et al. (2008). The bottom five quadrats were scraped free of organisms in 1980 and the top five left to serve as controls.

Several camera systems were used over the course of the time series. From year 1980 to 2003 an analogue Hasselblad Super Wide Camera with a Biogon 38 mm lens and a correction lens was used in a Hasselblad underwater casing with a Zeiss corrective glass port. From 2004 to 2013, a digital Nikon D100 6-mpx with a Nikkor 14mm lens F/2.8 AF-D was used, and this was replaced in 2015 by a Nikon D750 full-frame with a 20mm lens and two external Sea and Sea YS-D2 flashes.

2.3 Image analysis and species identification

Images were saved in variable resolutions throughout the time series. Analogue images from year 1980-2003 and digital images in 2004 were saved as ~6 mega pixels TIF files, whereas images from 2006-2013 where only available as ~2.5 mega pixels JPG files. From 2015 the resolution was strongly improved as the images were available as ~9 mega pixel NEF files.

A total of 109 images were analyzed in the present study, consisting of five images from every second year (1980-2012 + 2013 +2015 +2017), and four additional images from 1980 (one image missing) before the clearing treatment was applied as well as five images of the control plots in 2017. The analysis was restricted to images from every other year due to the time-consuming nature of image analysis and for comparability with the control quadrats. This seemed reasonable given the generally slow rate of recolonization in Arctic hard-bottom communities (Beuchel and Gulliksen, 2008, Konar, 2007). All images were renamed as a random number between 1 and 109 and randomized prior to the image analysis in order to minimize analyzer bias.

The remaining images of the control quadrats were analyzed by former UiT master students Susanne Kortsch (year 1980-2010) (Kortsch, 2010) and Carl Ballantine (years 2012 + 2013 + 2015). Image analysis was performed in Adobe Photoshop CC 2017 after the semi-automated method developed by (Beuchel et al., 2010). This method quantifies the abundance and area covered by each taxonomic group by utilizing different selection tools. First, the area of each image is calibrated to the original size of the frame (50cm x 50cm), allowing accurate measurements. Next, images are processed by adjusting saturation, hue, brightness, contrast, high-pass filter etc. when needed to correct images with lower resolution and over or underexposed areas. Each taxon is then identified and assigned a specific RGB color until the entire image is color-coded (Figure 3) and the abundance (individuals per image) of solitary organisms and cover (cm^2 per image) of colonial organisms exported as a csv file. For a more detailed description of the image analysis, see Beuchel et al. (2010).

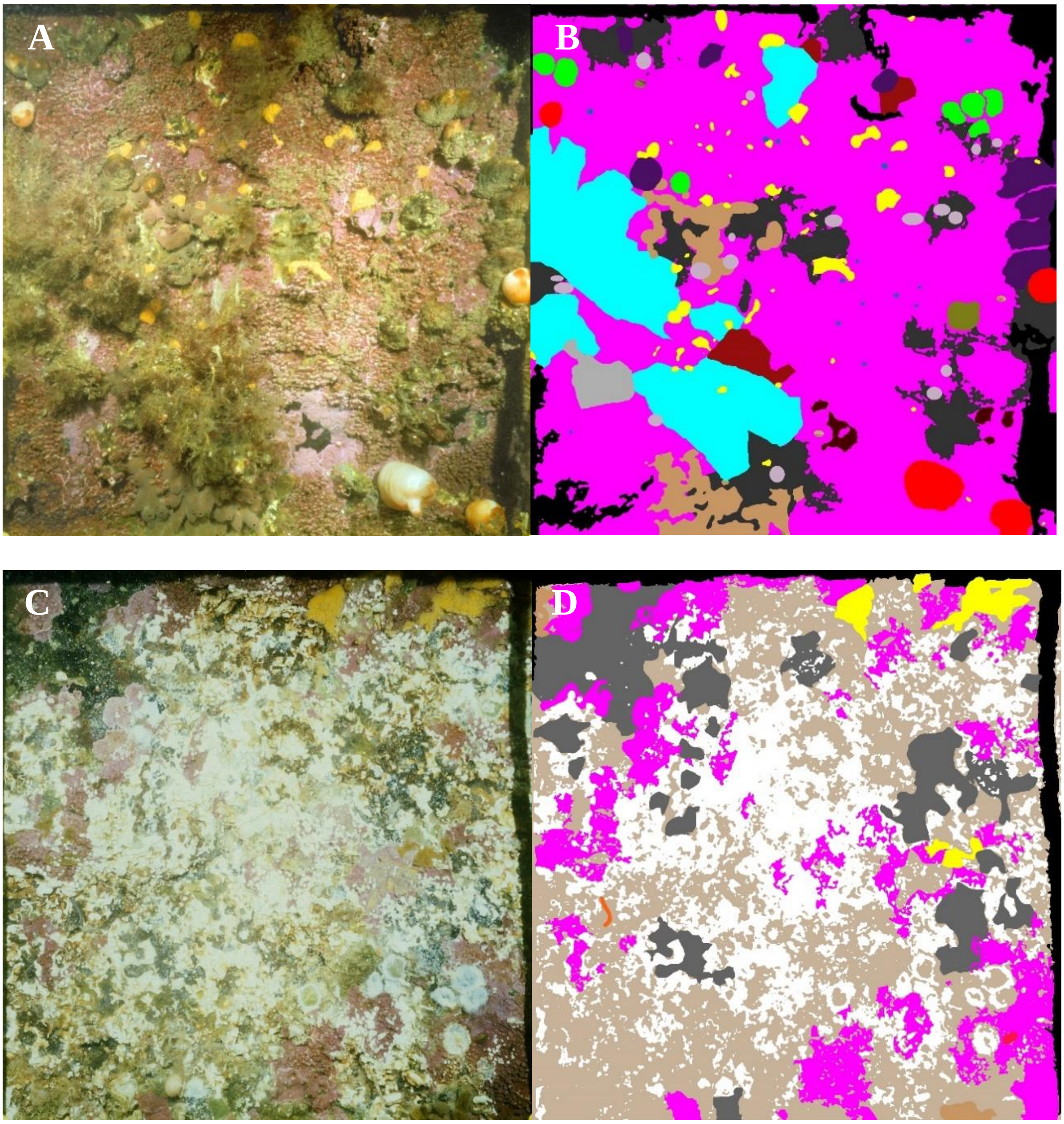


Figure 3 A-D. Images from 1980 before and after image analysis. Control quadrat 3 before (A) and after (B) image analysis. Cleared quadrat 3 after the clearance-of-substrate manipulation (C) and after image analysis (D).

Identification of organisms was performed to the highest possible taxonomic resolution, following a list of taxa provided from the analysis of the control plots (Kortsch et al., 2012). Calibration in taxonomic identification was performed in training sessions with MSc. Frank Beuchel, Dr. Susanne Kortsch, and MSc. Carl Ballentine. In addition, expert opinion was sought when needed from Prof. Bjørn Gulliksen and Prof. Bodil Bluhm. Some difference in identification between analyzers was detected and difficulties in differentiating between the ascidians *Dendrodoa aggregata* and *Styela* spp., the different crabs, and ophiuroids from the images led to the decision of these taxa being pooled in to the family Styelidae, the infraorder Brachyura, and the class Ophiuroidea, respectively. Assemblages of two or three different taxa were specified when the quantitative assessment of component taxa was impossible.

These include assemblages of algae and hydrozoans, algae and bryozoans, hydrozoans and bryozoans, and lastly algae, hydrozoans, and bryozoans. See Appendix 1 for a list of all taxa identified in the present study.

Physical identification of benthic invertebrates and macroalgae from dredge and trawl samples in Smeerenburgfjorden was conducted during the AB-321 Ecology of Arctic Marine Benthos cruise with R/V Helmar Hanssen in August 2017. Here I learnt that differentiating between *Lebbeus polaris*, *Eualus* sp., and *Spironthocaris* sp. in images is practically impossible, so these were pooled to the paraphyletic group Natantia and will be referred as such. In addition, personal observation of the organisms on site during photographic sampling in June 2017 further confirmed the taxonomic inventory of the site. All names where checked and standardized to the currently accepted taxonomy with the World Register of Marine Species (WoRMS) (Horton et al., 2018).

2.4 Data analysis

The five images of the control and the five of the cleared quadrats from each year were pooled and treated as two transects due to the autocorrelation in space. Abundances of solitary taxa were calculated as individuals per m^2 and cover of colonial organisms as percentage cover in the univariate analyses and cm^2/m^2 in the multivariate analyses. Macroalgae were included in the colonial category for practical reasons and taxa which occurred in less than 1% of the samples were excluded. Unidentified and shaded areas were subtracted from the total area.

All data analyses and graphical illustrations were performed in R studio (Team 2017). Maps were created with the “PlotSvalbard” package (Vihtakari, 2017), multivariate analyses with the “ca” package (Nenadic and Greenacre, 2007) and “vegan” package (Oksanen et al., 2017).

2.4.1 Data analysis for objective 1

What is the successional pattern in a cleared rocky benthic community in Smeerenburgfjorden, and when is the state of the control community reached?

The successional pattern was investigated graphically by displaying the most conspicuous taxa over time, and the differences between the abundance/cover of those taxa in the cleared and control areas where quantified to assess when the two converged. These differences were calculated by subtracting the abundance/cover of the taxa in the control area from the cleared, resulting in a positive value if the cleared transect contained more of the given taxa, and negative if the control transect did.

The succession and potential convergence of the entire community in each of the transects were explored with a correspondence analysis (CA). This multivariate, indirect ordination method relies on chi-squared distances between samples (see equation below).

$$x_{x,y} = \sqrt{\sum_{j=1}^{J} \frac{1}{c_j}(x_j - y_j)^2}$$

Where $\chi_{x,y}$ is the chi-square distance between the profiles of two years x and y, c_j is the proportion of the j-th species in the data set (Greenacre and Primicerio, 2013). An underlying assumption of CA is that the data is measured on the same scale. This was not the case in the present study, as the data consisted of both abundance and cover, but the problem was overcome by weighting the two tables of abundance and cover data differently to balance their inertia.

2.4.2 Data analysis for objective 2

Which functional traits are involved in the different stages of recolonization and succession of the community after a perturbation?

The first and important step in a functional traits analysis is choosing the appropriate traits capable of addressing the research question. The first six traits in Table 1 were coded by Kortsch (unpublished) (Appendix 2), whereas I added an additional three traits which might be relevant for recolonization (Table 1). Information on trait modalities exhibited by each taxon was gathered from databases, literature searches and expert consultation (see Table 1 for references) and if information on a trait of a given taxon was unavailable, the trait of the closest related taxon was coded. Each trait contained different modalities and if a certain trait category was expressed by a species it was coded 1, and if a trait was not expressed 0, in addition, species displaying more than one modality within a trait was coded with multiple 1's. This is similar to the commonly used "fuzzy coding" procedure (Bremner et al., 2006) except traits were coded as presence/absence. To illustrate which taxa exhibited similar traits, a complete linkage dendrogram was constructed.

The community weighted mean (CWM) trait approach was employed to assess which traits characterized the different stages of recolonization by constructing an area-weighted-traits per year matrix. This approach inherently assumes that the traits of the dominant taxa will have the greatest effect on the ecosystem (Frainer et al., 2017). To overcome the challenge of defining traits for the four algae, hydrozoan, and bryozoan assemblages, these areas were divided into equal parts and added to the area of the "parent" taxa. Only the invertebrate community was considered in the traits analysis, thereby excluding all macroalgae. Autotrophic organisms are functionally very dissimilar to the invertebrate community and would in addition drive much of the observed traits analysis due to their extensive cover on all images. The relative changes in trait modalities over time were investigated with stacked barplots. For the computation, first a traits-by-taxa matrix of the most dominant taxa was compiled and analyzed with a CA to map the traits characterization of different taxa. The CWM of each sample was then calculated for the first and the second CA axis, depicting the overall change in the functional identity of the community throughout the time series.

Table 1. List of functional traits and their modalities. The traits in bold print were coded as part of this MS thesis and the other traits used in the analysis were coded by Dr. Susanne Kortsch.

Trait	Trait category	Labels
Relative adult body size	Small	Small
	Small-medium	small_medium
	Medium	medium
	Medium-large	medium_large
	Large	large
	Indeterminate	indeterminate
Living habitat	Free living	free_living
	Crevice dwelling	crewice_dwelling
	Tube dwelling	tube_dwelling
	Burrowing	burrowing
	Epi/endo zoic/phytic	epi_endozoic_phytic
	Attached	attached
Feeding mode	Surface deposit feeder	surface_deposit_feeder
	Filter/suspension feeder	filter_suspensionfeeder
	Grazer	grazer
	Opportunist/scavenger	opportunist_scavenger
	Predator	predator
Relative adult mobility	None	mob_no
	Low	mob_low
	Medium	mob_med
	High	mob_high
Sociability	Solitary	soc_sol
	Gregarious	sol_greg
	Colonial	sol_col
Longevity	1-2 years	1_2yr
	3-5 years	3_5yr
	6-10 years	6_10yr
	11-20 years	11_20yr
	>20 years	over_20yr
Egg/larval dispersal	1-10m	disp_1_10m
	10-100m	disp_10_100m
	100-1000m	disp_100-1000m
	1-10km	disp_1_10km
	>10km	disp_over_10km
Reproduction mode	Asexual	asexual
	Sexual	sexual
Development mode	Lecithotrophic	lecithotrophic
	Planktotrophic	planktotrophic

3 Results

3.1.1 Results addressing objective 1 - single-taxa succession

In this study, a total of 45 taxa from the phyla Rhodophyta, Ochrophyta, Porifera, Cnidaria, Annelida, Arthropoda, Mollusca, Bryozoa, Echinodermata, and Chordata were identified. The most common taxa were red crustose coralline algae, *Phycodrys rubens*, *Desmarestia* spp., *Haliclona* spp., Hydrozoa, *Spirorbis spirorbis*, *Balanus balanus*, Natantia, *Hiatella arctica*, *Tonicella* spp., *Margarites* spp., Bryozoa, *Dendrodoa aggregata* and *Styela* spp. (pooled to family Styelidae in the taxonomic analysis), *Halocynthia pyriformis*, and *Botryllus* spp. and trends of these taxa are depicted in the following. See Appendix 1 for a full taxonomic list and Appendix 3 for their cover and abundance.

Early colonizers in the cleared transect include sessile hydrozoans, and the solitary motile chitons and gastropods of the genus *Margarites* sp. Red coralline algae and Natantia shrimps were also present early but are not characterized as pioneers.

Polyps in the group Hydrozoa showed a rapid increase in the cleared transect following the perturbation (Figure 4.a) and displayed a high but variable cover in the first two decades. The cover was generally comparable to the control area (Figure 4.b), with the exception of year 1980 prior to the clearing, here the control community showed five-fold larger area covered by hydrozoans. The cleared area did however display a much larger area covered the algae/hydrozoan assemblage (see Appendix 3), and this assemblage was generally dominated by hydrozoans with little turfing algae.

The chitons *Tonicella* spp. were quick to invade after the substrate was cleared and were present throughout the whole study and in relatively high numbers in the 1980’s and ‘90’s (Figure 4.c). The abundance dropped in the 2000’s until a drastic increase in 2017. Chitons in the control transect fluctuated in a synchronized manner, though with approximately half of the abundance of the cleared transect in the first two decades (Figure 4.d). The snail *Margarites* spp. was not nearly as abundant as the chitons but did show an initial increase in 1982 beyond levels of the control transect and again in 1988 hereafter fluctuating in both cleared and control plots (Figure 4.e-f).

Red crustose coralline algae were not completely removed in the scraping experiment due to their strong adherence to the substrate, hence recolonized fast, covering almost half of the transect by 1982 (Figure 4.g). Succeeding this was a period with a cover of coralline algae at 40-50% over the next decade after which the algae showed a general – though variable - decrease until the two very last years of the study. The control transect showed a similar trend but had a slightly higher coralline algae cover throughout the study period (Figure 4.h), particularly in the 2000’s. Shrimp of the paraphyletic group Natantia were also present in high numbers early in the succession on the cleared transect compared to the control. They showed similar fluctuations in abundance in both control and cleared plots, though with lower numbers in the 2000’s (Figure 4 i-j).

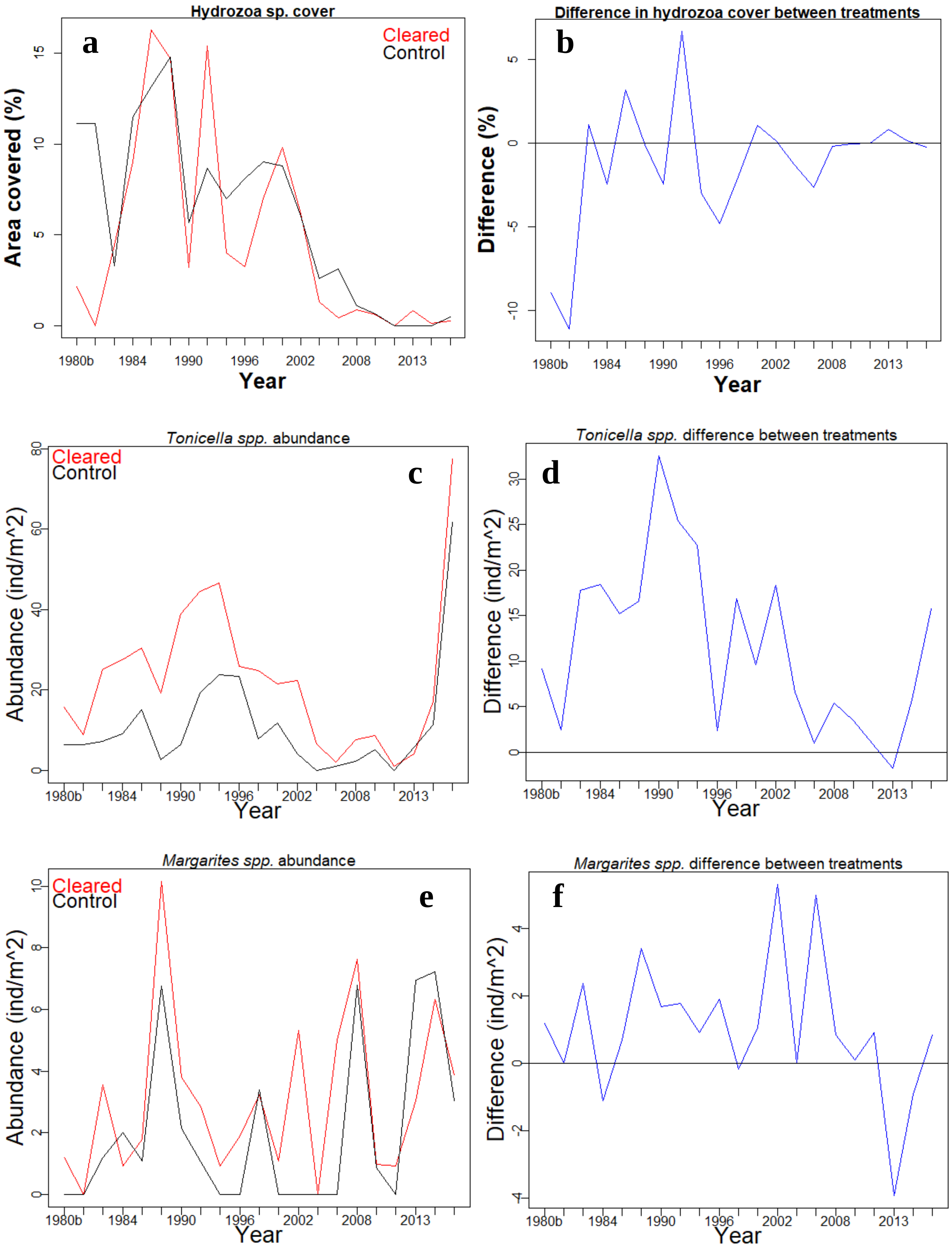
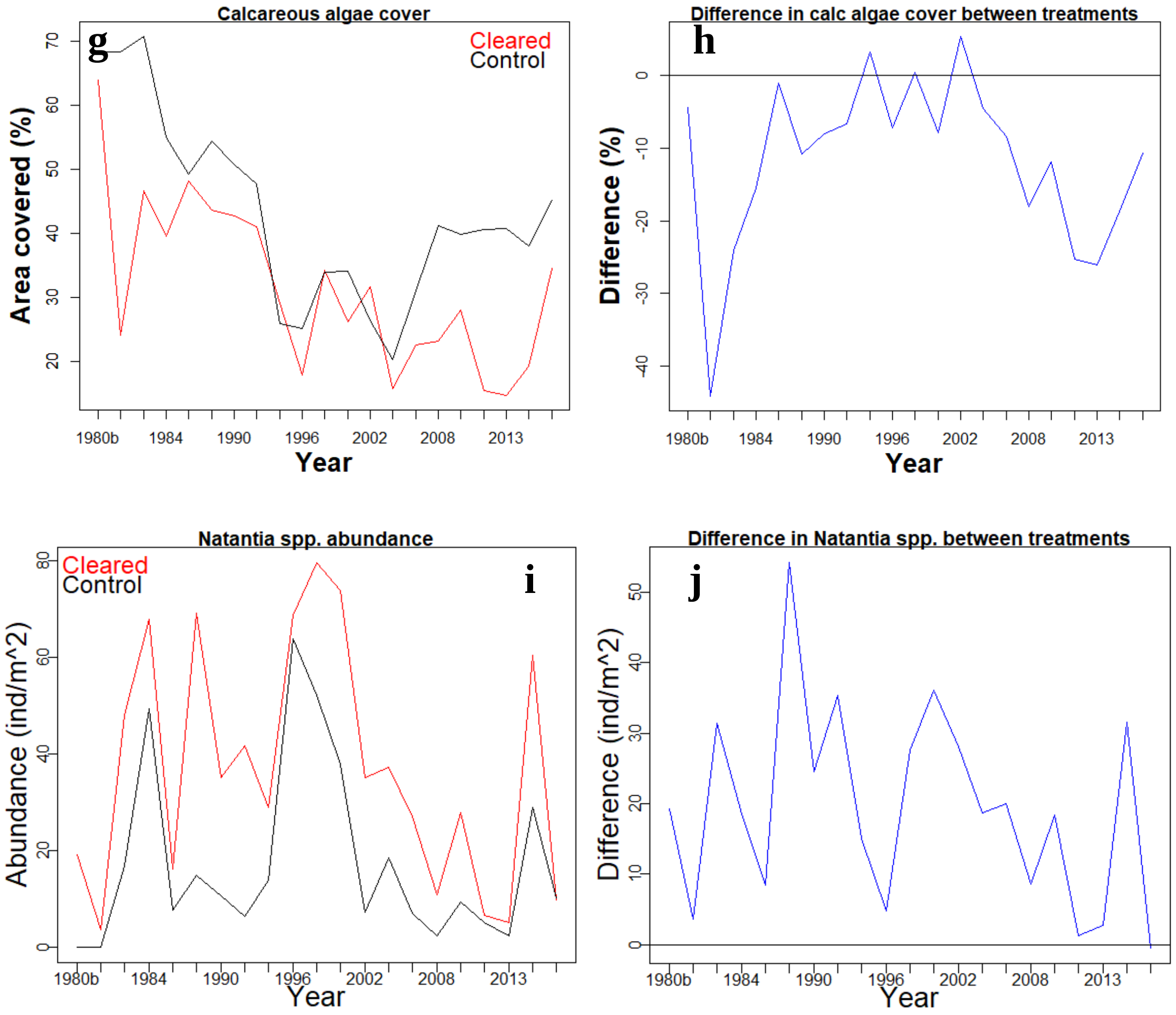


Figure 4 (continues on next pages). Early colonizers in cleared (red) and control (black) transects from 1980-2017. The first point on the x-axis (1980b) is the cover/abundance of the taxa in 1980 before the clearing and the following point is after. a. Hydrozoa cover. b. Difference between Hydrozoa cover in cleared and control transect c. *Tonicella* spp. abundance. d. Difference in *Tonicella* spp. abundance in cleared and control transect. e. *Margarites* spp. abundance. f. Difference in *Margarites* spp. abundance in cleared and control transects. g. Red crustose coralline algae cover. h. Difference in red crustose coralline algae cover in cleared and control transects. i. Natantia spp. abundance. j. Difference in Natantia spp. abundance in cleared and control transects.



Sponges, ascidians, and barnacles required a decade or more to recolonize in numbers and cover comparable to the control areas. The sponges *Haliclona* spp. reached to pre-treatment cover approximately ten years after the area was cleared and covered about a tenth of the total area in the 1990's, but then remained at a cover of about half of the control area for over a decade after this (Figure 5.a-b). The colonial ascidian *Botryllus* spp. showed greater variability, covering over 10% of the area before the area was cleared, increasing to a cover similar to pre-treatment and control cover 8 years after clearing (Figure 5.c) and essentially tracked control transect values from then on (Figure 5.d).

Solitary ascidians *Halocynthia pyriformis* and Styelidae (*Styela* spp. and *Dendrodoa aggregata*) along with *Balanus balanus* and *Hiatella arctica* recolonized particularly slowly. *H. pyriformis* were present in the cleared transect in much smaller numbers compared to the control for over 15 years, only in 2000 did this species exhibit an abundance comparable to pre-treatment and control transect (Figure 5.e-f). Styelidae were present in much lower numbers in the cleared transect compared to the control throughout the entire study. It reached about half of the pre-treatment levels in the 90's but only showed a large increase in the last two years of the time series (Figure 5.g-h). The barnacle *B. balanus* recovered slowly after the substrate was cleared, only reaching pre-treatment and control abundance approximately a decade later (Figure 5.i-j). From then on, *B. balanus* gradually declined in both transects with some fluctuations only to increase drastically in 2017. The bivalve *H. arctica* was abundant before the substrate was cleared but did not reach similar numbers until the last two years of the study (Figure 5.k-l). The control area, on the other hand, had markedly higher, though variable, abundances.

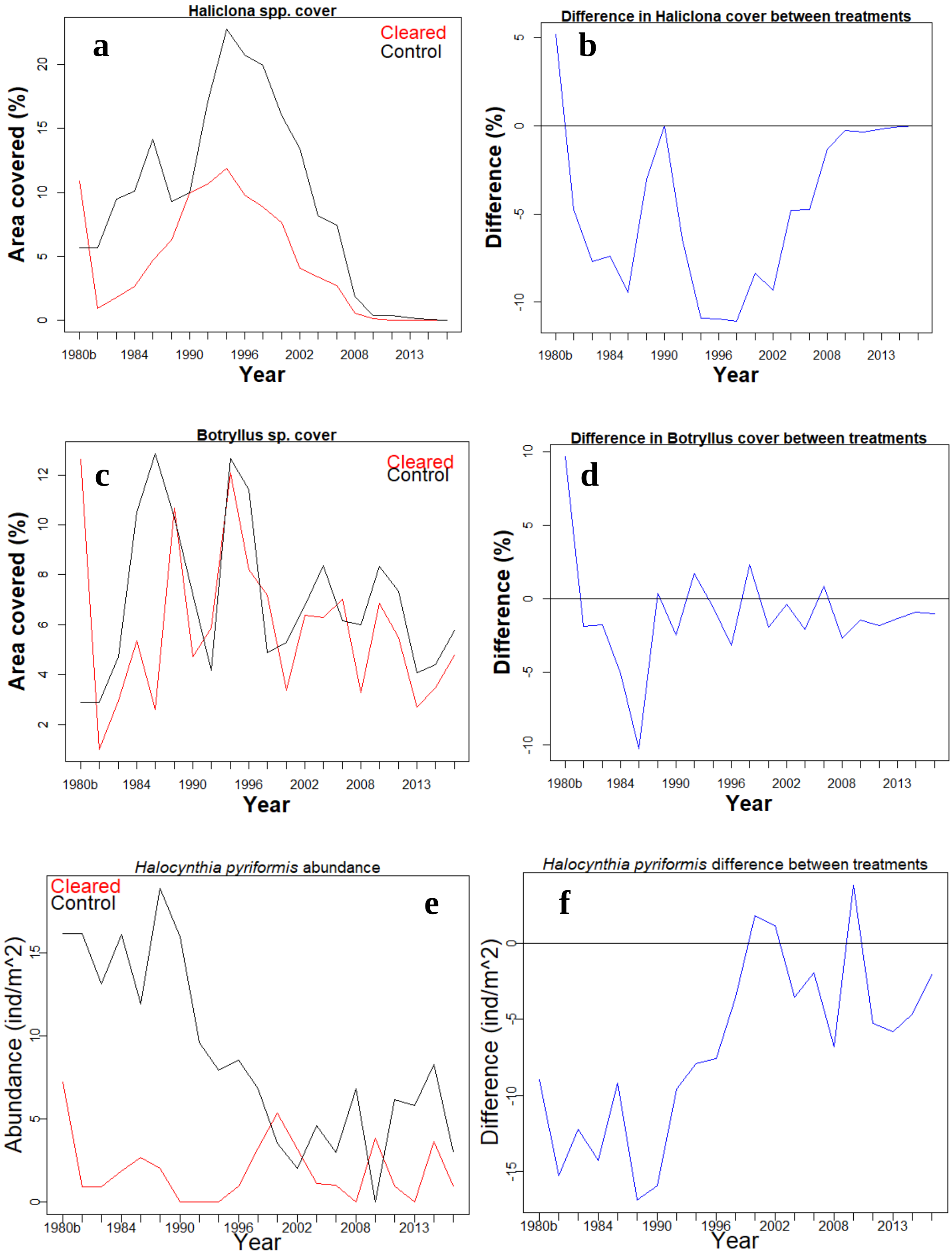
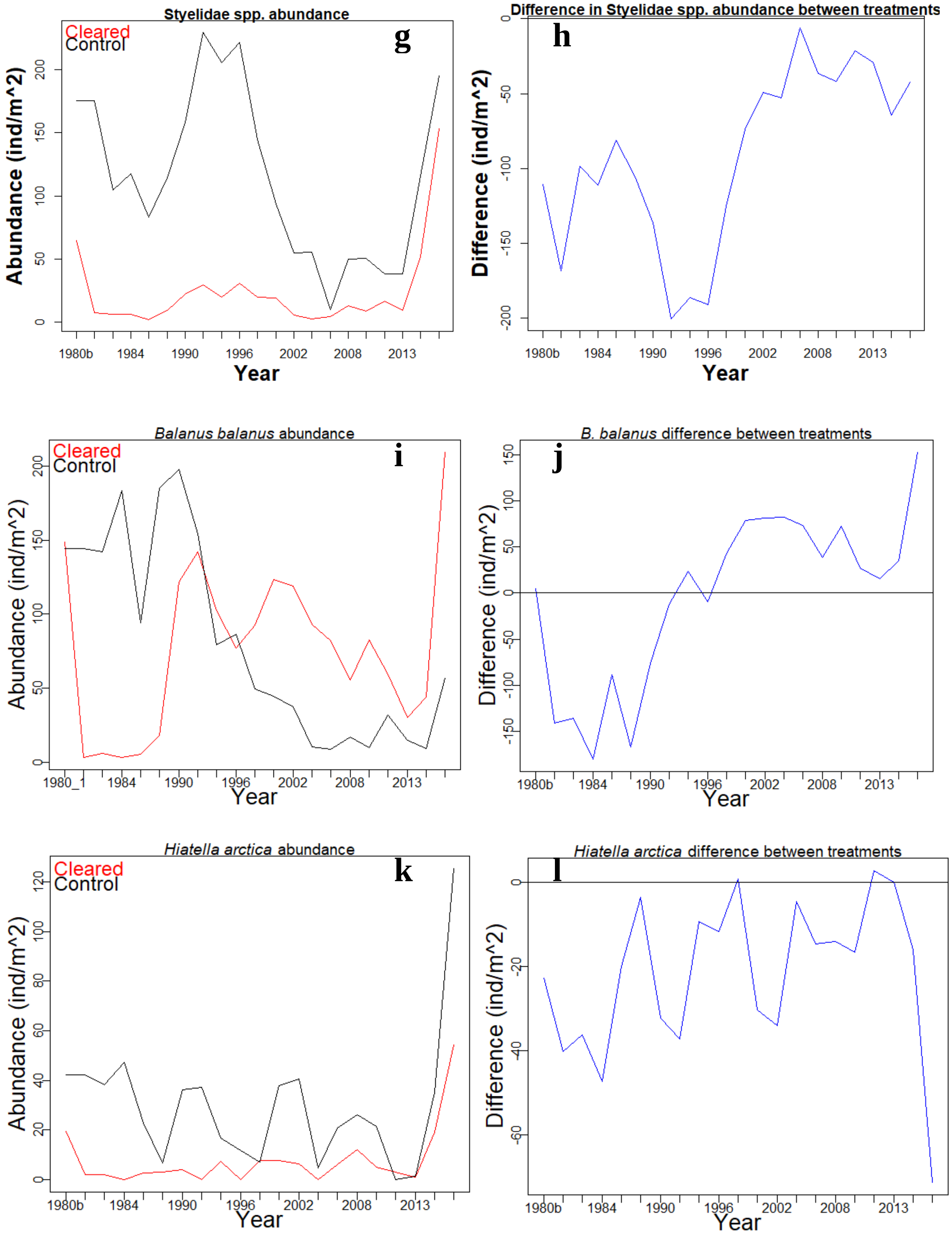


Figure 5 a-l (continues on next pages). Late colonizers in cleared (black) and control (red) transects from 1980-2017. *Haliclona* spp. cover in cleared and control transect over time (a) and the difference between the transects (b). *Botryllus* spp. cover (c) and difference (d). *H. pyriformis* abundance (e) and difference (f). Styelidae abundance (g) and difference (h). *B. balanus* abundance (g) and difference (h), and *H. arctica* abundance (k) and difference (l).



The communities in both cleared and control transects were characterized by drastic reorganizations approximately 20 years after the clearing manipulation. Abundance and cover of most taxa in the two transects had converged by then and this period will be dealt with in section 3.1.3. Convergence of the amount of available substrate i.e. cleared substrate, bedrock, and dead calcareous algae, was colonized by living organisms in the cleared transect to a degree comparable to the control community after ten years (Figure 6).

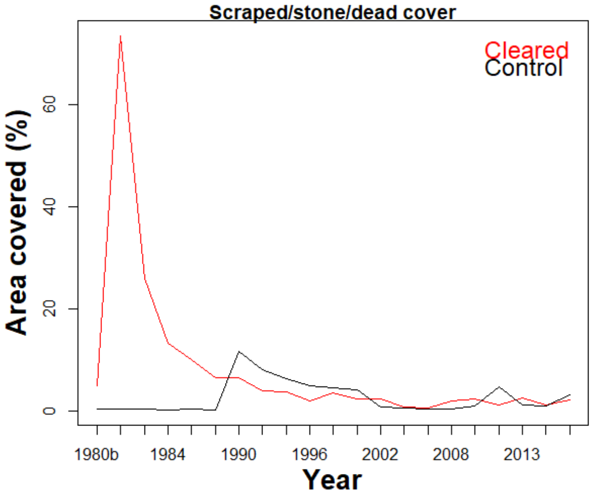


Figure 6. Cover of non-living organisms including stone/bedrock, dead calcareous algae, and scraped area.

3.1.2 Results addressing objective 1 - ecosystem succession

Similarities between the community structure of the control and cleared transects were low in the first two decades. The control communities in the first 22 years displayed a relatively similar structure, as depicted in the bottom left sector of the CA biplot (Figure 7). The community of the pre-treatment (cleared) area is also located here, confirming the similarity of the control and manipulated communities prior to the treatment. These communities are characterized by a high presence of *B. balanus*, Styelidae spp., *Haliclona* spp., and to a lesser degree the coralline algae. The cleared community was highly dissimilar during the two decades following the manipulation, with large interannual variability. The observed differences in community structure were here driven by Natantia, hydrozoans, *Tonicella* spp., and the algae/Hydrozoa assemblage. Cleared and control communities showed similar patterns and trends from year 2002 and 2004, respectively, by moving towards the right side of the biplot, a structural change driven by an increase in *P. rubens*, bryozoans, *S. spirorbis*, and to a lesser degree macroalgae excluding *P. rubens*.

A total of 62% of the variation was summarized by the first two CA dimensions, the first axis accounting for 47% of the observed variation, was associated with the climate-driven regime shift, whereas the second dimension, accounted for 15% of the variation, was related to the difference between the manipulated and control transects (i.e. clearing treatment).

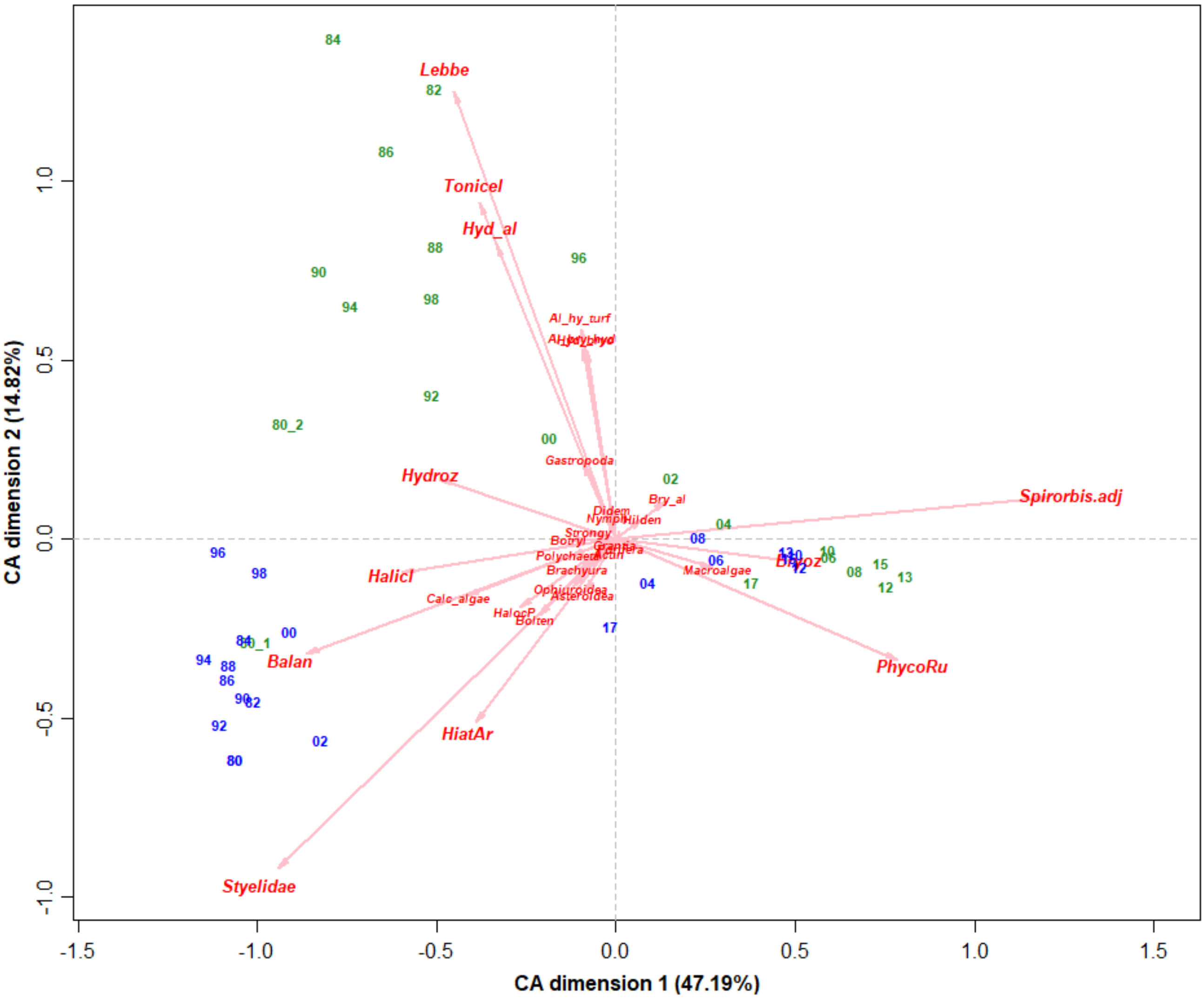


Figure 7. Correspondence analysis biplot depicting variation in community structure of cleared (green) and control (blue) transects from year 1980-2017. Red labels in large font refer to the taxonomic groups with the greatest contributions to the observed variation in community structure. 80_1 is the community of the cleared transect in year 1980 before the substrate was cleared and 80_2 after.

A drastic reorganization in the benthic community was observed in the late 1990's and early 2000's (Figure 8a-d). Taxa that had not previously been present or present only in small numbers suddenly occurred in high numbers and cover. Particularly conspicuous was the dramatic increase in macroalgae cover (Figure 9.c), primarily of the red algae *Phycodrys rubens*, and to a lesser degree the brown macrophyte *Desmarestia* spp., but also cover of bryozoans (moss animals) (Figure 8.a), and abundance of the polychaete *Spirorbis spirorbis* (Figure 8.e) increased markedly.

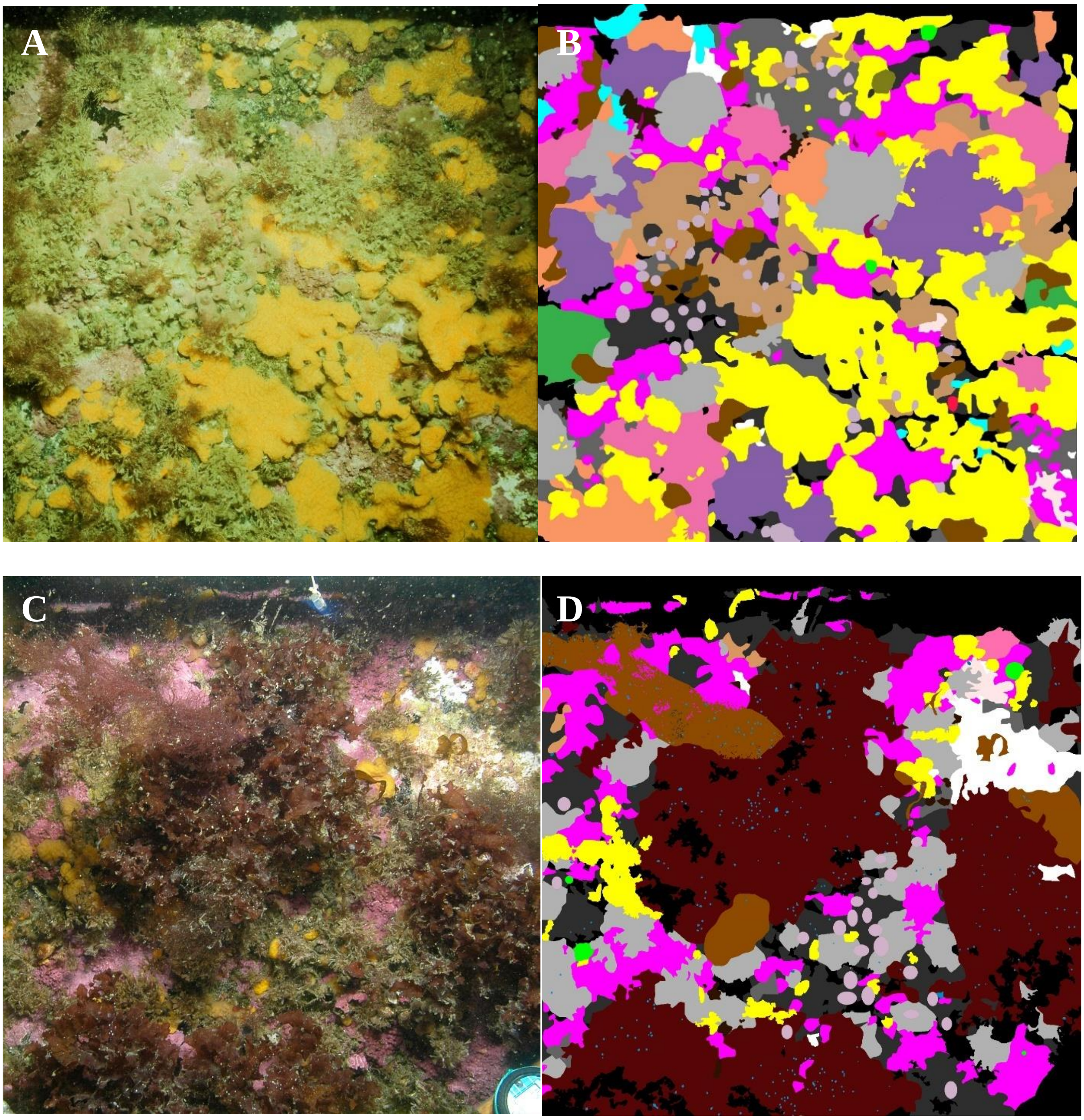
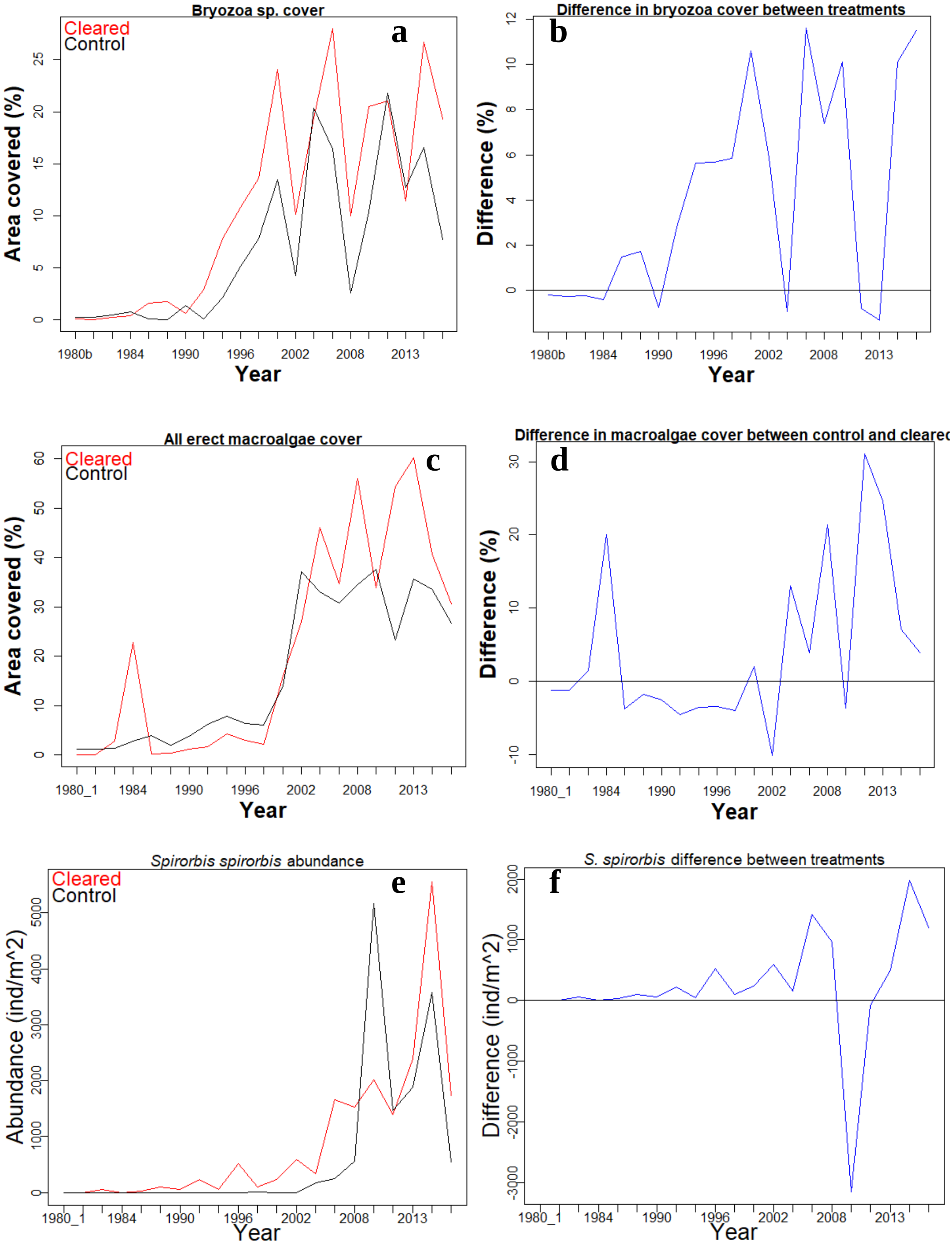


Figure 8 a-d. Community before (a-b) and after regime shift (c-d). Image 3 of the cleared community in 1994 before (a) and after the image analysis (b) is characterized by sponges and ascidians. The same image from 2008 before (c) and after (d) image analysis illustrate the large cover of *Phycodrys rubens*, *Desmarestia* spp. and bryozoans.

Bryozoans were nearly absent in the study site until the early 1990s when a 38-fold and 10-fold increase in cover occurred between 1990 and 2000 in the cleared and control transect, respectively (Figure 9a-b). Here after, the bryozoan cover fluctuated between 10 and 28% of the cleared plots and 4 and 20% of the control plots. Foliose macroalgae, largely *Phycodrys rubens* but also *Desmarestia* spp. (see Appendix 3 for cover of specific taxa), showed the most striking trend with a 23-fold increase in cover from 1998 to 2004 in the cleared transect, here after sustaining a cover of 30-60% of the area for the rest of the period (Figure 9.c). There was a spike in cover of mainly *Desmarestia* spp. in 1984 in the cleared transect, aside from this, the cover in the control transect followed a similar trend to the cleared but with slightly lower values through the 2000’s (Figure 9.d). The polychaete *Spirorbis spirorbis* was largely absent in both cleared and control transects prior to the increase macroalgae cover in where after it appeared in very high numbers in both transects though with differences in densities (Figure 9e-f).



Figures 9 a-g. Cover and abundance of taxa in cleared (red) and control areas (black) from year 2015-2017. Bryozoa cover (a) and difference between transects (b). Cover of all macroalgae (c) and difference (d). Abundance of *S. spirorbis* (e) and difference (f).

To sum up the findings of the taxonomic analysis, early-succession taxa appearing in the cleared transect were hydrozoans, *Tonicella* spp., and *Margarites* sp. to a smaller degree, also coralline algae and Natantia were present. 10 to 20 years after the clearing, sponges, ascidians, barnacles and *H. arctica* recolonized to pre-treatment and/or control area abundance/cover. In the late 1990's/early 2000's a drastic increase in bryozoans, foliose macroalgae and *S. spirorbis* was observed. The CA supported these findings and highlighted the cleared community showed high interannual variability in the first two decades. It also illustrated a more uniform composition of the control community in the first two decades, structured by barnacles, Styelidae, and *H. arctica*, where after the control community converged with the cleared.

3.2 Results addressing objective 2

Results from the literature review are presented in Table 2 and provide the trait modalities expressed by the most dominant taxa. A list of all traits is provided in Appendix 2.

Table 2. Traits and references. See Appendix 2 for remaining traits.

Taxa	**Longevity**	**Dispersal**	**Reproduction mode**	**Development mode**
Balanus balanus	6-10 & 10-20yr (Gulliksen and Svensen, 2004)	>10km (Marlin, 2006)	Sexual	Planktotrophic (Marlin, 2006)
Boltenia echinata	3-5yr (artdatabanken)	1-10m (est. from other solitary ascidians)	Sexual	Lecithotrophic (Svane and Lundälv, 1982)
Botryllus spp.	1-2yr (Marlin, 2006)	1-10m (Grosberg, 1987)	Asexual (Ali and Tamilselvi, 2016) p. 10	Lecithotrophic (Grosberg, 1987, Marlin, 2006)
Bryozoa	3-10yr (Gth)	1-100m (Mcedward, 1995)	Asexual (Zimmer and Woollacott, 1977) Sexual	Lecithotrophic (Dethier et al., 2003)
Dendrodoa aggregata	1-2yr (Gth)	1-100m (est. Gth)	Sexual & asexual	Lecithotrophic (est. from other sol. ascidians)
Didemnum albidum	1-2yr (Gth)	1-10m (Jackson, 1986)	Asexual (Ali and Tamilselvi, 2016) p.10 sexual (Gth)	Lecithotrophic (Marlin, 2006)
Grantia sp.	>20yr (est. from *Haliclona* spp.)	1-100m (Mcedward, 1995)	Sexual & asexual	Lecithotrophic (est. Porifera) (Dethier et al., 2003)
Halocynthia pyriformis	3-5yr (Svavarsson, 1990)	1-100m (est. from other ascidians)	Sexual	Lecithotrophic (Svane and Lundälv, 1982)
Henricia sp.	3-5yr (Marlin, 2006)	>10km (Marlin, 2006)	Sexual	Lecithotrophic (Gth)
Hiatella arctica	>20yr (Sejr et al., 2004)	>10km (Gth)	Sexual	Planktotrophic (Gth)
Hyas sp.	3-10yr (Gth)	>10km (Gth)	Sexual	Planktotrophic (Anger and Dawirs, 1981)
Hydrozoa	1-2yr (Gth & MarLIN, 2006)	1-100m (Gth & MarLIN, 2006)	Sexual & asexual	Lecithotrophic (Gth, MarLIN, 2006, Ruppert 2004)
Margarites	1-2yr (Arctic ocean diversity)	1-10m (est. since brooder) (Strathmann, 1990)	Sexual	Lecithotrophic (Hadfield and Strathmann, 1990)
Natantia	3-10yr (Gth, Gulliksen and Svensen, 2004)	>10km (Gth)	Sexual	Planktotrophic (Gth)
Sea spider (*Nymphon* sp.)	1-2yr (Marlin, 2006)	10-100m (Marlin, 2006)	Sexual	Planktotrophic (Marlin, 2006)
Ophiura sp.	3-10yr (Gth)	>10km (Gth)	Sexual	Planktotrophic (Gth)
Pagurus sp.	3-10yr (Gth and MarLIN, 2006)	1-10km (Gth)	Sexual	Planktotrophic (Dethier et al., 2003, Lovrich and Thatje, 2006)
Polychaet indet	NA	NA	Sexual	NA
Pteraster spp.	NA	NA	Sexual	Lecithotrophic (McEdward)
Sea anemone	>20yr (Gulliksen and Svensen, 2004)	>10km (est. from long 11-30 days larval duration) (MarLIN, 2006)	Sexual & asexual	Lecithotrophic & planktotrophic (Ruppert et al., 2003, Shick, 1991)
Spirorbis spirorbis	1-2yr (Ni et al., 2018)	1-100m (Mcedward, 1995)	Sexual	Lecithotrophic (Rouse, 2005)
Haliclona spp.	>20yr (Teixidó et al., 2011)	1-100m (Mcedward, 1995)	Sexual & asexual	Lecithotrophic (Carballo and Ávila, 2004)

Strongylocentrotus droebachiensis	>20yr (Blicher et al., 2007)	>10km (MarLIN, 2006)	Sexual	Planktotrophic (MarLIN, 2006)
Styela spp.	1-2yr (MarLIN, 2006)	1-100m (MarLIN, 2006)	Sexual & asexual	Lecithotrophic (MarLIN, 2006)
Tonicella spp.	3-5yr (est. from *Lepidochitona cinereal*) (Fish and Fish, 1989)	10-1000m (est from larval duration) (Barnes and Gonor, 1973)	Sexual	Lecithotrophic (Dethier et al., 2003)

See all web-based references in web resources section of bibliography.

Taxa that have similar functional traits are clustered together in the dendrogram (Figure 10). Three distinct clusters of taxa group together. The first cluster contains the echinoderms *Pagurus* spp., *Hyas* spp., *Henricia* sp., *Strongylocentrotus* sp., *Pteraster* spp., *Nymphon* sp., but also polychaetes and *Tonicella* spp. The second group is more heterogenous and consists of the ascidians *D. aggregata*, *Styela* spp., *Botryllus* spp., *Didemnum albidum*, the sponges *Haliclona* spp., *Grantia* sp., as well as hydrozoans, bryozoans and *S. spirorbis*. The third and last group contains *Boltenia echinata*, *H.* pyriformis, sea anemones, barnacles, *Hiatella arctica*, and Ophiura.

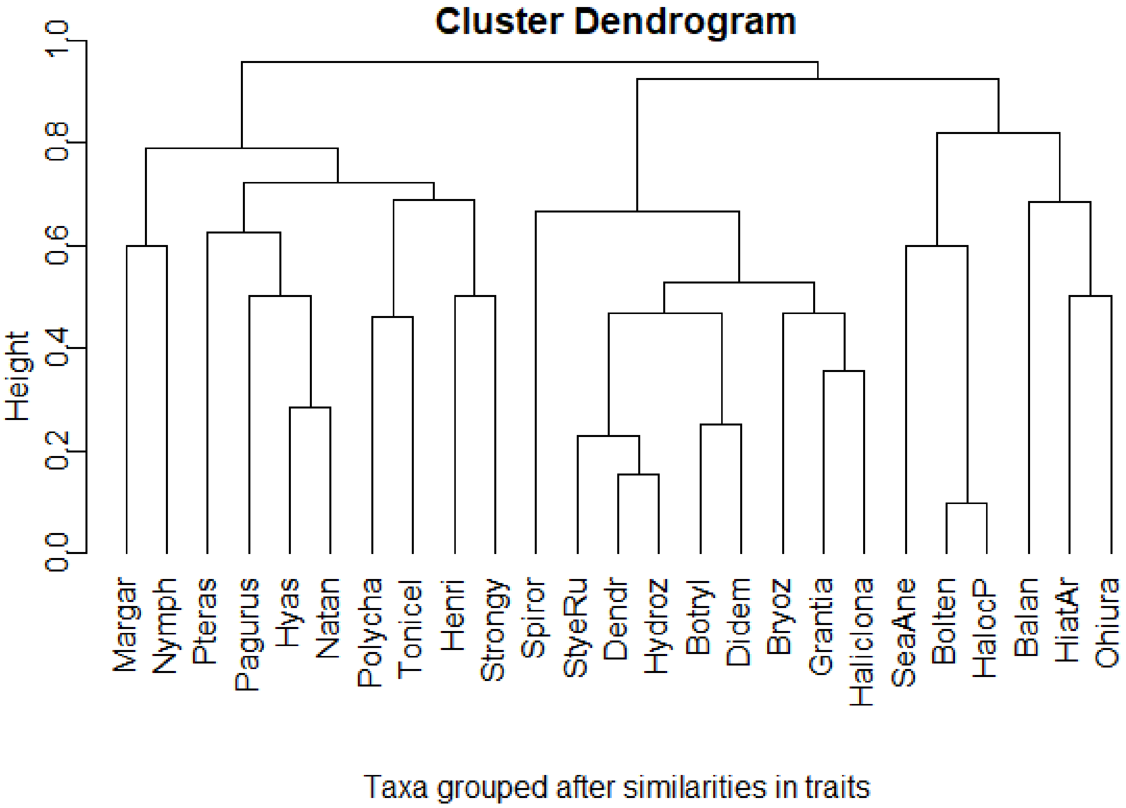


Figure 10. Complete-linkage dendrogram clustering taxa with similar functional traits together.

3.2.1 Single trait succession

Size and longevity traits showed the greatest change over time. A reduction in size was observed in the years following the manipulation (Figure 11a). Large and indeterminate (taxa with indefinite growth) sizes were dominant in 1980 but decreased in their contribution for the rest of the study, whilst a medium size was dominant in the 1980's and early 1990's, where after medium-large became the principal size. The life span of the invertebrate community also showed a reduction in the long-lived taxa and a concurrent increase in short-lived in the eighties (Figure 11.b). From 1990, the short-lived taxa declined throughout the rest of the study, whilst the long-lived increased for a bit, then declined to almost zero, while the 3-5- and 6-10-year-old taxa became more abundant.

The community mobility trait was dominated by no mobility throughout the whole-timeseries, but a small increase in low, medium, and high mobility was observed following the clearing in 1980 (Figure 11c). A similar small trend was evident in the feeding habit trait (Figure 11d). Filter/suspension feeding was by far the most common trait in all years, but grazing, predation and surface-deposit feeding rose a little after the manipulation.

Sociability trait was completely dominated by colonial lifeforms, and gregarious and solitary taxa were reduced after the perturbation until the mid-2000's where gregarious behavior was expressed more (Figure 11e). Dispersal capacities showed little or no trend, a short dispersal capacity (10-100m) governed the community, second by even shorter distance dispersal (1-10m) (Figure 11f). The 10-100m category increased slightly after 1980. Development was completely dominated by lecithotrophic development with minor fluctuations throughout the timeseries (Figure 11g).

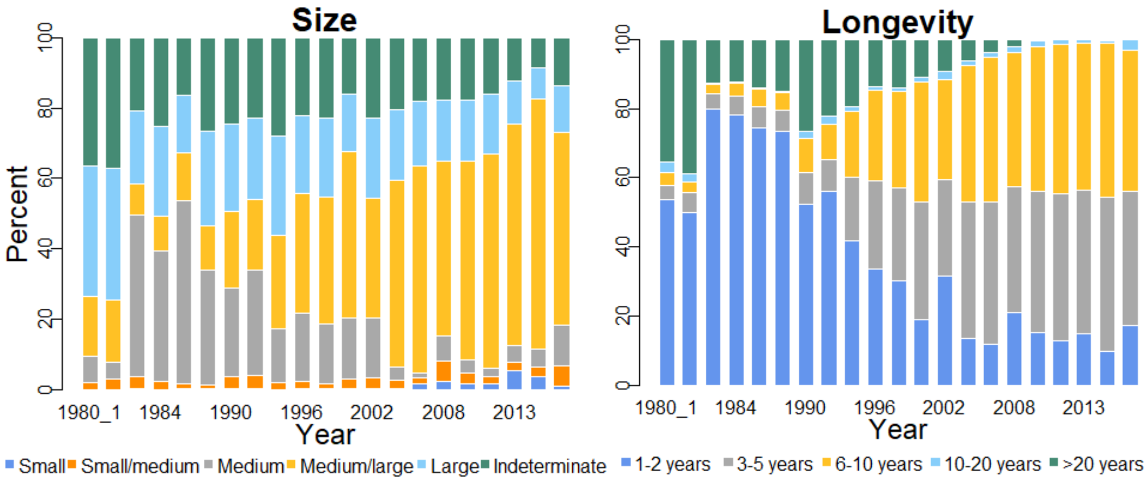
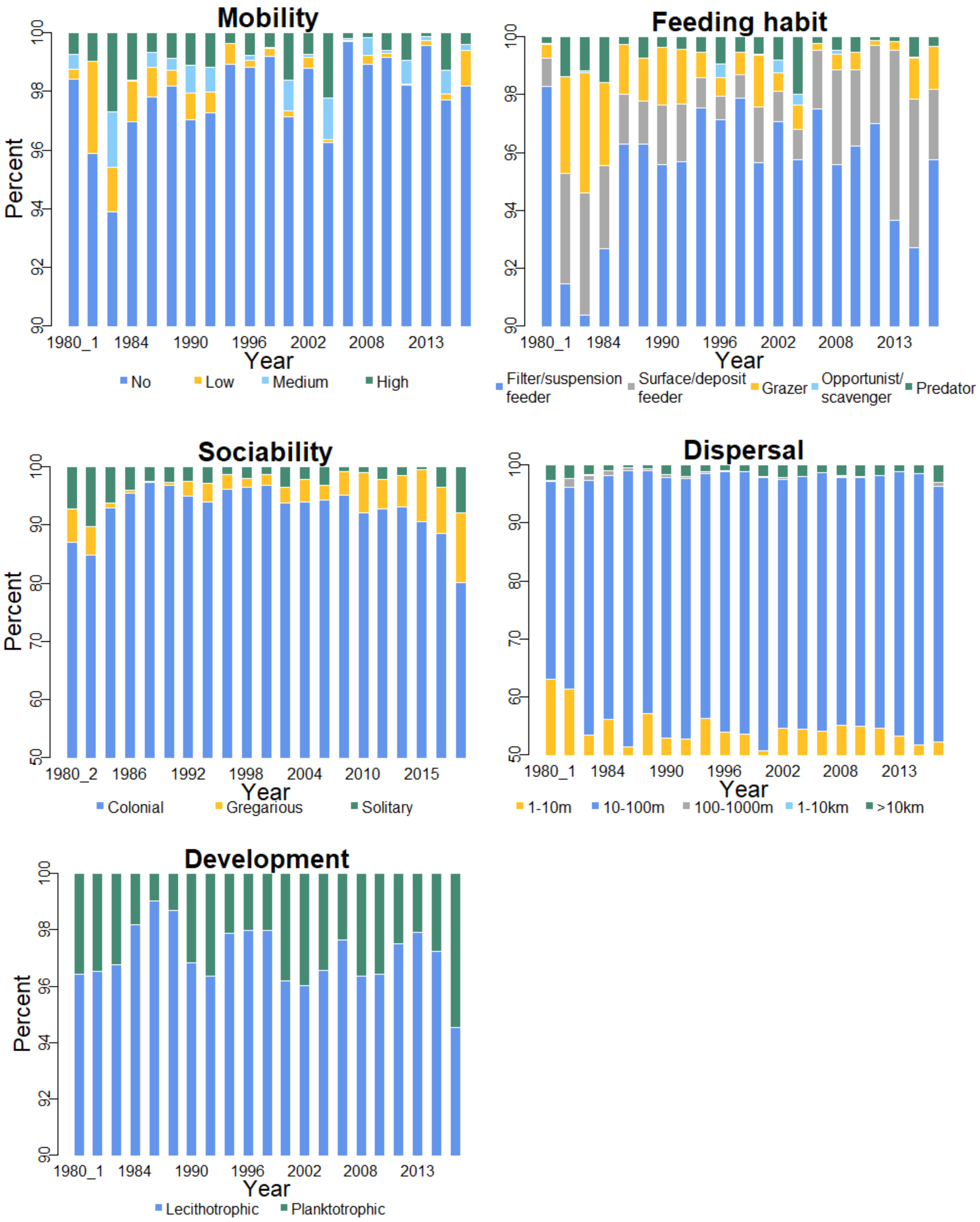


Figure 11a-g (continues on next page). Development in CWM trait expression over time in size (a), longevity (b), mobility (c), feeding habit (d), sociability (e), dispersal capacities (f) and development mode (g). Note the different scales on y-axes!

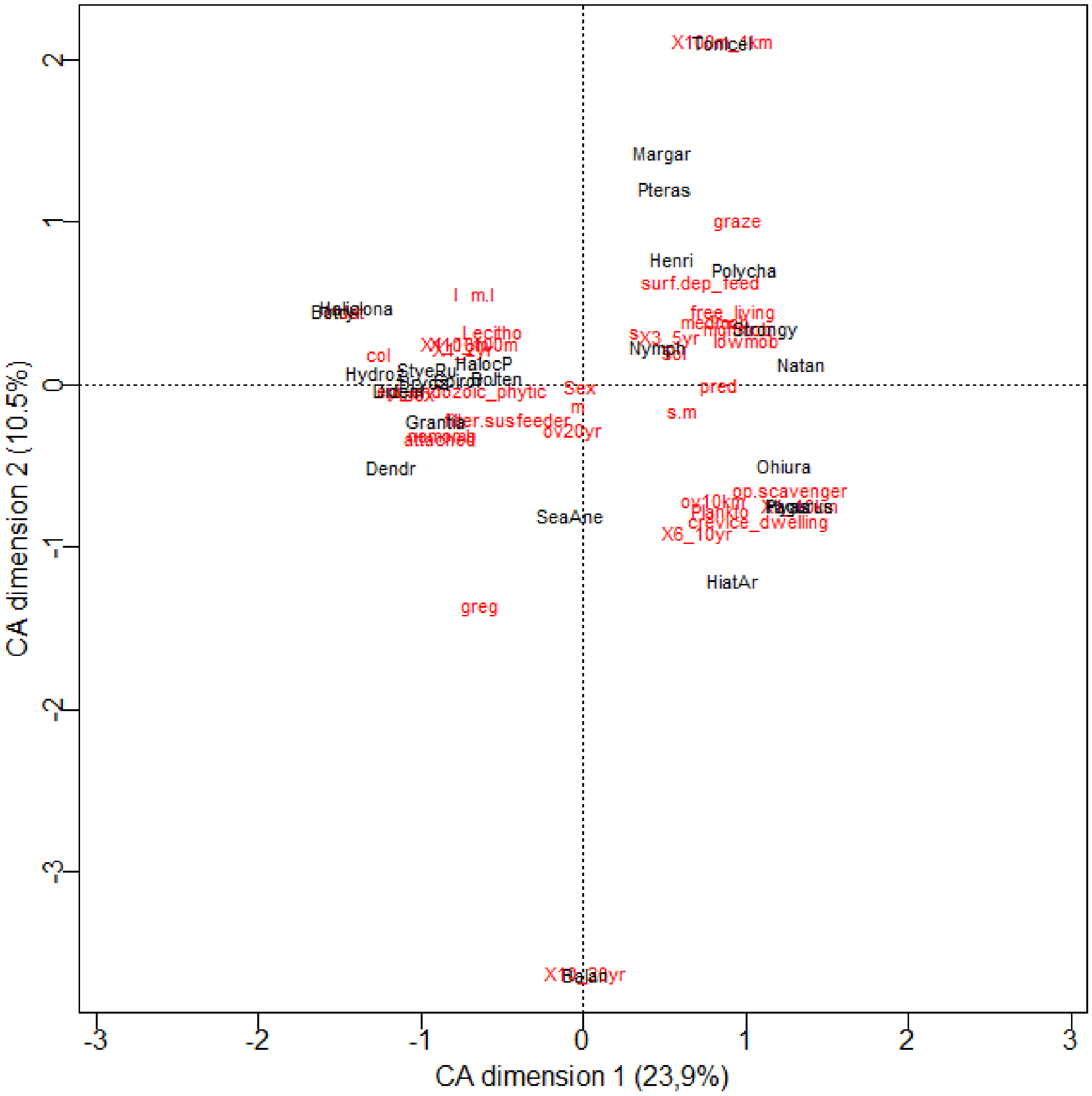

Mobility
Percent
90
92
94
96
98
100
1980_1
1984
1990
1996
2002
2008
2013
Year
No
Low
Medium
High
Feeding habit
90
92
94
96
98
100
1980_1
1984
1990
1996
2002
2008
2013
Year
Filter/suspension feeder
Surface/deposit feeder
Grazer
Opportunist/ scavenger
Predator
Sociability
Percent
50
60
70
80
90
100
1980_2
1986
1992
1998
2004
2010
2015
Year
Colonial
Gregarious
Solitary
Dispersal
50
60
70
80
90
100
1980_1
1984
1990
1996
2002
2008
2013
Year
1-10m
10-100m
100-1000m
1-10km
>10km
Development
Percent
90
92
94
96
98
100
1980_1
1984
1990
1996
2002
2008
2013
Year
Lecithotrophic
Planktotrophic

3.2.2 Multiple trait succession

Correspondence analysis of the traits supported the clusters of similar taxa found in the dendrogram and yielded a total inertia of 2.2 with the two first axes accounting for 34.4% of the variation together (Figure 12). The first CA axis accounted for 23.9% of the observed variation and illustrated a gradient of organisms characterized by colonial, filter/suspension feeding organisms with short dispersal capacity, lecithotrophic development, and indeterminate growth on the negative side and solitary, opportunists/scavengers, grazers with long dispersal, planktotrophic development and small/medium size in the positive side. This corresponds to the taxa identified in the dendrogram as functional group 2 along with *Boltenia echinata* and *Halocynthia pyriformis* from group 3 in the negative side and group 1 and the rest of group 3 on the positive side of CA axis 1. The second axis did not show as clear a gradient, but could be interpreted as a change in mobility, with mobile organisms, primarily of group 1 in the positive side of the biplot and no mobility and the remaining taxa of group 3 in the negative side. This axis accounted for 10.5% of the variation in the trait space.

The community weighted means on the CA axes was used as an indicator of the change in the functional identity over time (Figure 13a-b). The values on the y-axis in Figure 13a and Figure 13b corresponds to the values on the first and second CA dimensions, respectively in Figure 12. They illustrate a gradual and directional change in the mean trait value of the community throught the time series. In 1980 the functional identity (Figure 13a-b) moved from the coordinates -1.3 (1st axis) and 0.25 (2nd axis) approximately where *Botryllus* sp., *Haliclona* sp. and Hydrozoa are located, to -1 (1st axis) and -0.1 (2nd axis) in 2017 which corresponds to the area where Bryozoa, *S. spirorbis,* and *Styela rustica*, and *Grantia* sp. are (Figure 12).

In summary, three groups of functionally similar taxa were identified, a decrease in size and longevity, and small increase in mobility, grazing and deposit feeding, and colonial life habit was observed in the community trait expression following the clearing. Dispersal and development showed no clear trend, whereas the functional identity displayed a directional change throughout the study.



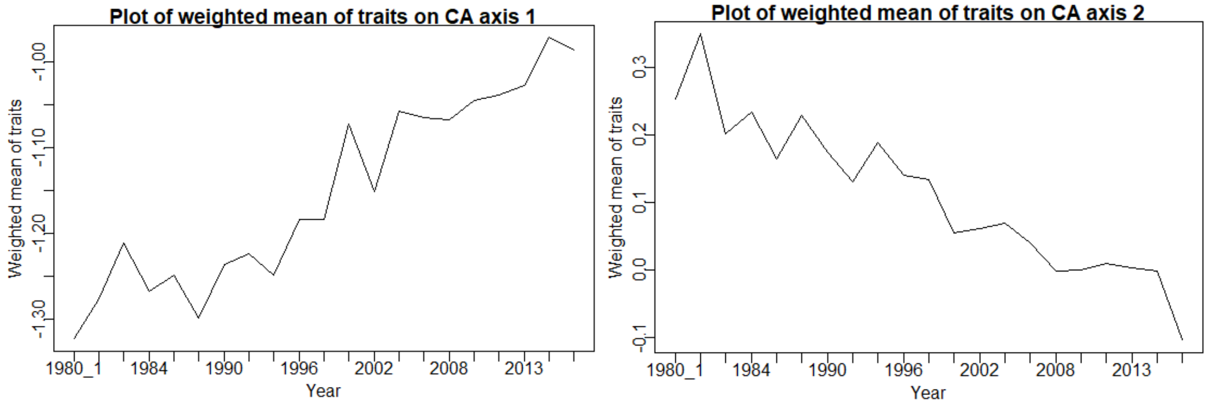


Figure 12 (top). Correspondence analysis of traits and dominant taxa. Figure 13a-b. Community weighted mean of traits over time on 1st and 2nd CA axis of figure 11.

4 Discussion

The present study investigates recolonization and succession in a coastal hard-bottom benthic community in Smeerenburgfjorden, Svalbard. Spanning nearly four decades, this study confirms observations of slow rates of recolonization in polar benthic ecosystems (Barnes and Conlan, 2007, Beuchel and Gulliksen, 2008, Dunton et al., 1982, Konar, 2013) and table below. Single taxa showed different return rates and fluctuating abundance and cover throughout the time-series. The cleared substrate was covered by living organisms comparable to the control area ten years after the manipulation, whereas the convergence of the two transects' community compositions appeared to take more than two decades. Early colonists included sessile hydrozoans and mobile grazers *Tonicella* spp. and *Margarites* spp., whereas ascidians, sponges, barnacles, and the bivalve *Hiatella arctica* were slow colonists. In addition, a regime shift occurred, resulting in an abrupt increase in macroalgae, bryozoans, and spirorbid polychaetes around year 2000, supporting observations from the control transect and a similar study in Kongsfjorden (Kortsch et al., 2012). Decrease in size and longevity traits of the community were observed following the clearance, whereas mobility, grazing, and deposit feeding increased to some degree, while dispersal and development traits did not show any trend. The results of both taxonomic and traits analysis suggest that recolonization at the study site depends on a standing stock of organisms, representative of the local population.

4.1 Recolonization patterns

4.1.1 Recolonization patterns on the taxon level

All recorded taxa are common to hard-bottom habitats in Svalbard (Hop et al., 2002, Kortsch et al., 2012, Laudien and Orchard, 2012, Palerud et al., 2004) and organisms identified in the manipulated transect were also present in the control transect, thereby representative of the local community. The time-series can be divided into three markedly different periods. The first period (1980-1990) was characterized by recolonization processes in the cleared transect, while the community in the control transect corresponds to the "Balanus" community described from Kongsfjorden after the most dominant structuring invertebrate taxa of that community (Voronkov et al., 2016). This period was followed by a "Developed" community stage (1990-2000), dominated by sponges and ascidians, where after the community transitioned to a "Branched bryozoan" community in 2000 and has remained as such since.

Hydrozoans were among the most conspicuous pioneers to appear in the first years following the manipulation. This class increased rapidly in cover after the manipulation and covered a larger area in the cleared transect than to the control when the algae/hydrozoan assemblage was included and could be associated with an underlying colonization process. Hydroids are fast-growers but poor competitors and are easily overgrown (Meyer et al., 2017). They are identified as early-colonizers in Arctic hard-bottom ecosystems following a perturbation (Dunton et al., 1982, Konar, 2007, Meyer et al., 2017), and are also recognized as early sessile colonizers in Antarctica and NE Greenland after ice-scour events (Gutt et al., 1996).

Motile grazers such as *Tonicella* spp. and *Margarites* spp. (in low numbers) were quick to invade after the substrate was cleared. They are common in Arctic hard-bottom habitats where they feed on small recruits of algae, hydrozoans, and bryozoans that grow on rocks and are known to immigrate areas after a perturbation (Beuchel and Gulliksen, 2008). Invertebrate grazing is an important process known to drive community structure and colonization in temperate hard-bottom (Aguilera and Navarrete, 2007, Johnson et al., 2011), but has not been extensively investigated in polar regions (Konar, 2013). It could explain the slow rate of colonization found in this study since grazers feed on newly established recruits, although this assumption was not confirmed in a study of the Boulder Patch in the Beaufort Sea. In that study, the author found that grazing did not have a significant effect on recolonization of cleared boulders where grazers were excluded, compared to uncaged and cage control boulders (Konar, 2007). This single observation, however, may not necessarily apply to all hard-bottom regions in the Arctic, since differences in sedimentation, inclination and type of substrate, geographic position, local and regional processes are likely to influence the observed patterns in ecological interactions, such as grazing.

Red crustose coralline algae and shrimps were also present in the early stages of recolonization in the cleared transect but categorizing them as pioneers would be misleading. Coralline red algae are considered late-succession taxa as they are slow-growing superior competitors (Meyer et al., 2017), but were found to rapidly recolonize the cleared transect in the present study. This may be an artifact of incomplete clearing in the scraping treatment, leaving small patches of remaining red crustose algae capable of quickly regaining high coverage through vegetative growth. An analogous observation was made in another recolonization study from the Boulder Patch, where red coralline algae in three years almost doubled in cover on boulders where they had not been completely removed (Dunton et al., 1982). Natantia also appeared in the early stages of recolonization in the present study, likely to feed on the newly settled recruits of hydrozoans (Birkely and Gulliksen, 2003), but the high mobility of this group restricts making general assumptions on their opportunistic behavior.

The second period (Figure 5) characterized by Porifera and Ascidia. These taxa were slow to regain cover and abundance following the clearing and are characterized as strong competitors and late succession groups (Meyer et al., 2017). Sponges of the genus *Haliclona* are slow-growing and can live to over 20 years of age (Teixidó et al., 2011). They displayed a slow, stable incline in cover during the recolonization period, converging with the area of the control transect ten years after the initiation of the study. Styelidae showed a trend similar to *Haliclona* spp., with a very slow recovery in the cleared areas, only reaching pre-treatment numbers after 35 years and convergence with the control after 26 years. The control transect did however start out with ~100 individuals per square meter more than in the cleared transect and this difference persisted with up to 200 individuals throughout the two first decades. This might be associated with their patchy, gregarious behavior, given that the tadpole larvae appear to prefer to settle next to or on the parent (Gulliksen and Svensen, 2004), an observation that was also evident in the images. This aggregated behavior might explain the slow recovery since the individual ascidians would likely not disperse far from the parent. *Halocynthia pyriformis* also recovered slowly, with the abundance in the cleared transect merging with the control transect in year 2000, potentially due to poor competitive abilities. The pattern for *Botryllus* spp. differed in that the cover highly fluctuated which could be associated with the cycles of growth and senescence in the short-lived zooids of this genus (Chadwick-Furman and Weissman, 1995). Another explanation could be the patchy distribution of this genus which may be linked with the larvae favoring settlement close to the parent (Grosberg, 1987), this apply to all ascidians in the present study. Sponges and ascidians were slow to recolonize, one common characteristic in these groups are the limited dispersal capacity (see Table 2). This is in line with a recruitment study on settlement plates submerged for one year at different depths in three Svalbard fjords, here they found no recruitment of sponges and ascidians and suggested limited dispersal capacity as a proximate reason (Meyer et al., 2017). In the present study, they appeared to colonize from the edges of the images (pers. obs.) which may be attributed their short dispersal distance and/or vegetative growth. Vegetative encroachment by organisms from the margins of an area was suggested as the primary means of recovery after a disturbance (Bulleri, 2005).

Hiatella arctica and *Balanus balanus* were interestingly also among the late colonizers contrary to other hard-bottom colonization studies from Jan Mayen, Svalbard, and the Beaufort Sea (Gulliksen et al., 1980, Konar, 2007, Meyer et al., 2017). The late occurrence of these species can be explained by the slow growth and high longevity (Gulliksen and Svensen, 2004, Sejr et al., 2004). Another possible explanation is that they were present in the early successional stages but had not reached a measurable size in the images (see also method discussion). *Spirorbis spirorbis* was essentially absent in both control and transect areas prior to the macroalgae expansion in year 2000. This is contrary to other studies which have found spirorbid worms to be amongst the first colonizers in polar areas (Barnes, 2017, Barnes and Conlan, 2007, Konar, 2007). In the present study, they only occurred in very small numbers in both control and cleared transects prior to the regime shift, where after they increased greatly. *S. spirorbis* grew almost exclusively on the foliose macroalgae, suggesting a facilitation association between the macroalgae and *S. spirorbis*. This last period characterized by a regime shift in the community structure lasted from year 2000 until the end of the time-series and will be discussed in section 4.1.3.

The present results from the analysis of single taxa over time demonstrated the high interannual variability in abundance and cover of many taxa, and some of these did not converge with the control taxa, as illustrated in the difference plots in the result section.

Table 3.Recolonization studies, recovery time, early- and late colonists

Location	Habitat type	Type of disturbance	Recovery rate	Early colonizers	Late colonists	Reference
Smeerenburgfjorden	Vertical hard bottom wall	Clearing of substrate	10-24 years	Hydrozoans, *Tonicella* spp., *Margarites* sp.	Sponges, ascidians, barnacles	This study
Kongsfjorden, Svalbard	Horizontal hard-bottom (15m)	Clearing of substrate	10-13 years	*Tonicella* spp., *Margarites* sp., urchins	Sea anemones, Porifera	(Beuchel and Gulliksen, 2008)
Boulder Patch, Beaufort Sea	Small boulders (6-7m)	Clearing of substrate	>7 years	Barnacles, spirorbids		(Konar, 2007, Konar, 2013)
South Africa	Intertidal hard-bottom	Clearing of substrate	3 years			(Dye, 1998)
Ascension Island, North Atlantic		Settlement plates		Spirorbidae, ascidians		(Barnes, 2017)
SE England	Soft-bottom	Dredging	7yr (low intensity site) >11yr (high intensity site)	NA	NA	(Hussin et al., 2012)
Cornwallis Island, Barrow Strait	Soft-bottom (12-24m)	Ice-scour	10-14 years (estimate)	Capitellid, dorvilleid, hesionid, phyllodocid, and spionid polychaetes, cumaceans, ophiuroids, juvenile bivalves	Bivalves, cirratulid, paranoid, pholoid and ampharetid polychaetes, Cingula spp., ostracod and tanaid crustaceans	(Conlan and Kvitek, 2005)
NE Hongkong	Soft-bottom (0.1-1m)	Defaunation	<15 months	Polychaetes, gastropods		(Lu and Wu, 2000)

4.1.2 Ecosystem succession

Determining when a dynamic community is fully recovered has been defined differently in the past. In a recent review, more than twenty different definitions of ecosystems recovery were identified, illustrating the lack of consensus in the scientific community (Duarte et al., 2015). Recovery is regularly referred to as a return to a “normal” state, but this state is often not known, or natural fluctuations may mask this “baseline” state (Lotze et al., 2011). Referring to the objectives of this study, I will use recovery as convergence of the cleared community structure with that of the control community.

The available bare substrate (i.e. stone, scraped surface) in this study was covered by living organisms to a numerically comparable degree to the control transect after ten years (Figure 6), but over 80% of the surface was covered by living organisms already after four years. This was primarily driven by the regrowth of crustose coralline algae and is faster compared to a study in the Beaufort Sea where only 2% of the available substrate was colonized four years after boulders were cleared of substrate (Konar, 2007). Nevertheless, plenty of bare substrate was available for recruitment in the present study and this suggests low and/or sporadic recruitment. Recruitment is suggested to occur slowly in the Arctic (Meyer et al., 2017), and this could explain why the cleared community of the present study took so long to recover. Another, earlier recolonization study from the Boulder Patch in the Beaufort Sea also showed a slow return rate, with 50-70% of the available substrata remaining bare after 4 years (Dunton et al., 1982). These authors suggested temporal variability in composition and abundance of larvae and spores, predation, herbivory, competition, and growth rates of settlers to govern the slow return. Styrofoam floats at the same site showed different recolonization pattern on the other hand, being covered by organisms after 12 months. Smothering and grazing can inhibit successful settlement of larvae and spores, so the lack of sedimentation and grazing were the proposed drivers causing the faster recolonization on the Styrofoam floats (Dunton et al., 1982). Sedimentation can be excluded as a mechanism inhibiting recolonization in the present study, given the vertical nature of the substratum and periodically strong current at the site, and the availability of bed rock makes competition for space seem unlikely. Predation and herbivory cannot be excluded since grazers were observed in the early stages of recolonization, but further studies investigating their influence are needed to establish whether they may have such a strong influence. Sporadic recruitment seems plausible to influence the observed pattern and relates to the traits of the local community. Many other ecological interactions and environmental pressures are likely to influence the slow rate of recolonization but discussing them all is beyond the scope of this study.

In contrast to the pure regrowth of organisms on the bare rock, results from the multivariate analysis suggested a much longer recovery time (~24 years) required for the composition of the cleared and control communities to converge (Figure 7). Large interannual variability was evident in the cleared community throughout the first two decades, in contrast to the less variable structure of the control community, an observation also made in a recolonization study from South Africa (Dye, 1998). The interannual variability in the present study may indicate a reorganization in the cleared community structure associated with an ongoing recolonization process. This larger variability could also be a result of external forcing acting differently on the less resilient community of the cleared areas and keeping benthos at an intermediate successional stage, though evidence for a "climax" stage is difficult to obtain in dynamic system with constant external forcing. Climate variability has been linked to altered benthic community structure in Smeerenburgfjorden (Kortsch et al., 2012) and in Kongsfjorden (Beuchel et al., 2006). In Kongsfjorden, changes in the North Atlantic Oscillation (NAO) index were associated with 45% of the observed variability in the benthic community structure (Beuchel et al., 2006). Such a strong correlation between NAO and the community structure was not observed in Smeerenburgfjorden (Kortsch, 2010). This difference could be related to the lower inflow of Atlantic water over the shallow sills in Smeerenburgfjorden, compared to Kongsfjorden which has no sill (Svendsen et al., 2002). This reduced inflow might also have led to slower recruitment in Smeerenburgfjorden, since Atlantic water influenced fjords in Svalbard appear to have faster recruitment compared to Arctic water influenced fjords (Meyer et al., 2017). Smeerenburgfjorden is strictly speaking not influenced by Arctic water but given its more northern location and the presence of sills, it may be considered more "Arctic-like" than the open Kongsfjorden.

Polar near-shore habitats are suggested to be some of the most disturbed habitats globally, due to the frequency of ice-scours, storm events, and the high seasonality in environmental conditions (Barnes, 1999). According to the intermediate disturbance hypothesis (IDH), communities are anticipated to display the highest diversity at intermediate disturbance regimes by allowing pioneers and superior competitors to co-exist (Connell, 1978). It would thus be intuitive to expect that these Arctic coastal ecosystems are well-adapted to disturbances by housing a mosaic local community with pioneers and superior competitors co-existing, and capable of a relatively fast recovery. This was not the case in the present study, where available space remained unoccupied for a decade. While the disturbance history of the time series site is not recorded, the study site and its vicinity showed no sign of ice-scour in the images nor *in* *situ* (pers. dive obs.) and the site at 15 m seems to be below the depths directly impacted by ice in Svalbard. This observation suggests that the community may in fact not be disturbance-adapted, which is supported by the local community being highly dominated by superior competitors, with few pioneers. This interpretation is supported by results from a microbial manipulation study where diversity did not increase at the *local* scale if the community was skewed towards high competitors, whereas IDH was supported at a higher spatial scale (Cadotte, 2007). Facilitation in the traditional sense where pioneers modify the environment thereby facilitating the establishment of late-colonizers (Connell and Slatyer, 1977) did not seem to be significant in the present study given the modest presence of pioneers. The tolerance model could however be applied to the current system, since it appears that the later colonists are neither facilitated nor inhibited by pioneers, they rather seem to show this slow recolonization as a result of their life-histories (Connell and Slatyer, 1977).

4.1.3 Regime shift

Results from this study found evidence of a regime shift and support the findings of a previous study from Smeerenburgfjorden and Kongsfjorden (Kortsch et al., 2012). The climate-driven regime shift was characterized by an abrupt increase in macroalgae cover with a subsequent reorganization of the invertebrate community (Kortsch et al., 2012). As ecosystem engineers, macroalgae affect both the structure and function of ecosystems, most notably by providing habitat, food, shelter from predation, ameliorating waves action and currents (Paar et al., 2016), as well as altering light regime (Bartsch et al. 2016). Many sessile and mobile taxa are associated with macroalgae (Hop et al., 2002) and in the present study, bryozoans and spirorbid polychaetes were found to increase in cover and abundance in conjunction with the increase in macroalgae cover.

The macroalgae expansion was suggested to be triggered by an increase in light availability caused by the prolonged ice-free season (Kortsch et al., 2012) as elaborated in a recent modelling study of the same location (Scherrer, 2015). The sudden increase of *Desmarestia* spp. cover in 1984 in the cleared transect of this study corroborates this finding. This year was unusually warm in Svalbard, which caused a higher number of ice-free days (Kortsch et al., 2012), increasing the annual light availability that in turn could have promoted the observed growth of *Desmarestia* spp. This event suggests that the absence of extensive foliose macroalgae cover prior to year 2000 was not a result of competitive exclusion by crustose coralline algae. If this had been the case, then the removal of corallines with the manipulation in 1980 in the present study would have led to an increase in the cover of foliose macroalgae.

The 1984 algal occurrence also shows that foliose macroalgae have been present throughout the studied time-period, but that conditions presumably did not favor extensive growth until the late nineties.

Another explanation of the sudden increase in macroalgae cover is a general upward shift of macroalgae belts in coastal Svalbard waters as recently reported from Kongsfjorden (Bartsch et al., 2016). This process is also suggested to be climate warming-induced due to reduced light availability caused by increased turbidity from melting glaciers and river run-off (Bartsch et al., 2016, Weslawski et al., 2010). Several observations in the present study could support this observation. First, the dominant macroalgae species in this study is the Arctic/cold-temperate red algae *Phycodrys rubens*. This is a common understory species from 15-30m depth (Hop et al., 2012), it is shade-adapted and does not tolerate high UV exposure (Hop et al., 2002). The present study site at 15 m is at the upper limit of *P. rubens*, given the maximum density at present is at ~8 m, I suggest that deteriorated light regime has allowed this shade-adapted species to persist at such shallow depth.

4.2 Ecosystem function

The functioning of the ecosystem following the clearing was explored with a traits analysis. Nine traits representing different ecosystem functions (Degen et al., 2018) were chosen to explore the recolonization process of the benthic community. Size, longevity, mobility, feeding habit, and sociability showed a trend in the recolonization stage, whereas the remaining traits did not show any clear pattern. The multivariate analysis showed gradual transition in the function of the community, but the traits only explained 35% of the species composition, thereby limiting the scope for broad generalizations.

4.2.1 Single-traits in the recolonization stage

Following the perturbation, a reduction in the adult size and longevity of the organisms inhabiting the community was observed. Size has been characterized as one of the most vital traits in ecosystem functioning (Weigel et al., 2016), affecting physiology, trophic strategies and ecological interactions (Degen et al., 2018). Large animals are more vulnerable to mechanical disturbance, leaving small, and sometimes early life-stage organisms dominating in the recovering system (Norkko et al., 2013). In this study, removing large, slow-growing organisms with indeterminate growth affected the traits structure of the community, since these will require longer time to recover than smaller organisms with fast growth. Related to decreasing size, longevity displayed an increase in short-lived – and often smaller - organisms in conjunction with a reduction in long-lived ones. Organisms in a disturbed habitat is often characterized by short life span and high turnover rate, and longevity is considered a *response* trait since it determine how a given organism responds to a disturbance or a change in the environment (Degen et al., 2018). Pioneer species are often characterized by r-strategy life history traits such as rapid growth and short life-span (Newell et al., 1998), so a rise in ephemeral taxa in the years following the disturbance could suggest that pioneers colonized the area. Slow growth and high longevity are characteristic for many polar animals (Barnes and Conlan, 2007, Beuchel and Gulliksen, 2008, Degen et al., 2018), which plausibly explains the long recolonization process compared to lower latitudes. High longevity promotes local competitive abilities of sessile organisms but often involves a trade-off between colonization and competition (Potthoff et al., 2006). This trade-off was evident in the present study, which showed that long-lived competitively superior taxa were slow to recolonize, in line with the results of a similar recolonization study in Kongsfjorden (Beuchel and Gulliksen, 2008).

Mobility of the invertebrate community increased slightly in the first years following the manipulation. Species living in disturbed environments may comprise of small mobile opportunists capable of taking advantage of newly released resources (Newell et al., 1998). The increase in mobility in the present study is consistent with the observation of mobile taxa appearing in the early successional stages since they are able to move freely around the substrate and are not limited to disperse by early mobile life stages or by rafting (Jackson, 1986). This mobility may, however, also allow the animals to leave the area before the image is taken, so their estimate might be biased and could explain the low signal.

Feeding habit shifted with surface-deposit feeding, grazing, and predation increasing moderately after the manipulation in 1980. This is in line with the hypothesis that grazers appear in the early stages of recolonization to feed on newly established recruits. Grazing can be an important factor driving recolonization patterns (Beuchel and Gulliksen, 2008), and the grazers may attract predators which in turn feed on them, explaining the increase in predation. Filter/suspension feeding was still the dominant feeding habit by large, which is not uncommon for hard substrate communities in Svalbard (Hop et al., 2002) and vertical walls in general (Laudien and Orchard, 2012).

Colonial lifeforms dominated the study area throughout the time-series. This strategy was expressed even further after the clearing. Colonial invertebrates are common inhabitants in shallow marine areas and constitute a great component of marine biodiversity (Hughes, 2005), so their contribution to the functioning of these ecosystems is expected to be substantial. This trait is associated with many other traits such as longevity, larval dispersal, reproduction, and development mode, size (indefinite growth), mobility, and feeding habit (Strathmann, 1990). A characteristic of colonial organisms is the capability of vegetative growth of modules (Edwards and Stachowicz, 2010), and the results of this study indicate that invertebrates capable of this type of growth dominated the community even further following the perturbation. Recolonization of colonial animals occur primarily through recruitment of sexually reproduced larvae and propagules and through vegetative encroachment from the margins of study area (Bulleri, 2005, Konar, 2013). This later process is likely the dominant form of colonization by sessile, colonial invertebrates in the present study as they appeared to grow in to the cleared area from the surrounding untouched areas (pers. obs.).

Larval dispersal and development traits did not show any clear trends during the recolonization stage, contrary to *a priori* expectations of early recruits possessing broad dispersal capacities, i.e. long dispersal distance and planktotrophic larvae. These expectations stem from literature on early successional and colonizing taxa (Horn, 1974, Wangensteen et al., 2016), suggesting that opportunists generally displaying long-distance dispersal of larvae dominate in early successional stages (Wangensteen et al., 2016). Long dispersal capacities are interestingly not always the dominant trait in the most common polar taxa, many of which are characterized by short pelagic or benthic dispersal and lecithotrophic larvae or direct development (Barnes and Conlan, 2007). Such a strategy is supposedly expressed to reduce dispersal distance and undesirable conditions that would arise for planktotrophic larvae due to the large seasonal variations in food availability in polar regions (Potthoff et al., 2006). This idea, known as Thorson's rule, has been the prevailing paradigm for decades and could explain the low presence of taxa with planktotrophic larvae in this study, though the emergence of polar taxa that do not follow this rule has recently questioned its generality (Barnes and Conlan, 2007). There are several evolutionary consequences of a decreased larval period which could explain the predominance of this trait in the present community: more regular recruitment, less irregular year classes, decreased dispersal away from favorable habitats, and adaptions to local conditions (Strathmann, 1990). Explanations of the lack of a trend in larval dispersal and development traits after the clearing could again support the above notion that recolonization in the present study is mostly driven by nearby local populations rather than long-distance disperser. A modelling study in a high disturbance regime in Antarctica indicated that a long pelagic larval phase was in fact not needed for a pioneer species to persist regionally (Potthoff et al., 2006). This appear to apply for the community of the present study, as a long pelagic larval phase would otherwise have been selected for.

These results suggest that the early recolonization depended on the standing stock of the local population (which was supported in the taxonomic analysis) of medium-sized short-lived organisms. Mobility, grazing, and deposit feeding also increased to some degree, though sessile life style and filter feeding were still dominant traits in the community.

4.2.2 Succession of functional identity

A directional change in the functional identity was evident throughout the timeseries. This indicate that the functioning of the invertebrate community was altered in a generally consistent direction through all three time periods. It was not, however, a particularly strong signal, as illustrated by the small area in the CA plot where this change was manifested along with the modest explanatory power of the correspondence analysis. This could be an artifact of displaying numerous taxa’s many traits in just two dimensions, the generally low taxonomic resolution, or simply just illustrate the heterogeneity of the dataset. Nevertheless, a clear trend was demonstrated, suggesting a functionally dynamic system.

4.3 Methodological constraints and suggestions for future solutions

The results of the present study support findings from an identical study in Kongsfjorden (Beuchel and Gulliksen, 2008), suggesting that they can be carefully generalized as a trend typical of the fjords of NW Svalbard, and potentially be considered a replicate to the Kongsfjorden study. The study design at both these localities is such that the treatment and control plots are spatially autocorrelated, and so are the individual quadrats of each plot. The latter are not interspersed so there are no independent replicates in the study. This challenge was overcome by pooling the five quadrats into one area (transect) which gave rise to another issue, namely having only a single sample for the control and one for the cleared area each year. This limits broad generalizations on the findings of this study, since they merely provide a trend from a small connected area, but the unique and valuable nature of this time series outweighs these issues by far. In addition, the site was only visited once a year and not at the exact same time, thereby providing only a snapshot in time and not considering the variability in abundance and cover of the organisms over the course of a year. This possible variability might only apply for mobile and annual taxa but given that most Arctic biota are long-lived and that sessile organisms dominated in the present study, I would argue that this seasonality only played a minor role. Lastly, the autocorrelation in time results in consecutive years being more similar.

It is unfortunately not likely that sampling could be expanded to occur biannually in the near future, due to the costs and logistics of conducting such expeditions but establishing another monitoring site is not necessarily associated with much additional costs once the site has been chosen and set up. Obtaining the photographs does not take a long time in itself so adding another site nearby would in the long run provide the benefit of replication with little additional costs. Another interesting, but a little more extensive suggestion to future studies would be to perform the clearing of substrate manipulation again and compare the rate and process of recolonization of present times to the results from the 1980s. Another suggestion is to re-design the experimental set-up with interspace between the manipulated and control areas, as well as between the quadrats.

Photographic sampling provides the best option when considering multiple aspects, compared to other sampling methods. Dredging and trawling may provide identification to higher taxonomic levels but does not allow a quantitative repeated sampling of a site, grabs and box corer sampling cannot be applied on hard-bottom substrates, whereas SCUBA diving-based *in situ* observations may yield high taxonomic resolution, but are time consuming and require divers with extensive taxonomic knowledge (Beisiegel et al., 2017). Benthic imagery does however have some shortcomings which includes a generally low taxonomic resolution of the identification, underestimation of small and cryptic taxa may as a result of the variable resolution of the images, and a two-dimensional representation of a three-dimensional habitat. These main shortcomings were ameliorated by collecting physical samples in the vicinity of the site, providing a more solid taxonomic identification.

The occasional large differences between the abundance/cover of single taxa in the control and cleared transects might have been magnified as an artefact of bias since three different people analyzed the images. A possible solution would be to have all three analyze a subsample of the same images and calibrate from these results. Given the extensive training I received from the other analyzers, it is more likely that these differences where in fact biological and/or ecological.

A very important methodological difference distinguishing the present study from the similar study in Kongsfjorden (Beuchel and Gulliksen, 2008, Beuchel et al., 2006) is the calculation of different community layers. In that study, three different community layers were calculated to adjust for the top-down view of the camera resulting in foliose macroalgae and large solitary organisms "over-shading" small solitary animals and encrusting colonial organisms (Beuchel et al., 2010). This method was not applied in the present study for several reasons. First, the cover of foliose macroalgae is smaller in Smeerenburgfjorden compared to that of Kongsfjorden therefore the shading effect is not as extensive. Second, a multivariate graphical comparison yielded no substantial difference between the "layered" and "unlayered" community structure. Third, avoiding unnecessary assumptions of the shaded part of the community and potential overestimation of small taxa reduces the risk of bias and sampling artifacts.

The high occurrence of colonial organisms in benthic samples complicates the use of abundance data and many ecological indices based on counts (Voronkov et al., 2013). One could either investigate solitary and colonial organisms separately or attempt to combine the two datasets to achieve an analysis of the entire community. The latter has commonly been performed with multivariate tools based on Bray-Curtis dissimilarity (Beuchel and Gulliksen, 2008, Kortsch et al., 2012), but the use of this measure has recently been criticized since it confounds the "size" (overall measure, i.e. abundance/cover) and "shape" (relative composition) of the different components in a community (Greenacre, 2017). Since the "size" of the community was assessed in univariate space and based on discussion with Prof. M. Greenacre (pers. com.), I chose to examine the relative community structure by weighting the abundance and cover data sets differently to get a similar total inertia and perform a correspondence analysis.

Lack of trait information on Arctic benthos resulted in much information being gathered from lower latitudes. This inherently assumes that organisms do not show any adaptions or plasticity in trait expression related to a latitudinal or environmental gradient, which may not always be the case (Degen et al., 2018). The relatively low taxonomic resolution achieved from the photographic sampling might also have influenced the trait analysis as well as the use of cover as will have underestimated the effect of small organisms.

4.4 Conclusions and outlook

Results from this study add valuable baseline information on the structure and function of Arctic hard-bottom ecosystems, important knowledge in a time of rapidly changing Arctic environments. Here, evidence of slow recolonization and recovery rates was found in an Arctic nearshore hard-bottom community after a disturbance, supporting observations from previous studies. Cleared substrate was covered by living organisms comparable to the control area after ten years, whereas the community composition of the cleared areas converged with the control after 24 years. Colonists were representative of the local community, comprised of strong competitors and few pioneers, indicating a low disturbance habitat despite the high interannual variability in the community structure. The tolerance model of succession seems applicable for the given community, suggesting succession was primarily driven by life-history traits of the local species such as slow growth and high longevity.

Modifications of the physical environment in the Arctic caused by anthropogenic climate change will alter ecological interactions, promote species invasions, and increase human activities in the region. Large coastal areas of available hard-bottom habitats are expected to open up for colonization in Arctic fjordic regions such as those in Svalbard, the Canadian Arctic Archipelago and Greenland as glaciers retreat. Another significant implication of Arctic warming is the rapidly decreasing sea ice, presently resulting in a giant light experiment as the number of ice-free days and areas available to new settling biota are increased. Both changes will cause dramatic shifts in macroalgae-dominated benthic ecosystems, as illustrated in this and other studies, and will have repercussions for higher trophic levels utilizing coastal habitat. These developments highlight the need for research such as the present study on the processes of succession at previously ice-influenced hard-bottom coasts.

Future studies should attempt to identify ecological drivers of the interannual variability in community structure in hard-bottom communities. Here, I strongly recommend increased environmental sampling effort in Smeerenburgfjorden in particular, in conjunction with the ongoing photographic sampling since only coarse satellite data from the West Spitsbergen Current outside the fjord appear readily available. I also suggest establishing other sampling sites within the fjord and at multiple depths, perhaps even implementing a new clearance-of-substrate manipulation. Expanding the study to comparative sites in Greenland and Franz Josef Land could further illuminate the generality of the findings to a pan-Arctic scale. The importance and uniqueness of this and other time-series cannot be overemphasized and the valuable information in contains may provide the foundation for monitoring, management, and conservation programs of Arctic ecosystems.

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Works cited

Aguilera, M. A. & Navarrete, S. A. 2007. Effects of Chiton granosus (Frembly, 1827) and other molluscan grazers on algal succession in wave exposed mid-intertidal rocky shores of central Chile. *Journal of Experimental Marine Biology and Ecology,* 349**,** 84-98.

Ali, H. a. J. & Tamilselvi, M. 2016. *Ascidians in Coastal Water: A Comprehensive Inventory of Ascidian Fauna from the Indian Coast*, Springer.

Anger, K. & Dawirs, R. 1981. Influence of starvation on the larval development of Hyas araneus (Decapoda, Majidae). *Helgoländer Meeresuntersuchungen,* 34**,** 287.

Barnes, D. K. 1999. The influence of ice on polar nearshore benthos. *Journal of the Marine Biological Association of the United Kingdom,* 79**,** 401-407.

Barnes, D. K. 2017. Marine colonization and biodiversity at Ascension Island and remote islands. *Journal of the Marine Biological Association of the United Kingdom,* 97**,** 771-782.

Barnes, D. K. & Conlan, K. E. 2007. Disturbance, colonization and development of Antarctic benthic communities. *Philosophical Transactions of the Royal Society of London B: Biological Sciences,* 362**,** 11-38.

Barnes, J. & Gonor, J. 1973. The larval settling response of the lined chiton Tonicella lineata. *Marine Biology,* 20**,** 259-264.

Bartsch, I., Paar, M., Fredriksen, S., Schwanitz, M., Daniel, C., Hop, H. & Wiencke, C. 2016. Changes in kelp forest biomass and depth distribution in Kongsfjorden, Svalbard, between 1996–1998 and 2012–2014 reflect Arctic warming. *Polar Biology,* 39**,** 2021-2036.

Beisiegel, K., Darr, A., Gogina, M. & Zettler, M. L. 2017. Benefits and shortcomings of non-destructive benthic imagery for monitoring hard-bottom habitats. *Marine pollution bulletin,* 121**,** 5-15.

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**,** 913-924.

Beuchel, F., Gulliksen, B. & Carroll, M. L. 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**,** 35-48.

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

Birkely, S.-R. & Gulliksen, B. 2003. Feeding ecology in five shrimp species (Decapoda, Caridea) from an Arctic fjord (Isfjorden, Svalbard), with emphasis on Sclerocrangon boreas (Phipps, 1774). *Crustaceana,* 76**,** 699-715.

Blicher, M. E., Rysgaard, S. & Sejr, M. K. 2007. Growth and production of sea urchin Strongylocentrotus droebachiensis in a high-Arctic fjord, and growth along a climatic gradient (64 to 77 N). *Marine Ecology Progress Series,* 341**,** 89-314.

Bremner, J., Rogers, S. & Frid, C. 2006. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecological Indicators,* 6**,** 609-622.

Bulleri, F. 2005. Experimental evaluation of early patterns of colonisation of space on rocky shores and seawalls. *Marine Environmental Research,* 60**,** 355-374.

Cadotte, M. W. 2007. Competition-colonization trade-offs and disturbance effects at multiple scales. *Ecology,* 88**,** 823-829.

Carballo, J. L. & Ávila, E. 2004. Population dynamics of a mutualistic interaction between the sponge Haliclona caerulea and the red alga Jania adherens. *Marine Ecology Progress Series,* 279**,** 93-104.

Chadwick-Furman, N. E. & Weissman, I. L. 1995. Life histories and senescence of Botryllus schlosseri (Chordata, Ascidiacea) in Monterey Bay. *The Biological Bulletin,* 189**,** 36-41.

Cochrane, S. K., Denisenko, S. G., Renaud, P. E., Emblow, C. S., Ambrose Jr, W. G., Ellingsen, I. H. & Skarðhamar, J. 2009. Benthic macrofauna and productivity regimes in the Barents Sea—ecological implications in a changing Arctic. *Journal of Sea Research,* 61**,** 222-233.

Conlan, K. E. & Kvitek, R. G. 2005. Recolonization of soft-sediment ice scours on an exposed Arctic coast. *Marine Ecology Progress Series,* 286**,** 21-42.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science,* 199**,** 1302-1310.

Connell, J. H. & Slatyer, R. O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist,* 111**,** 1119-1144.

Degen, R., Aune, M., Bluhm, B. A., Cassidy, C., Kędra, M., Kraan, C., Vandepitte, L., Włodarska-Kowalczuk, M., Zhulay, I. & Albano, P. G. 2018. Trait-based approaches in rapidly changing ecosystems: A roadmap to the future polar oceans. *Ecological Indicators,* 91**,** 722-736.

Dethier, M. N., Mcdonald, K. & Strathmann, R. R. 2003. Colonization and connectivity of habitat patches for coastal marine species distant from source populations. *Conservation Biology,* 17**,** 1024-1035.

Deyoung, B., Barange, M., Beaugrand, G., Harris, R., Perry, R. I., Scheffer, M. & Werner, F. 2008. Regime shifts in marine ecosystems: detection, prediction and management. *Trends in Ecology & Evolution,* 23**,** 402-409.

Duarte, C. M., Borja, A., Carstensen, J., Elliott, M., Krause-Jensen, D. & Marbà, N. 2015. Paradigms in the recovery of estuarine and coastal ecosystems. *Estuaries and Coasts,* 38**,** 1202-1212.

Dunton, K. H., Reimnitz, E. & Schonberg, S. 1982. An arctic kelp community in the Alaskan Beaufort Sea. *Arctic***,** 465-484.

Dye, A. 1998. Dynamics of rocky intertidal communities: analyses of long time series from South African shores. *Estuarine, Coastal and Shelf Science,* 46**,** 287-305.

Edwards, K. F. & Stachowicz, J. J. 2010. Multivariate trade-offs, succession, and phenological differentiation in a guild of colonial invertebrates. *Ecology,* 91**,** 3146-3152.

Fish, J. D. & Fish, S. 1989. *A Student's Guide to the Seashore.,* London, Unwin Hyman Limited.

Frainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A. V., Fossheim, M. & Aschan, M. M. 2017. Climate-driven changes in functional biogeography of Arctic marine fish communities. *Proceedings of the National Academy of Sciences,* 114**,** 12202-12207.

Grebmeier, J. M., Overland, J. E., Moore, S. E., Farley, E. V., Carmack, E. C., Cooper, L. W., Frey, K. E., Helle, J. H., Mclaughlin, F. A. & Mcnutt, S. L. 2006. A major ecosystem shift in the northern Bering Sea. *Science,* 311**,** 1461-1464.

Greenacre, M. 2017. 'Size' and 'shape' in the measurement of multivariate proximity. *Methods in Ecology and Evolution,* 8**,** 1415-1424.

Greenacre, M. & Primicerio, R. 2013. *Multivariate analysis of ecological data,* Bilbao, Fundacíon BBVA.

Grosberg, R. K. 1987. Limited dispersal and proximity-dependent mating success in the colonial ascidian *Botryllus schlosseri*. *Evolution,* 41**,** 372-384.

Gulliksen, B., Haug, T. & Sandnes, O. K. 1980. Benthic macrofauna on new and old lava grounds at Jan Mayen. *Sarsia,* 65**,** 137-148.

Gulliksen, B. & Svensen, E. 2004. *Svalbard and life in polar oceans,* Kristiansund, Kom.

Gutt, J., Starmans, A. & Dieckmann, G. 1996. Impact of iceberg scouring on polar benthic habitats. *Marine Ecology Progress Series,* 137**,** 311-316.

Hadfield, M. G. & Strathmann, M. F. 1990. Heterostophic shells and pelagic devolopment in trochoideans: implications for classification, phylogeny and palaeoecology. *Journal of Molluscan Studies,* 56**,** 239-256.

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

Hop, H., Wiencke, C., Vögele, B. & Kovaltchouk, N. A. 2012. Species composition, zonation, and biomass of marine benthic macroalgae in Kongsfjorden, Svalbard. *Botanica Marina,* 55**,** 399-414.

Horn, H. S. 1974. The ecology of secondary succession. *Annual review of ecology and systematics,* 5**,** 25-37.

Horton, T., Kroh, A., Ahyong, S., Bailly, N., Boury-Esnault, N., Brandão, S. N., Costello, M. J., Gofas, S., Hernandez, F., Mees, J., Paulay, G., Poore, G. C. B., Rosenberg, G., Decock, W., Dekeyzer, S., Lanssens, T., Vandepitte, L., Vanhoorne, B., Verfaille, K., Adlard, R., Adriaens, P., Agatha, S., Ahn, K. J., Akkari, N., Alvarez, B., Anderson, G., Angel, M., Arango, C., Artois, T., Atkinson, S., Bank, R., Barber, A., Barbosa, J. P., Bartsch, I., Bellan-Santini, D., Bernot, J., Berta, A., Bieler, R., Blanco, S., Blasco-Costa, I., Blazewicz, M., Bock, P., Böttger-Schnack, R., Bouchet, P., Boxshall, G., Boyko, C. B., Bray, R., Breure, B., Bruce, N. L., Cairns, S., Campinas Bezerra, T. N., Cárdenas, P., Carstens, E., Chan, B. K., Chan, T. Y., Cheng, L., Churchill, M., Coleman, C. O., Collins, A. G., Corbari, L., Cordeiro, R., Cornils, A., Coste, M., Crandall, K. A., Cribb, T., Cutmore, S., Dahdouh-Guebas, F., Daly, M., Daneliya, M., Dauvin, J. C., Davie, P., De Broyer, C., De Grave, S., De Mazancourt, V., De Voogd, N., Decker, P., Decraemer, W., Defaye, D., D'hondt, J. L., Dijkstra, H., Dohrmann, M., Dolan, J., Domning, D., Downey, R., Drapun, I., Ector, L., Eisendle-Flöckner, U., Eitel, M., Encarnação, S. C. D., Enghoff, H., Epler, J., Ewers-Saucedo, C., Faber, M., Feist, S., Figueroa, D., Finn, J., Fišer, C., Fordyce, E., Foster, W., Frank, J. H., et al. 2018. World Register of Marine Species (WoRMS). WoRMS Editorial Board.

Hughes, R. N. 2005. Lessons in modularity: the evolutionary ecology of colonial invertebrates. *Scientia Marina,* 69**,** 169-179.

Hussin, W. R. W., Cooper, K. M., Froján, C. R. B., Defew, E. C. & Paterson, D. M. 2012. Impacts of physical disturbance on the recovery of a macrofaunal community: a comparative analysis using traditional and novel approaches. *Ecological Indicators,* 12**,** 37-45.

Iken, K., Bluhm, B. & Dunton, K. 2010. Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. *Deep Sea Research Part II: Topical Studies in Oceanography,* 57**,** 71-85.

Jablonski, D. & Lutz, R. A. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews,* 58**,** 21-89.

Jackson, J. 1986. Modes of dispersal of clonal benthic invertebrates: consequences for species' distributions and genetic structure of local populations. *Bulletin of Marine Science,* 39**,** 588-606.

Johnson, C. R., Banks, S. C., Barrett, N. S., Cazassus, F., Dunstan, P. K., Edgar, G. J., Frusher, S. D., Gardner, C., Haddon, M. & Helidoniotis, F. 2011. Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *Journal of Experimental Marine Biology and Ecology,* 400**,** 17-32.

Jueterbock, A., Tyberghein, L., Verbruggen, H., Coyer, J. A., Olsen, J. L. & Hoarau, G. 2013. Climate change impact on seaweed meadow distribution in the North Atlantic rocky intertidal. *Ecology and evolution,* 3**,** 1356-1373.

Konar, B. 2007. Recolonization of a high latitude hard-bottom nearshore community. *Polar Biology,* 30**,** 663-667.

Konar, B. 2013. Lack of recovery from disturbance in high-arctic boulder communities. *Polar biology,* 36**,** 1205-1214.

Kortsch, S. 2010. *Long-term patterns (1980-2008) in the structure of a rocky-bottom macrobenthic community in Smeerenburgfjord, northwest Svalbard: assessment of density and cover using image analysis.* Universitetet i Tromsø.

Kortsch, S., Primicerio, R., Beuchel, F., Renaud, P. E., Rodrigues, J., Lønne, O. J. & Gulliksen, B. 2012. Climate-driven regime shifts in Arctic marine benthos. *Proceedings of the National Academy of Sciences,* 109**,** 14052-14057.

Krause-Jensen, D. & Duarte, C. M. 2014. Expansion of vegetated coastal ecosystems in the future Arctic. *Frontiers in Marine Science,* 1**,** 77.

Krumhansl, K., Jamieson, R. & Krkosek, W. 2016. Using species traits to assess human impacts on near shore benthic ecosystems in the Canadian Arctic. *Ecological indicators,* 60**,** 495-502.

Laudien, J. & Orchard, J.-B. 2012. The significance of depth and substratum incline for the structure of a hard bottom sublittoral community in glacial Kongsfjorden (Svalbard, Arctic)—an underwater imagery approach. *Polar biology,* 35**,** 1057-1072.

Lotze, H. K., Coll, M., Magera, A. M., Ward-Paige, C. & Airoldi, L. 2011. Recovery of marine animal populations and ecosystems. *Trends in Ecology & Evolution,* 26**,** 595-605.

Lovrich, G. A. & Thatje, S. 2006. Reproductive and larval biology of the sub-Antarctic hermit crab Pagurus comptus reared in the laboratory. *Journal of the Marine Biological Association of the United Kingdom,* 86**,** 743-749.

Lu, L. & Wu, R. 2000. An experimental study on recolonization and succession of marine macrobenthos in defaunated sediment. *Marine Biology,* 136**,** 291-302.

Marlin 2006. BIOTIC - Biological Traits Information Catalogue. *Marine Life Information Network.* www.marlin.ac.uk/biotic: Plymouth: Marine Biological Association of the United Kingdom. .

Mcedward, L. R. 1995. *Ecology of marine invertebrate larvae*, CRC press.

Meyer, K. S., Sweetman, A. K., Kuklinski, P., Leopold, P., Vogedes, D., Berge, J., Griffiths, C., Young, C. M. & Renaud, P. E. 2017. Recruitment of benthic invertebrates in high Arctic fjords: Relation to temperature, depth, and season. *Limnology and Oceanography,* 62**,** 2732-2744.

Molis, M., Beuchel, F., Laudien, J., Wlodarska-Kowalczuk, M. & Buschbaum, C. in press. Ecological drivers of and responses by Arctic benthic communities, with an emphasis on Kongsfjorden, Svalbard. In: Hop H, Wiencke C (eds) The ecosystem of Kongsfjorden, Svalbard. *Advances in Polar Ecology,* 1, Springer Verlag.

Nenadic, O. & Greenacre, M. 2007. Correspondence Analysis in R, with two- and three-dimensional graphics: The ca package. *Journal of Statistical Software 20(3):1-13.*

Newell, R., Seiderer, L. & Hitchcock, D. 1998. The impact of dredging works in coastal waters: a review of the sensitivity to disturbance and subsequent recovery of biological resources on the sea bed. *Oceanography and Marine Biology: An Annual Review,* 36**,** 127-178.

Ni, S., Taubner, I., Böhm, F., Winde, V. & Böttcher, M. E. 2018. Effect of temperature rise and ocean acidification on growth of calcifying tubeworm shells (Spirorbis spirorbis): an in situ benthocosm approach. *Biogeosciences,* 15**,** 1425.

Norkko, A., Villnäs, A., Norkko, J., Valanko, S. & Pilditch, C. 2013. Size matters: implications of the loss of large individuals for ecosystem function. *Scientific reports,* 3**,** 2646.

Oksanen, J., Blanchet, F. G., Friendly, M., Roeland Kindt, Pierre Legendre, Dan Mcglinn, Peter R. Minchin, R. B. O'hara, Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens, Szoecs, E. & Wagner, H. 2017. Vegan: Community Ecology Package. R package version 2.4-3. https://CRAN.R-project.org/package=vegan.

Paar, M., Voronkov, A., Hop, H., Brey, T., Bartsch, I., Schwanitz, M., Wiencke, C., Lebreton, B., Asmus, R. & Asmus, H. 2016. Temporal shift in biomass and production of macrozoobenthos in the macroalgal belt at Hansneset, Kongsfjorden, after 15 years. *Polar Biology,* 39**,** 2065-2076.

Palerud, R., Gulliksen, B., Brattegard, T., Sneli, J.-A. & Vader, W. 2004. The marine macro-organisms in Svalbard waters. *A catalogue of the terrestrial and marine animals of Svalbard. Norsk Polarinstitutt Skrifter,* 201**,** 5-56.

Potthoff, M., Johst, K. & Gutt, J. 2006. How to survive as a pioneer species in the Antarctic benthos: minimum dispersal distance as a function of lifetime and disturbance. *Polar Biology,* 29**,** 543-551.

Renaud, P. E., Sejr, M. K., Bluhm, B. A., Sirenko, B. & Ellingsen, I. H. 2015. The future of Arctic benthos: Expansion, invasion, and biodiversity. *Progress in Oceanography,* 139**,** 244-257.

Rouse, G. W. 2005. Annelid sperm and fertilization biology. *Hydrobiologia,* 535**,** 167-178.

Ruppert, E. E., Barnes, R. D. & Fox, R. S. 2003. *Invertebrate Zoology: A Functional Evolutionary Approach*, Brooks Cole.

Scherrer, K. 2015. *Light, temperature and competition: understanding the causes for climate-driven regime shifts in arctic marine benthos.* Uppsala Universitet.

Sejr, M. K., Petersen, J. K., Jensen, K. T. & Rysgaard, S. 2004. Effects of food concentration on clearance rate and energy budget of the Arctic bivalve Hiatella arctica (L) at subzero temperature. *Journal of Experimental Marine Biology and Ecology,* 311**,** 171-183.

Shick, M. J. 1991. *A Functional Biology of Sea Anemones,* University of California, Chapman & Hall.

Strathmann, R. R. 1990. Why life histories evolve differently in the sea. *American Zoologist,* 30**,** 197-207.

Svane, I. & Lundälv, T. 1982. Population dynamics and reproductive patterns of boltenia echinata (Ascidicea) on the Swedish west coast. *Netherlands Journal of Sea Research,* 16**,** 105-118.

Svavarsson, J. 1990. Life cycle and population dynamics of the symbiotic copepod Lichomolgus canui Sars associated with the ascidian Halocynthia pyriformis (Rathke). *Journal of experimental marine biology and ecology,* 142**,** 1-12.

Svendsen, H., Beszczynska-Møller, A., Hagen, J. O., Lefauconnier, B., Tverberg, V., Gerland, S., Børre Ørbæk, J., Bischof, K., Papucci, C. & Zajaczkowski, M. 2002. The physical environment of Kongsfjorden–Krossfjorden, an Arctic fjord system in Svalbard. *Polar research,* 21**,** 133-166.

Teixidó, N., Garrabou, J. & Harmelin, J.-G. 2011. Low dynamics, high longevity and persistence of sessile structural species dwelling on Mediterranean coralligenous outcrops. *PloS one,* 6**,** e23744.

Vihtakari, M. 2017. PlotSvalbard: PlotSvalbard - plot research data from Svalbard on maps. R package version 0.1.16. https://github.com/MikkoVihtakari/PlotSvalbard.

Voronkov, A., Hop, H. & Gulliksen, B. 2013. Diversity of hard-bottom fauna relative to environmental gradients in Kongsfjorden, Svalbard. *Polar Research,* 32**,** 11208.

Voronkov, A., Hop, H. & Gulliksen, B. 2016. Zoobenthic communities on hard-bottom habitats in Kongsfjorden, Svalbard. *Polar Biology,* 39**,** 2077-2095.

Wangensteen, O. S., Turon, X. & Palacín, C. 2016. Reproductive strategies in marine invertebrates and the structuring of marine animal forests. *Springer International Publishing AG*.

Wassmann, P., Duarte, C. M., Agusti, S. & Sejr, M. K. 2011. Footprints of climate change in the Arctic marine ecosystem. *Global change biology,* 17**,** 1235-1249.

Weigel, B., Blenckner, T. & Bonsdorff, E. 2016. Maintained functional diversity in benthic communities in spite of diverging functional identities. *Oikos,* 125**,** 1421-1433.

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

Zimmer, R. & Woollacott, R. 1977. *Biology of bryozoans,* New York, Academic Press.

Web resources

Artdatabanken; http://artfakta.artdatabanken.se/

Ght - Marine Macrofauna Genus Trait Handbook; http://www.genustraithandbook.org.uk/

MarLIN – Biological Traits Information Catalogue; http://www.marlin.ac.uk/biotic/

WoRMS – World Register of Marine Species; http://www.marinespecies.org/

Appendix – taxonomic list

Taxonomic level	Identified taxa	Colonial/solitary
Rhodophyta		
Genus	*Lithothamnium* spp. (crustose coralline algae)	Colonial
Genus	*Hildenbrandia* sp.	Colonial
Class	Rhodophyta indet.	Colonial
Species	*Callophyllis cristata*	Colonial
Species	*Polysiphonia arctica*	Colonial
Species	*Phycodrys rubens*	Colonial
Species	*Turnerella pennyi*	Colonial
Genus	*Ptilota* sp.	Colonial
Ochrophyta		
Class	Phaeophyceae indet.	Colonial
Species	*Sacchoriza dermatodea*	Colonial
Species	*Desmarestia aculeata*	Colonial
Species	*Desmarestia viridis*	Colonial
Porifera		
Phylum	Porifera indet.	Colonial
Genus	*Haliclona* spp.	Colonial
Genus	*Grantia* sp.	Colonial
Cnidaria		
Class	Hydrozoa	Colonial
Order	Actiniaria	Solitary
Annelida		
Species	*Spirorbis spirorbis*	Solitary
Class	Polychaeta indet	Solitary
Family	Polynoidae	Solitary
Class	Calcareous polychaete	Solitary
Family	Sabellidae	Solitary
Arthropoda		
Crustacea		
Species	*Balanus balanus*	Solitary
Unaccepted suborder	Natantia	Solitary
Genus	*Hyas* spp.	Solitary
Infraorder	Brachyura	Solitary
Genus	*Pagurus* spp.	Solitary
Pycnogonida		
Genus	*Nymphon* sp.	Solitary
Mollusca		
Species	*Hiatella arctica*	Solitary
Genus	*Tonicella* spp.	Solitary
Class	Gastropoda indet.	Solitary
Genus	*Margarites* spp.	Solitary
Species	*Chlamys islandica*	Solitary
Phylum	Bryozoa	Colonial
Echinodermata		
Genus	*Henricia* sp.	Solitary
Species	*Ophiopholis aculeata*	Solitary
Species	*Strongylocentrotus droebachiensis*	Solitary
Genus	*Ophiura* spp.	Solitary
Genus	*Pteraster* spp.	Solitary
Chordata		
Species	*Dendrodoa aggregata*	Solitary
Genus	*Styela* spp.	Solitary
Species	*Halocynthia pyriformis*	Solitary
Genus	*Botryllus* spp.	Colonial
Species	*Boltenia echinata*	Solitary
Species	*Didemnum albidum*	Colonial
Class	Ascidiacea indet	Solitary
Assemblages		
	Algae/Hydrozoa	Colonial
	Algae/Bryozoa	Colonial
	Hydrozoa/Bryozoa	Colonial
	Algae/Hydrozoa/turf	Colonial
	Algae/Hydrozoa/Bryozoa	Colonial

Appendix 2 - Traits

Species	s	s/m	m	m/l	l	indet	infauna	epibenthic	hyper_benthic	free_living	crevice_dwelling	tube_dwelling	burrowing	epi_endozoic_phytic	attached
Balan	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1
Bolten	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1
Botryl	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1
Bryoz	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1
Dendr	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1
Didem	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1
Grantia	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1
HalocP	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1
Henri	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0
HiatAr	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0
Hyas	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0
Hydroz	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1
Margar	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0
Natan	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0
Nymph	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0
Ohiura	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0
Pagurus	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0
Polycha	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0
Pteras	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0
SeaAne	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1
Spiror	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Haliclona	0	0	0	1	1	1	0	1	0	0	0	0	0	0	1
Strongy	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0
StyeRu	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1
Tonicel	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0

Species	surf/dep_feed	filter/susfeeder	graze	op/scavenger	pred	nomob	lowmob	medmob	highmob	sol	greg	col	1_2yr	3_5yr	6_10yr	10_20yr	ov20yr	1_10m	10_100m	100m_1km	1_10km	ov10km	Asex	Sex	Lecitho	Plankto
Balan	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1
Bolten	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0
Botryl	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	1	1	0
Bryoz	0	1	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	0	1	1	1	0
Dendr	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	1	1	0
Didem	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	1	1	0
Grantia	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	1	0
HalocP	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	1	1	0
Henri	1	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0
HiatAr	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1
Hyas	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	1
Hydroz	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	1	1	0
Margar	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0
Natan	1	0	1	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	1
Nymph	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1
Ohiura	1	1	0	1	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	1
Pagurus	0	0	0	1	1	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	1
Polycha	1	1	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Pteras	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0
SeaAne	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1
Spiror	1	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0
Haliclona	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	1	1	1	0
Strongy	1	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1
StyeRu	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	1	1	1	0
Tonicel	1	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	1	1	0

Appendix 3 – Abundance and cover

Treatment	Asci	Balan	Bolten	Brachy	Dendr	Gastro	HalocP	Henri	HiatAr	Hyas	Lebbe	Margar	Ohiura	OphiAc	Pagurus	Polycha	Polypol	Pteras	Actin	Nymph	Spirorbis	Strongy	StyeRu	Tonicel	Wo	Chlamys	Sabel	Porifera
Manipulat	1.200729	148.8904	3.602188	0	37.22261	0	7.204376	3.602188	19.21167	0	19.21167	1.200729	1.200729	0	0	0	0	0	0	0	0	0	26.41604	15.60948	4.802917	0	0	0
Manipulat	0	3.558043	0	0	4.447554	0	0.889511	0	1.779022	0	3.558043	0	0	0	0	0.889511	0	0	0	0	0	0	2.668532	8.895108	0	0	0	0
Manipulat	0	6.233881	0	0	3.562218	0	0.890554	0	1.781109	0	48.08994	3.562218	0	0	0.890554	0	0	0	0	0	58.12471	0.890554	2.671663	24.93552	25.82608	0	0	0
Manipulat	0	3.666368	0	0	4.58296	0	1.833184	0	0	0	67.82781	0.916592	0	0	0	0.916592	0	0	0	0	0	0	1.833184	27.49776	72.41077	0	0	0
Manipulat	1.786479	5.359438	0	0	0	0	2.679719	0	2.679719	0	16.07831	1.786479	0	0	0	0	0	0	0	0	31.52957	0.89324	0	30.37015	22.33099	0	0	0
Manipulat	0	18.29483	1.016379	1.016379	8.131035	0	2.032759	0	3.049138	0	69.1138	10.16379	0	0	0	0	0	0	0	0	103.567	1.016379	1.016379	19.31121	98.5888	0	0	0
Manipulat	2.849297	121.57	0.949766	0.949766	9.497657	0	0	0	3.799063	0	35.14133	3.799063	0	0	0	0	0	0	0	0	54.39878	0.949766	9.497657	38.94039	75.03149	0	0	0
Manipulat	0.948123	142.2184	2.844368	0	21.80682	0	0	0	0	0	41.7174	2.844368	0	0	0	0	0	0	0	0	226.6905	1.896245	6.636859	44.56177	33.1843	0	0	0
Manipulat	0	102.2701	0.929728	0	17.66483	0	0	0	7.437825	0	28.82157	0.929728	0.929728	0	0	0.929728	0	0	0	2.789184	48.29751	0	1.859456	46.4864	0	0	0	0
Manipulat	3.816258	77.27923	1.908129	0	20.03536	0	0.954065	0	0	0.954065	68.69265	1.908129	0	0	2.862194	0.954065	0	0	0	1.908129	523.5754	0	6.678452	25.75974	39.11665	0	0	0
Manipulat	1.076699	92.59612	0	0	15.07379	0	3.230097	0	7.536894	0	79.67573	3.230097	0	0	0	1.076699	0	0	0	0	106.1281	0	3.230097	24.76408	54.91166	0	0	0
Manipulat	1.071646	123.2392	0	0	11.7881	0	5.358228	0	7.501519	0	73.94355	1.071646	0	0	1.071646	0	0	0	0	0	237.6674	3.214937	6.429874	21.43291	5.358228	0	0	0
Manipulat	0	119.1551	1.063884	0	3.191653	0	3.191653	1.063884	6.383306	1.063884	35.10818	5.319422	0	0	0	0	0	0	0	2.127769	595.888	0	2.127769	22.34157	31.91653	0	2.127769	1.063884
Manipulat	0	92.91837	1.093157	0	1.093157	0	1.093157	0	0	1.093157	37.16735	0	0	0	0	0	0	1.093157	0	1.093157	333.4436	1.093157	1.093157	6.558944	3.279472	0	0	0
Manipulat	1.99534	81.80895	0.99767	0	0.99767	0	0.99767	0	5.986021	0	26.93709	4.988351	0	0	0	0	0	0	0	0	1665.772	0	0.99767	1.99534	1.99534	0	0	0
Manipulat	0	55.63195	0	0	13.08987	3.272468	0	1.090823	11.99905	0	10.90823	7.635758	0	0	1.090823	0	0	0	0	0	1532.163	0	0	7.635758	14.18069	0	0	0
Manipulat	0	82.57644	0	0	3.840765	0	3.840765	0.960191	4.800956	0	27.84554	0.960191	0	0	0	0	0	0	0	0.960191	2015.025	0	4.800956	8.641721	4.800956	0	0	0
Manipulat	0	59.28469	0.926323	0	16.67382	0	0.926323	1.852647	2.77897	0	6.484263	0.926323	0	0	0	0	0	0	0	0	1392.414	0	0	0.926323	3.705293	0	0	1.852647
Manipulat	0	30.41931	0	0	9.125794	0	0	0	1.013977	0	5.069886	3.041931	0	0	0	0	0	0	0	0	2393.294	0	0	4.055908	3.041931	0	0	0
Manipulat	0	44.19952	0.902031	0	46.00358	0	3.608124	0	18.94265	0	60.43608	6.314217	0	0	0.902031	0	0	0	0	0	5561.167	1.804062	5.412186	17.13859	5.412186	0	0	2.706093
Manipulat	0	209.3182	1.938131	0	102.721	0	0.969066	0	54.26768	0	9.690657	3.876263	3.876263	0	0	0	0.969066	0	1.938131	0	1735.475	0.969066	50.39142	77.52526	31.0101	0	12.59785	0
Control	0	144.4415	9.701297	0	134.7402	0	16.16883	1.077922	42.03895	7.545453	0	0	1.077922	0	0	0	0	0	0	0	0	0	40.96103	6.467531	0	0	0	0
Control	0	144.4415	9.701297	0	134.7402	0	16.16883	1.077922	42.03895	7.545453	0	0	1.077922	0	0	0	0	0	0	0	0	0	40.96103	6.467531	0	0	0	0
Control	0	141.8353	7.151362	0	56.019	2.383787	13.11083	4.767575	38.1406	0	16.68651	1.191894	0	4.767575	0	7.151362	4.767575	0	0	0	0	0	48.86764	7.151362	0	0	0	0
Control	0	183.2872	11.0778	0	57.40314	1.007073	16.11316	0	47.33242	4.028291	49.34656	2.014145	0	1.007073	0	3.021218	0	0	1.007073	0	0	1.007073	60.42436	9.063654	0	0	0	0
Control	0	94.03342	9.727595	0	50.79966	1.080844	11.88928	0	22.69772	0	7.565907	1.080844	0	0	0	0	0	0	0	0	0	3.242532	32.42532	15.13181	0	0	0	0
Control	0	184.9981	1.350351	0	86.42249	0	18.90492	1.350351	6.751757	0	14.85386	6.751757	0	0	0	0	0	0	1.350351	0	0	0	28.35738	2.700703	0	0	0	0
Control	0	197.8021	4.253808	0	143.566	0	15.95178	0	36.15737	0	10.63452	2.126904	1.063452	2.126904	0	2.126904	0	0	0	0	0	1.063452	14.88833	6.380712	0	0	0	0
Control	0	154.4013	7.453858	0	155.4662	1.064837	9.583532	1.064837	37.26929	0	6.389021	1.064837	0	1.064837	1.064837	2.129674	0	0	0	0	0	0	74.53858	19.16706	0	0	0	0
Control	0	79.14461	9.893076	0	128.61	0	7.914461	0.989308	16.81823	0	13.85031	0	0	2.967923	0.989308	0.989308	0	0	0	0	0	0	77.16599	23.74338	0	0	0	0
Control	0	86.30601	4.262025	0	188.5946	0	8.52405	0	11.72057	1.065506	63.93038	0	0	3.196519	0	26.63766	0	0	0	0	0	1.065506	33.03069	23.44114	0	0	0	0
Control	0	49.80875	3.396051	0	131.314	1.132017	6.792102	1.132017	6.792102	0	52.07278	3.396051	0	1.132017	0	0	0	0	0	0	11.32017	0	13.5842	7.924119	0	0	0	0
Control	0	44.90558	0	0	51.99593	0	3.545177	0	37.81523	0	37.81523	0	0	7.090355	0	0	0	0	0	0	0	3.545177	41.3604	11.81726	0	0	0	0
Control	0	37.44632	0	0	43.5187	0	2.024126	3.036188	40.48251	2.024126	7.084439	0	0	2.024126	0	1.012063	0	1.012063	0	1.012063	0	2.024126	11.13269	4.048251	0	0	0	0
Control	0	10.37332	0	0	42.64589	0	4.610366	1.152592	4.610366	0	18.44147	0	0	0	0	0	0	0	0	0	172.8887	0	12.67851	0	0	0	0	0
Control	0	8.853127	0	0	5.902084	0	2.951042	0.983681	20.6573	0	6.885765	0	0	0	0	0	0	0	0	0	245.9202	0	3.934723	0.983681	0	0	0	0
Control	0	16.99657	0	0	35.12624	0	6.798628	1.133105	26.06141	0	2.266209	6.798628	0	1.133105	0	21.52899	0	0	0	0	566.5523	1.133105	14.73036	2.266209	0	0	0	0
Control	0	10.2685	0	0	50.48681	0	0	0	21.39272	0	9.412796	0.855709	0	0	0.855709	0	0	0	0	0	5168.48	0	0	5.134252	0	0	0	0
Control	0	31.90696	0	0	38.08249	0	6.17554	0	0	0	5.146283	0	0	0	0	0	0	0	0	0	1471.837	1.029257	0	0	0	0	0	0
Control	0	15.07117	0	0	38.25759	0	5.796604	0	1.159321	0	2.318642	6.955925	1.159321	0	2.318642	0	0	0	1.159321	1.159321	1889.693	2.318642	0	5.796604	0	0	0	0
Control	0	9.299048	0	0	115.7215	0	8.265821	0	35.12974	0	28.93037	7.232593	5.166138	0	1.033228	0	0	0	1.033228	2.066455	3574.967	5.166138	0	11.3655	0	0	0	0
Control	0	56.6983	1.01247	1.01247	110.3592	0	3.037409	1.01247	125.5462	0	10.1247	3.037409	0	0	2.024939	0	0	0	2.024939	0	540.598	5.062348	85.04744	61.76064	29.36162	1.01247	9.112226	5.062348

Al_bry_hy	Botryl	Brownal	Bryoz	Bry_al	Dead_al	Des	Didem	Grantia	Stone	Halicl	Hilden	Hydroz	Hyd_al	Hyd_bryo	Litho	PhycoRu	Phymato	Redal	Sacc	Shade	Un_org	Al_hy_tur	Polysiph	Callo	Ptilota	Scraped_t	Epi_bryo	Undet_al	Turne	Calc_algae
0	1261.822	0	5.610653	0	163.6607	0	1.234403	0	337.0771	1089.834	45.69595	215.6582	21.9181	0	6391.111	0	0	0	0	1127.882	876.0635	0	0	0	0	0	0	0	0	6391.111
0	99.68988	0	0	0	3321.284	0	0	0	1033.932	92.56492	11.97244	0	7.40073	0	2410.844	0	0	0	0	805.767	315.4856	0	0	0	0	2991.059	0	0	0	2410.844
0	293.9778	259.4414	20.02599	0	761.856	14.86058	0	0	969.439	178.8941	49.02408	442.8889	523.4701	0	4666.994	0	0	0	0	821.9109	376.5772	858.2516	0	0	0	1145.672	0	0	0	4666.994
29.39889	535.8604	0	34.82318	0	105.8189	2275.012	0	0	1046.92	267.0871	61.0532	902.2067	484.0642	37.84278	3947.898	0	0	0	1.623506	1097.933	396.5961	0	0	0	0	178.9664	0	0	0	3947.898
0	261.4263	0	155.9904	0	151.1904	18.62405	7.360295	0	850.4866	470.3551	63.81763	1630.871	1111.045	46.44846	4820.956	0	0	0	0	705.2888	546.6261	326.9013	0	0	0	108.9671	0	0	0	4820.956
0	1067.251	5.945819	172.3359	0	102.6662	23.05148	1.740982	0	548.9363	626.21	110.8407	1468.745	1094.392	278.0791	4361.141	0	0	0	0	1783.628	950.3794	0	0	0	0	0	0	0	0	4361.141
701.4999	472.3285	94.08379	63.41408	18.69139	259.8956	0	63.09294	0	394.39	1000.429	73.85215	322.4165	1671.303	203.5654	4271.537	3.585788	0	0	17.59916	909.3086	1001.574	196.9909	0	0	0	65.66364	0	0	0	4271.537
307.365	585.7019	84.79612	288.4341	0	215.9191	11.82309	86.59329	0	181.0761	1067.904	211.2155	1539.951	807.9539	188.2118	4098.167	45.97447	0	0	0	1098.912	887.5709	0	16.87658	1.846925	0	0	0	0	0	4098.167
632.5544	1207.152	132.5234	777.0479	166.309	155.0879	92.43356	20.75153	0	218.4233	1188.84	90.10598	401.6753	1320.813	330.1092	2898.664	37.07756	0	138.1283	0.939025	938.276	676.2878	0	0	17.11309	0	0	0	0	0	2898.664
1065.438	819.2248	92.34939	1079.942	681.2786	110.0023	109.6125	52.48309	2.890816	97.45638	977.7144	88.1492	327.4327	1581.153	847.1508	1785.433	97.12377	0	0	0	1002.833	885.2274	0	0	0.810955	0	0	0	0	0	1785.433
507.1009	718.8264	29.07088	1360.097	275.2223	115.6091	39.84898	9.505792	0.31341	245.2814	887.7099	118.3126	699.2504	577.4543	689.1968	3424.654	125.6994	0	0	0	2702.494	868.0336	0	0	9.492455	0	0	0	0	4.500602	3424.654
22.97664	335.4606	0	2408.105	116.0174	54.57493	1264.98	1.591866	0	194.9478	762.6388	100.8073	981.2177	54.22298	430.1241	2615.046	209.269	0	0	33.26189	2389.687	1011.262	0	0	23.85511	0	0	0	0	60.6371	2615.046
188.4262	636.4514	40.34759	1015.256	168.7273	111.5947	1318.894	0.548465	0	126.4792	408.3329	121.2775	617.2644	93.92744	433.5269	3167.473	1248.651	0	13.91568	0	2672.208	893.4125	0	0	83.76987	0	0	0	0	0	3167.473
7.539497	627.1413	0	1937.341	385.7848	78.07652	1875.885	0	0	9.94614	340.2121	62.02252	130.7967	0	34.5743	1571.7	1633.949	0	0	0	2721.53	958.3785	0	1046.194	0	0	0	0	0	45.71347	1571.7
0	702.0308	0	2801.683	142.0505	9.720939	978.8039	3.491845	0	48.75508	268.7872	55.96398	45.23132	0	0	2254.898	2423.297	0	53.00249	0	1205.672	1584.409	0	0	6.544716	0	0	4.406729	0	0	2254.898
0	328.5503	0	999.0024	64.7585	157.1549	526.3158	49.28655	0	48.2689	53.95284	57.05702	89.63289	99.3194	0	2313.836	4686.603	0	0	176.8756	2466.972	1164.748	0	203.4825	0	0	0	0	0	0	2313.836
0	686.757	0	2048.25	384.12	145.6113	755.9582	3.187075	0	84.6057	10.56759	100.4296	60.88799	59.21499	12.30965	2790.634	2537.583	0	43.52547	14.59033	987.7024	1021.04	0	23.6688	10.91737	0	0	0	0	0	2790.634
0	549.922	19.22351	2098.827	0	34.3033	252.2939	5.071148	0	89.65611	3.226951	58.18398	0	0	0	1535.06	5018.692	0	0	0	827.3149	744.0159	0	120.5424	30.29568	0	0	0	0	0	1535.06
0	270.1338	0	1139.668	478.1609	158.6773	362.9137	11.37682	0	93.19686	0	77.65067	83.45032	0	0	1463.11	5189.683	0	0	0	2052.594	793.714	0	479.6064	0	0	0	9.443918	0	0	1463.11
0	346.8023	0	2668.665	366.6797	25.65904	393.3116	5.446498	0	90.55257	0	83.19881	12.31227	0	0	1919.583	3595.96	0	0	2.355693	531.3982	863.2864	0	14.29719	12.4249	46.49497	0	29.81632	0	0	1919.583
0	475.9557	0	1919.299	52.80439	66.12916	94.08659	0.823706	0	153.3656	0	160.1365	25.65117	5.756251	14.5263	3441.473	2838.235	0	0	0	754.5415	1349.373	0	36.01048	18.55717	65.61308	0	0	28.16105	0	3441.473
0	290.2736	21.12727	26.72168	0	10.07857	0	4.193116	0	23.77896	568.5283	12.26675	1112.782	0	0	6754.981	0	72.11297	95.05115	0	1443.445	1898.63	0	0	0	0	0	0	0	0	6827.094
0	290.2736	21.12727	26.72168	0	10.07857	0	4.193116	0	23.77896	568.5283	12.26675	1112.782	0	0	6754.981	0	72.11297	95.05115	0	1443.445	1898.63	0	0	0	0	0	0	0	0	6827.094
0	471.6681	0	43.53988	0	20.73895	0	9.034554	0	26.92488	947.5078	0	331.561	72.08573	0	7081.16	0	0	132.1095	0	3799.781	1295.374	0	0	0	0	0	0	0	0	7081.16
0	1050.478	24.70349	77.65537	0	0	0	0	0	21.64199	1007.707	16.34479	1150.409	56.33565	0	5487.64	0	14.91475	247.8809	0	876.4553	1521.717	0	0	0	0	0	0	0	0	5502.554
0	1286.755	250.2478	7.187612	0	33.96011	0	0	0	0	1416.284	0	1314.155	0	0	4927.102	0	0	142.1958	0	1923.221	1450.752	0	0	0	0	0	0	0	0	4927.102
0	1028.306	174.1953	0	0	28.64095	0	2.72771	0	0	928.5286	6.414169	1479.891	176.6935	0	5415.638	0	26.66944	27.76322	0	4717.088	2060.393	0	0	0	0	0	0	0	0	5442.308
29.81919	720.2441	8.699037	138.7273	0	414.7994	0	3.360508	0	749.4677	998.2411	22.47074	570.0953	307.7417	0	5076.292	27.69229	0	311.6446	21.35411	1421.708	1439.308	0	0	0	0	0	0	0	0	5076.292
0	415.4354	394.8202	6.601988	5.94179	331.718	0	2.587554	0	475.7798	1708.797	0	869.1198	145.5313	0	4650.196	58.48084	115.3112	163.8677	0	1823.107	1306.683	0	0	0	0	0	0	0	0	4765.507
0	1265.493	260.643	212.4043	0	316.4795	0	8.824623	0	311.5033	2280.651	0	699.1041	854.9794	0	2531.114	43.33167	49.04987	472.3548	0	966.0984	1341.541	0	0	0	0	0	0	0	0	2580.164
0	1140.049	179.8361	511.9118	0	187.2201	0	2.258873	0	316.5299	2072.719	27.39417	811.4683	1166.783	0	2503.247	96.11932	0	339.1293	26.63766	2037.61	920.4056	0	0	0	0	0	0	0	0	2503.247
0	486.3598	59.83842	775.6693	322.6022	174.2853	0	4.811072	0	282.3477	1996.368	0	902.659	562.3181	0	3384.142	241.1989	0	308.4067	0	3163.931	912.2132	0	0	0	0	0	0	0	0	3384.142
1.016284	530.7131	794.1788	1347.723	0	116.0455	0	8.425705	0	297.0977	1598.095	16.42599	878.3177	0	0	3202.17	290.1728	195.682	306.0906	0	3330.233	1309.919	0	0	0	0	0	0	0	0	3397.852
0	677.3837	3122.052	425.704	0	61.70547	0	0	0.283378	19.32028	1340.163	128.0259	601.3475	47.23297	0	2489.927	446.846	134.3716	148.2874	0	1804.437	653.4991	0	0	0	0	0	0	0	0	2624.299
0	838.2799	2648.46	2032.849	413.6767	23.50134	0	0	0	42.77267	821.7517	12.19442	260.4742	0	0	2025.611	549.5557	0	100.7019	0	3973.11	922.4536	0	0	0	0	0	0	0	0	2025.611
160.5465	617.1416	80.29786	1638.487	56.31572	32.49097	0	0	0	10.00403	743.5151	34.69442	312.0629	131.0164	0	3089.456	1269.745	6.187352	1725.917	0	944.3138	1158.146	0	0	0	0	0	0	0	0	3095.643
646.5609	599.707	1100.879	258.9257	0	42.16282	0	0	0	0	186.679	0	109.5259	207.1202	0	4119.153	1461.75	0	329.3595	560.1956	1671.737	2310.854	0	0	0	0	0	0	0	0	4119.153
0	834.2133	1988.436	1036.503	0	44.03477	0	3.902032	0	54.88516	36.66712	88.43749	64.57178	0	0	3980.064	846.681	0	920.2976	0	293.2257	339.1345	0	0	0	0	0	0	0	0	3980.064
0	735.445	609.1758	2177.701	0	28.70597	0	6.844557	0	456.9076	39.72931	0	0	0	0	4063.248	1720.474	0	0	0	1206.351	1621.614	0	0	0	0	0	0	0	0	4063.248
0	406.0637	3258.526	1272.331	0	1.51871	0	0.765152	0	115.2829	16.33483	358.775	0	0	0	4073.842	312.2515	0	0	0	1707.042	2781.466	0	0	0	0	0	0	0	0	4073.842
0	437.9438	1131.198	1656.677	0	67.61441	0	4.546201	0	29.16801	6.333685	185.578	0	0	0	3798.32	677.2393	0	1538.404	0	1148.763	1545.688	0	0	0	0	0	0	0	0	3798.32
0	578.515	0	772.8889	170.7327	135.7317	321.53	1.640201	21.06949	175.6837	0	283.0257	48.75041	0	16.74625	4518.601	1982.476	0	12.70649	0	1313.953	1348.539	0	333.062	8.778111	9.942451	0	0	0	0	4518.601