

Community analysis of large epibenthos in the Nordic Seas

Eric dos Santos



Faculty of Life and Environmental University of Iceland 2010

Community analysis of large epibenthos in the Nordic Seas

Eric dos Santos

90 ECTS thesis submitted in partial fulfillment of a Magister Scientiarum degree in marine biology

> Advisor(s) Jörundur Svavarsson Øle Tendal

Judicator Guðmundur Guðmundsson

Faculty of Life and Environmental Sciences School of Engineering and Natural Sciences University of Iceland Reykjavik, January 2010 Community analysis of large epibenthos in the Nordic Seas 90 ECTS thesis submitted in partial fulfillment of a *Magister Scientiarum* degree in marine biology

Copyright © 2010 Eric dos Santos All rights reserved

Faculty of Life and Environmental Sciences School of Engineering and Natural Sciences University of Iceland Sturtlugata 7 101 Reykjavik Iceland

Telephone: 525 4000

Bibliographic information:

Eric dos Santos, 2010, *Community analysis of large epibenthos in the Nordic Seas*, Master's thesis, Faculty of Life and Environmental Sciences, University of Iceland, pp. 47.

Printing: Háskólafjölritun / Háskólaprent, Fálkagötu 2, 101 Reykjavík Reykjavík, Iceland, January 2010

Hér með lýsi ég því yfir að ritgerð þessi er samin af mér og að hún hefur hvorki að hluta né í heild verið lögð fram áður til hærri prófgráðu.
I declare that this thesis is supported by my research work, written by myself and has not partly or as a whole been published before to higher educational degree.

Abstract

The aim of the presented project was to provide information about the community structure and diversity of epibenthic megafauna in the Nordic Seas. The focus was the importance of hard substrate in the formation and definition of animal communities.

The study was based on photographs from the Greenland-Iceland-Faeroes Ridge (GIF) and photographs and videos collected from the Jan Mayen Fracture Zone (JMFZ) and the Mohn Ridge. The GIF samples were collected from eight stations to the northwest of Iceland using a frame-mounted camera. Videos and stills collected from the JMFZ and the Mohn Ridge were recorded using an ROV. All animals large enough (>1 cm diameter for photographs, >5 cm diameter for videos) were identified to lowest possible taxonomic level.

On the GIF Ridge, community structure was found to vary somewhat between stations but also, within stations. Community structure was more strongly influenced by high habitat heterogeneity than by other measured environmental variables. The presence of hard surfaces in soft sediment areas caused a shift of community structure from that found on soft bottoms to one more like that found on hard bottoms. The wider scope provided by video data from the JMFZ and Mohn Ridge areas showed distribution of epifauna in patches where high dominance of a few taxa was observed. This patchiness seems to be the result of presence or absence of hard surfaces to act as anchor sites for sessile and semi-sessile species.

Útdráttur

Markmiðið pappírsins er að bæta upplýsingar um samfélagsgerð og tegunda fjölbreytni stóra botndýra á norræna hafsvæðið. Áheyrslu var lagt á mikilvægi harðs botns í samfélagsmyndun og staðsetningu botndýrasamfélög.

Rannsóknin var byggð á ljósmyndum frá Grænlands-Íslands-Færeyja Hryggnum (GIF) og ljósmyndum og myndböndum safnaðar í Jan Mayen Fracture Zone (JMFZ) og Mohn Hrygginn (MR). Myndirnar frá GIF hrygginn voru teknar með ljósmyndavél sem var föst við rama. Fjarstírðan kafbát (ROV) var notaður til að safna myndböndin og ljósmyndirnar við JMFZ og MR. Öll dýr sem voru nóg stór (>1 sm þvermál á ljósmyndir, >5 þvermál á myndböndin) voru greind eins nákvæmlega og hægt var.

Á GIF Hryggnum tegundasamsetning var breytilegt milli stöðva jafn sem innan stöðva. Samfélagsgerð varð fyrir meira áhrif breytileika búsvæða heldur en önnur mældar breytur. Þar sem steinar voru til staðar á mjúkan botn var samfélagið meira líkt það sem finnst á hörðum botni. Bæði í JMFZ og MR var botndýralífið hnappdreift frekar en jafndreifð um allt. Hnappdreifingu botndýra virðist vera vegna framboði steina sem festingu fyrir staðbundin dýr.

Dedication I dedicate this paper to my loving wife who has supported me and assisted me throughout my education here in Iceland.

Table of Contents

L	List of Figures	X
L	List of Tables	Xi
A	Acknowledgements	xii
1	I Introduction	
	1.1 Background	
	1.2 Techniques	
	1.3 Aims	19
2	2 Methods	21
_	2.1 Study area	
	2.1.1 GIF Ridge	
	2.1.2 Jan Mayen Fracture Zone	
	2.1.3 Mohn Ridge	
	2.2 Data collection	
	2.2.1 GIF Ridge	23
	2.2.2 JMFZ and Mohn Ridge	24
	2.3 Visual analysis	25
	2.3.1 Photographic samples	
	2.3.2 JMFZ and Mohn Ridge samples	
	2.4 Statistical analysis	27
3	3 Results	29
	3.1 GIF Ridge	
	3.1.1 Present species and regional distribution	
	3.1.2 β–diversity and community analysis	
	3.1.3 Cover analysis	
	3.2 JMFZ and Mohn Ridge	
	3.2.1 Present species and regional distribution	37
	3.2.2 B-diversity and community analysis	38
4	4 Discussion	41
	4.1 Present species and regional distribution	41
	4.1.1 GIF Ridge	
	4.1.2 JMFZ and Mohn Ridge	42
	4.2 B-diversity and community analysis	43
	4.2.1 GIF Ridge	43
	4.2.2 JMFZ and Mohn Ridge	44
5	5 Concluding remarks	45
	References	
	Appendix I	
	Annendiy II	53 57
4	411112111111111	3 /

List of Figures

Figure 1. Sampled region. Grey boxes with numbers are Icelandic sampling stations. Black circle is area where Jan Mayen Fracture Zone video samples were collected. Black square is the area were Mohn Ridge video samples were collected.	22
Figure 2. Rarefaction of pooled abundance data by station.	32
Figure 3. Cluster diagram of Bray-Curtis similarity indices for samples pooled by station.	32
Figure 4 MDS plots of density data: a. density data from all photographs organized by station; b. density data omitting stations S3 and S4 to illustrate the relationship of the other six stations; c. density data organized by bottom type. (M: mud, S: sand, P: pebbles, St: stones)	33
Figure 5. Proportion of community structure represented by densities of present phyla.	34
Figure 6. Boxplot of percentage cover per station. Range for each station is the range of cover indices on ten photographs. Error bars indicate highest and lowest cover indices.	36
Figure 7. Dendrogram of Bray-Curtis similarity indices for the entire JMFZMR sample	39
Figure 8. Rarefaction of dives (D#) from the JMFZ/MR region	40
Figure 9. MDS grouping of JMFZ and MR frequency data by dive area. Very little variation is seen within the JMFZ sample and much more in the MR sample. The separation in the MR sample is caused by depth variation.	40

List of Tables

Table 1. Location, depth, and bottom type at GIF Ridge sampling stations	24
Table 2. Jan Mayen Fracture Zone (JMFZ) and Mohn Ridge sampling dives with depth and bottom type.	25
Table 3. List of species observed at a single station.	29
Table 4. Station average values of number of species (S), abundance (N), species diversity (d, H'), dominance (α, λ'), and evenness (J') for the Icelandic sample	31
Table 5. Rarefaction results for expected numbers of species from two samples of different size.	31
Table 6. Percentage of cover on ten slides per sampling station including station averages used in discussion of cover and standard deviation. Photographs are labeled P1–P10 for each station.	36
Table 7. Average proportion of observed cover represented by each taxon per site	37
Table 8. Average values for Abundance, species richness, and species diversity for dives from the Jan Mayen Fracture Zone and Mohn Ridge areas. Number of species (S), number of individuals (N), Margalef's diversity index (d), Fisher's diversity index(α), Shannon's diversity index (H'(log 10)), Simpson's index (dominance) (λ'), Pielou's evenness (J')	38
Table 9. Species identifications for the BIOICE sample. All identifications are conformis (cf.) names as physical specimens were not available for concrete identifications.	55
Table 10. Species identified from the Jan Mayen Fracture Zone and Mohn Ridge dive videos. All identifications are conformis (cf.) names as physical specimens were not available for concrete identifications	57

Acknowledgements

I wish to thank the Nordic Council of Ministers for its support through the MiFi (Miljö- og Fiskerisamarbejde). The Centre of Excellence in GeoBiology at the University of Bergen (funded by the Norwegian Research Council) and Dr. Christoffer Schander have my gratitude for letting me use ROV images and video from the Jan Mayen region. Also, I would like to thank Dr. Øle S. Tendal for the hospitality and expert guidance he provided at the Zoology Museum in Copenhagen, Denmark. I would like thank Dr. Stefán Áki Ragnarsson for supplying me with the photographs used to create the bulk of this work.

1 Introduction

1.1 Background

The Atlantic Ocean is traversed along an east-west axis by a single undersea ridge called the Greenland-Iceland-Faroe Ridge (GIF). The saddle depth of this ridge is more than 1000 m above the abyssal plains to both south and north and thus influences major ocean currents of varied physical and chemical qualities in the North Atlantic (Hansen & Østerhus 2000). The influence of major ocean currents also plays an important role in survivorship of all benthic marine life. Volcanic and tectonic forces that have shaped the ridge have left behind their mark in the form of gorges, canyons, chimneys, mounds, rises, and even mountains. This is, therefore, a region of complex bathymetry, hydrography, and ecology. Most of the region supports economically important fisheries. In addition, parts of the region have been shown to contain other valuable resources such as oil. It follows, that human disturbance is likely to increase as populations rise. However, until recent decades most of the research into sub-littoral benthic organisms in the region has been focused on identification of present species and compilation of large-scale species distribution information. On the GIF Ridge the two major study programs BIOICE (Benthic Invertebrates of Iceland) and BIOFAR (Biological Investigations of the Faroese Benthos) have compiled massive collections of samples of benthic organisms of the region. These programs have been used to further scientific knowledge about the distribution of benthic taxa of all sizes (e.g. Ringvold 1999, Schuchert 2000, Clausen 2004, Dijkstra et al. 2009). A number of other papers have been published in the last decade describing the taxa found on and around the GIF Ridge and especially the Icelandic margin (e.g. Piepenburg & von Juterzenka 1994, Svavarsson 1997, Sigurðsson et al. 2006).

There is a lack of studies of whole communities on the Icelandic margin. The majority of literature is concentrated on single taxa or species from a family rather than the structure of communities on a local scale. This information is a crucial part of understanding the ecology of an area if the goal is biodiversity conservation or sustainable use. In terms of conservation, species diversity is arguably the most common measure of biodiversity in any environment (Gray 1997). As one of the first steps of most analyses of animal communities, measuring the number of species in a given area can provide a wealth of information about that area. The present study is centered on the identification of species in a select area and then augmenting that information with the inclusion of environmental data to draw conclusions about the connection between the two. Species diversity can be used to analyze the importance of environmental variables in the functioning and structure of animal communities through multidimensional analysis and comparison of species diversities from more than one area of similar habitat. Some of the common environmental variables that explain observed species diversity are depth (e.g. Flach & de Bruin 1999; Jones et al. 2007b), bottom type (e.g. Mortensen & Buhl-Mortensen 2004; Jones et al. 2007a), hydrography (e.g. Gage et al. 2000), and climate (e.g. Gage 2001; Beuchel et al.

2006). Of these, climate is the only one not taken into account in the current study because it was outside the scale of the project.

Community and ecosystem diversity is another concept that will be discussed in the current paper. The concepts community and ecosystem have been combined by researchers because of the insightful observation that the community cannot truly be extracted from its environment, due to its dependency on ecosystem characteristics for existence (Gray, 1997). The current paper is just such a combination of these two concepts in that it focuses on megabenthos and a large proportion of the megabenthos is often an ecological feature in itself. That is, large emergent megafauna provide habitat for other species as well as influencing hydrographic effects near the bottom. Understanding this relationship between communities and their surroundings is crucial to understanding the sustainability of given species. The surroundings provide vital physical and nutritional characteristics that support the community and dictate, to some degree, which species will be able to teem. This relationship between fauna and their environment has been illustrated from both the perspective of organisms having an effect on their environment (e.g. Ambrose et al. 2001; Tendal & Dinesen 2005) and from the perspective of the environment shaping community structure (e.g. Seiderer & Newell 1999; Zajac 2008). For instance, mass occurrences of sponges carpeting the seafloor have been observed in areas of high bentho-pelagic diversity. While the abiotic ecosystem is shaping the community, the community is also altering its environment. This is one aspect of ecology where the use of photography provides information about the community in situ. Doing so allows the researcher to observe a community in its natural environment, with insight into possible interactions between community and environment. Such data about the connections between community and ecosystem is often lost by traditional sampling methods.

Using a blind sampling technique such as photography to collect samples also allows analysis of habitat diversity in a given region, which is often a second step after recognition of sampled species diversity. Much work has been done to link trends of species diversity with specific habitat (e.g. Barthel & Tendal 1993; Clarke & Ainsworth 1993; Maldonado & Young 1996; Mayer & Piepenburg 1996; Gage et al. 2000; Ojeda et al. 2003; Mortensen & Buhl-Mortensen 2004; Piepenburg 2005; Galparsoro et al. 2009). Photography provides direct visual evidence of the differences in megabenthic community structure and the surrounding habitat. To be referred to as a habitat, an area must have some identifying qualities that separate it from its surroundings. The area in question can be large (as in discussion of a pelagic versus a benthic habitat), it can be more localized (such as soft sediment versus hard bottom) or it can be even more specific and visually separable (as is the case in a polychaete reef or sponge mass occurrence).

At the smallest scale, habitat diversity is explored within a single habitat and is referred to as α -diversity. The effects of inter- and intraspecies competition are the primary forces influencing community structure at this scale (Gray 1997). Studies of α -diversity take the form of lists of species diversity in given habitat and they vary greatly in scale and scope. Many studies from the North Atlantic have examined a defined area of bottom different from its surroundings as a single habitat such as an undersea ridge (Piepenburg & von Juterzenka 1994), single seamount (Moore et al. 2004) or individual photographs of seafloor (Pech et al., 2004). Other researchers choose a single bottom type as a habitat of interest. Some commonly chosen habitats are soft sediment (Seiderer & Newell 1999; Sahade et al. 2004), rocky bottom (Mortensen & Buhl-Mortensen 2004; Serrano &

Preciado 2007), and reefs (Ross & Quattrini 2007 & 2009). In the context of the current paper, investigation of α -diversity is investigated in order to illustrate the trends and variety of species diversity in small localities.

The next larger scale of habitat diversity analysis, β -diversity, involves comparison of diversity figures from more than one area and most often more than one habitat. This is the main thrust of the current project. Community structure and its variations from one station to another will be investigated. The explanations for variation seen between habitats and locations at this scale are ecological forces, the most common examples of which are bottom type, water temperature, salinity, and depth (Gray 2007). Considering that the primary concern of β - diversity is comparison of samples from two locations, the first step is actually α - diversity analysis of each sample. Once diversity indices are calculated for each location, comparison is possible. Many studies describing β -diversity follow a gradient in an ecological factor such as depth (Weisshappel & Svavarsson 1998; Gage et al. 2000; Jones et al. 2007b), temperature (Bett 2001), substrate type (Mortensen & Buhl-Mortensen 2004), and habitat complexity (Serrano & Preciado 2007). To date no published paper has focused on the difference in overall faunal composition of communities in deep Icelandic waters, though some have investigated specific taxonomic groups in the region (e.g. Brandt &

Distribution of species is a central concept in biodiversity research. Megabenthos from the continental shelf and deeper waters is not distributed evenly in the total habitat. There are reported variations in distribution at a regional or global scale across latitudinal (e.g. Macpherson 2003; Hillebrand 2004) and longitudinal (e.g. Briggs 2007) gradients. However, both of these gradients have been the subject of skepticism since their inception. At a finer scale of investigation, depth is an important limitation on the distribution of species (e.g. Gage et al. 2000) and this is relevant to the current report. Here the distribution of species on the northwestern end of the GIF Ridge is investigated in detail in the main body of the paper and then it is investigated at somewhat lower resolution on videos from the deep-sea floor of the Jan Mayen Fracture Zone (JMFZ) and Mohn Ridge. Patchiness is a general pattern in the distribution of sessile and semi-sessile deep-sea megabenthos where species group together because of some environmental quality that they require (e.g. Schneider et al. 1987). Often this is explained by the presence or absence of a specific bottom type, but sometimes it is some other characteristic of the area. Estimation of the importance of patchiness was a major aim in analysis of the videos from the Jan Mayen Fracture Zone (JMFZ) and Mohn Ridge sampling stations.

The issue of rare species is another aspect of community analysis that inspires interesting questions. Two types of rarity have been investigated in the literature: low abundance—wide distribution species; and low abundance—small distribution species. The former has become known to be the norm in the deep sea where the majority of most samples is dominated by individuals from this group. The latter is a description of species in danger of extinction and, as such, is very rarely encountered. In the terms of the current paper, another aspect of rarity needs to be mentioned here—although it is far less often discussed in the literature—which is, the issue of species being extremely abundant in one area of their range but extremely rare in other areas of their range. There are those who suggest that the rare species observed in samples are not statistically important members of a community because their scarceness precludes their ability to have an ecological effect (Gage 2004; Fontana et al. 2008). They are seen as transients or species in such a state of

decline as to be not viable in the community. Major criticism has been lodged against statistical methods that give equal or more weight to the presence of species in extremely low number. On the other hand, many experts believe that the importance of rare species should never be underestimated because of the roles they play in recovery and development of the ecosystem and succession of species after disturbance. They assert that species found to have restricted range sizes may be representative of the regional pool from which the community composition is created and maintained but wide-ranging species do not necessarily do so (Ellingsen et al. 2007). This ties in to the recent popular theoretical shift toward a larger-scale approach to understanding marine life (Gage 2004). This is the interpretation of rare species used in the current thesis.

1.2 Techniques

Sampling techniques that have recently revolutionized the study of marine ecology especially in the benthic habitat—are photography (e.g. Pech et al. 2004; Jones et al. 2005; Abdo et al. 2006; Jones et al. 2007a) and underwater video (e.g. Ambrose et al. 2001; Bluhm et al. 2005; Jones et al. 2007c). One common reason for the selection of these methods in sampling regimes is that they do not disturb the communities or environment in the same way that traditional methods do. Towed gear are efficient in collecting large amounts of benthic fauna but they are selective in that delicate organisms tend to be lost or destroyed and their function is severely limited on rocky bottom. In addition, towed gears do not allow for investigation of distribution at small scales because in a single sample they collect organisms and sediment from the total length of the track. Grabs, the other most common benthic sampling tool, are also excellent for collecting infauna and the small epifauna. However, they do not function well on hard bottoms or as sampling tools for large emergent megabenthos or mobile forms such as fish. On the other hand, photography allows the sampling of all large epifauna and even some infauna at small enough scale as to enable estimation of local distribution and community composition. Video is usually recorded at a lower resolution than photographs and identification of small characteristics of the community is not possible without the combination of another sampling method. However, video does allow the viewing of communities in a continuous spatial progression and from a great enough distance to be able to illustrate spatial distribution patterns at a larger scale than photographs do. One aspect of species distribution that is captured well on video is patchiness. Most often, observed patchiness is related to geological aspects of a sampled area and video integrates a much better understanding of this relationship by recording the organisms in their natural habitat. Capture of video footage is most often accomplished using remotely operated vehicles (ROV) or towed sleds of various type.

In addition, photographs and video can provide valuable information about the amount of bottom covered by each species of the sessile megabenthos. As has been mentioned, many of the large sessile species provide habitat for other species. In order for researchers to be able to estimate the effect such species have in shaping a local community or ecosystem, they must first obtain some form of estimate of how extensive the population of the habitat-forming species is. Estimation of this type is easily accomplished with visual survey methods but in deep water trying to come to such an estimate using physical sampling methods can prove to be difficult or impossible. Physical sampling methods sample are designed to collect data from too small an area or too large an area in order to be of much use in determining the size and frequency of community patches in an area.

The practice of using bottom cover as an important measurement in benthic ecology is derived from similar approaches that have been used for many decades in botanical ecology. Through analysis of physical samples, an understanding of megabenthos commonly associated in a given area can be reached. It follows, then, that once such knowledge of the location of habitat-forming species can provide a foundation for further studies into the ecology of a region. That is, research effort on a specific group can be focused better on areas where it is most likely to occur. Furthermore, the identification of relationships of epibenthic organisms to pelagic organisms—such as commercial fish stocks—has often been an important tool in the management of those pelagic resources. In cases where benthic organisms have been shown to be important to non-benthic species, the abundance of the former increases the viability of populations of the latter (Turner et al., 1999; Lindholm et al., 2001; Pihl & Wennhage, 2002; Dinmore et al., 2003; Jaworski et al., 2006).

1.3 Aims

The purpose of the current thesis is to extend the understanding of deep-water benthic faunal communities in the Nordic Seas. There was a focus on three hypotheses:

- The species diversity of the three sampling areas—northwestern GIF Ridge, Jan Mayen Fracture Zone, and Mohn Ridge—is variable.
- The habitat heterogeneity is a cause of higher species richness and abundance of epifauna, and thus, bottom type has great effect on community composition.
- Community composition will change with depth in the JMFZ and Mohn Ridge communities and communities will exhibit patchy distribution overall.

Furthermore, the following report is presented as a test of methods of photographic and video analysis for use in marine ecology. As such, the current paper also represents a review of literature related to visual samples being used in the field to augment the more traditional sampling techniques. Here arguments for the use of these methods are given as well as arguments against. There was an attempt to include some of the disagreements in the literature as to methods and analyses that have been used to similar ends.

At the GIF Ridge stations, the focus is to identify every organism of suitable size and, using frequency data and a cover index, assess the amount of variation in community structure in terms of species diversity. Furthermore, the relationship between habitat heterogeneity and variation of species diversity is investigated. To this end, stones and pebbles are recorded, as well as shells if such are observed. A definition of bottom type will include mixed bottom types on two levels: primary type and secondary type. That is, a primary type is assigned describing the majority of area photographed. If other features are prevalent, a secondary type is assigned.

2 Methods

2.1 Study area

2.1.1 GIF Ridge

The North Atlantic Ocean is transected in a roughly east-west direction by the Greenland—Iceland—Faroes Ridge (GIF) (Figure 1). The effect of this ridge has powerful implications for the biology and oceanography of the region. The ridge has saddle depths of around 690 m between Iceland and Greenland and 560 m between Iceland and the Faeroes. Both to the north and south, lie ocean basins of more than 2000 meter depth. The shape and position of the ridge present a formidable barrier to the marine currents of the region (Hansen & Østerhus 2000, Søiland et al. 2008). A warm flow of Modified North Atlantic Water (MNAW) flowing north divides to the south of Iceland and a branch of it, known as the Irminger Current (IC), is redirected by the Reykjanes Ridge along the west coast of Iceland. The other branch, called the North Atlantic Current (NAC), turns west upon meeting the GIF Ridge and brings warm saline water to the south coast of Iceland before joining the IC to the west of the country. The IC forms a sort of buffer along the west coast by restricting the cold low-salinity water of the East Greenland Current (EGC) that flow southward out of the Arctic along the eastern coast of Greenland. Some of the IC also turns to flow eastward along the northern coast of Iceland, thereby shielding this region somewhat from the effects of the EGC water that washes into the Iceland Sea directly to the north of the country (Jónsson & Valdimarsson 2005). Mixing of these currents—the IC and the EGC—does occur to some degree and the result is the current flowing east along the Icelandic margin called the North Icelandic Irminger Current.

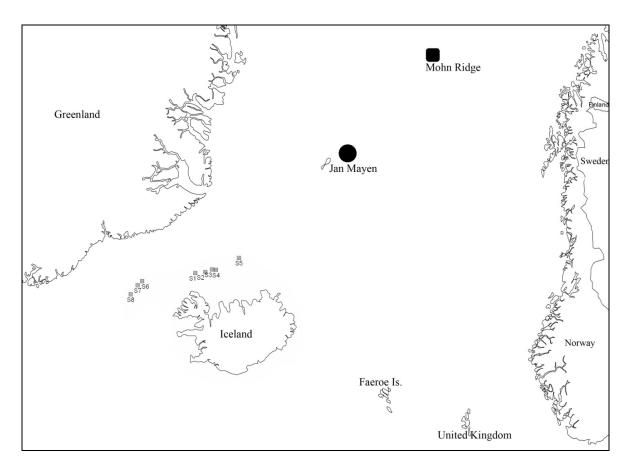


Figure 1. Sampled region. Grey boxes with numbers are Icelandic sampling stations. Black circle is area where Jan Mayen Fracture Zone video samples were collected. Black square is the area were Mohn Ridge video samples were collected.

Three of the GIF Ridge sampling stations are situated in an oceanographically complicated zone where the IC water mass flowing north along the western coast of Iceland mixes with the eastern limits of the EGC, which is itself a mixture of Arctic Intermediate Water (AIW), upper Polar Deep Water (uPDW), and Canadian Basin Deep Water (CBDW). North of Iceland, some of this mixture of water masses is redirected eastward by the GIF Ridge where they form the East Icelandic Current (Rudels et al. 2002; Blindheim & Rey 2004). The remaining five Icelandic stations are all located in this strong current of water colder than the North Atlantic, but somewhat warmer than the Arctic. None of the sampled stations is at a depth where hydrography is Arctic in nature. This mixing is indicated by the combination of salinity similar to that of the EGC water and temperature slightly lower than that of the IC water.

2.1.2 Jan Mayen Fracture Zone

The Jan Mayen Fracture Zone (JMFZ) is the geologically active southeastern face of the Mohn Ridge. It extends from the northern end of Kolbeinsey Ridge in the southwest to the Lofoten Basin in the northeast. These prominent seafloor features create the geological conditions that steer primary water masses in the Nordic Seas. To the south of the JMFZ lie the Iceland Plateau and the Lofoten Basins. To the north, on the other side of the Mohn Ridge, is the Greenland Basin. Major deep-water currents circle in each of these basins and circulation of water masses higher in the column are also steered somewhat by the effects

of regional bathymetry. Thirteen ROV dives were conducted to the east of Jan Mayen in the Jan Mayen Fracture Zone within 71°15'N—71°18'N and 5°46'W—5°51'W. Here two important water masses converge. One mass comes from the northwest is a cyclonic gyre known as the Jan Mayen Current (JMC) which is reflected east and northwards around the Greenland Basin. The other important mass is a branch of the Faroe Current (FC), which separates from the primary flow of the NAC between the Norwegian and Lofoten Basins. The depth range at which videos were collected is within the horizontal layer where these two water masses mix vertically and not deep enough to be within the deep water of the Greenland Basin (Blindheim & Rey, 2004).

2.1.3 Mohn Ridge

The Mohn Ridge lies between Jan Mayen and Spitzbergen (73°33'N—73°51'N, 7°33'E—8°18'E). The Mohn Ridge is a section of the Mid-Atlantic Ridge an estimated 400 km wide. The ridge is a wide flat area except for some trenches and fissures, especially near the eastern end where the dives were conducted. Thermal vents are common present at the eastern end of the ridge. However, they are widely spaced and not thought to be very old or stable (Schander et al., in publication). In this region, the ocean was strongly stratified with the FC at the surface and the JMC below that. However, sampling was conducted at the seafloor in a depth range of 895—2950 m, which places them within the range of the Arctic Ocean Deep Water, which forms the deep water of the Greenland Basin (Blindheim & Rey, 2004). As a result, the dives conducted in this region were in the coldest water of the three regions sampled for the current project.

2.2 Data collection

2.2.1 GIF Ridge

Color photographs were collected during a cruise of the Norwegian research vessel *Håkon Mosby* during the summer of 1999 (Table 1; Figure 1). This was a part of the BIOICE research program, which included physical samples widely distributed throughout the Icelandic EEZ. The camera used was a Photosea 1000A (Kongsberg-Simrad) mounted on a metal frame featuring a weighted trigger and a 150-watt strobe positioned for oblique illumination. Contact of the weighted trigger with the bottom fired the camera and flash unit. The film used was 35 mm 200 ASA Kodak color slide film. The camera was positioned on the frame to maintain a constant height of 1.19 m off the seafloor. Focus, aperture, and shutter speed were set prior to immersion. Due to the altitude of the camera (relative to the bottom) and the lens used, the total bottom surface area captured in each photograph was 0.83 m².

Table 1. Location, depth, and bottom type at GIF Ridge sampling stations.

Site	Latitude	Longitude	Depth (m)	Bottom type
S1	67°08'82" N	22°44'76" W	292	Mud + stones
S2	67°12'10" N	21°47'46" W	240	Sand + pebbles
S3	67°18'71" N	21°08'90" W	304	Mud
S4	67°18'06" N	20°45'96" W	316	Mud
S5	67°45'42" N	18°32'40" W	342	Rocky
S6	66°39'11" N	27°41'50" W	250	Mud + stones
S7	66°28'62" N	28°03'93" W	337	Sand + pebbles
S8	66°06'21" N	28°35'19" W	374	Pebbles

Eight BIOICE stations were chosen for photographic sampling. At each station, at least 50 photographs were taken to ensure the retrieval of useable images. The ship was allowed to drift during sampling, rather than attempting a straight transect with the camera frame suspended more than 250 m below the surface, so at each station the photographs were considered a repeated sampling of a single location. Stations were separated by at least 15 kilometers and overlap of sampled area between stations did not occur. Total distance between most remote stations was just over 475 km.

2.2.2 JMFZ and Mohn Ridge

Both of these samples were collected using the Argus Bathysaurus XL50 remotely operated vehicle (ROV). Sampling was conducted on three cruises of the Norwegian research vessel G.O. Sars during a search for hydrothermal vents and cold seeps in the North Atlantic. All dives in these two regions were conducted during the summers of 2005, 2006, and 2007. Image recording equipment included an Argus foc/Zoom HDTV camera and a low-light black and white camera. In addition, there were five other cameras including a high-resolution digital camera with a powerful zoom lens. Illumination for navigation and photography was provided by four 250W halogen lamps and four 150W Argus RS HID lights. Cameras and lighting systems are maneuverable to achieve the best angles possible. There is a live video feed from the ROV to the operation consol onboard by way of a 4000m Nexans Kevlar armored umbilical. Videos were collected during 19 dives of the ROV to various depths in separate locations within the two areas—JMFZ and Mohn Ridge (Table 2).

Table 2. Jan Mayen Fracture Zone (JMFZ) and Mohn Ridge sampling dives with depth and bottom type.

Area	Dive	Start latitude	Start longitude	Depth (m)	Bottom Type
JMFZ	D1	71°17.608' N	5°47.771' W	680	Rocky
	D2	71°17.835' N	5°47.057' W	645	Rocky
	D3	71°17.980' N	5°46.881' W	600	Rocky
	D4	71°15.727' N	5°50.503' W	750	Rocky
	D5	71°16.063' N	5°50.779' W	795	Rocky + soft
	D6	71°16.880' N	5°49.570' W	800	Rocky
	D7	71°18.010' N	5°46.750' W	600	Rocky + soft
	D8	71°17.880' N	5°47.100' W	645	Mud
	D9	71°17.710' N	5°47.025' W	620	Rocky + soft
	D10	71°17.870' N	5°46.370' W	530	Rocky
	D11	71°15.559' N	5°48.888' W	735	Rocky
	D12	71°17.988' N	5°46.839' W	612	Sand + stones
Mohn Ridge	D13	73°33.217' N	8°17.112' E	2900	Rocky
	D14	73°33.632' N	8°15.528′ E	2950	Mud
	D15	73°33.405' N	8°14.113′ E	2700	Mud + stones
	D16	73°50.276' N	7°36.575' E	895	Rocky
	D17	73°50.299' N	7°37.228' E	1129	Mud + stones
	D18	73°33.475' N	8°16.162' E	2927	Mud
	D19	73°52.643' N	7°33.302' E	1305	Sand + pebbles

2.3 Visual analysis

2.3.1 Photographic samples

A sample of ten photographs was chosen from the total collected at each of the eight BIOICE stations. Selection began with the first slide in the series from each area and then the first ten slides of acceptable quality were selected for analysis. Determination of acceptable quality was based upon focus, clarity, and lighting alone, i.e. images had to be properly focused and lit. In addition, many slides had to be omitted because of an abundance of suspended particles between the lens and the subject matter. Once these ten images were selected, the entire set was examined twice in order to gain an overview of the bottom type, degree of patchiness—if any, and presence of lebensspuren. Following this, each slide was projected onto a screen. Projection size was generally held at roughly twice actual size to increase ease of identification with as little loss of resolution as possible. Most animals down to 1 cm across were identifiable and some polychaetes could be identified by the shape, color and size of the feeding palps or by the shape of the tubes

constructed. Initially, species were identified as belonging to phyla and a list of descriptions, including drawings, of each observed organism type was developed. After the phyla were defined, family and genus names were sought through comparison of appearance with images found in identification keys and scientifically reviewed internet sites. These names were then verified as having been found in the region and recorded as conformis identifications. In this way, a list was formulated that included many species names with descriptions assigned by taxonomists writing in the literature. When the collection of 80 samples had been analyzed, all of them were placed into the projector and the completed species list was used to judge the consistency of identifications across all photographs. This was done to ensure that identifications of similar species as separate was not caused by differences in color quality or other artifacts of the photographic medium. During the photographic identification phase of analysis, taxonomic specialists (see acknowledgements) were consulted in order to determine which photographed specimens were too unclear to reach an acceptable identification and for assistance on some particularly difficult specimens.

The abundance of each species was calculated on each photograph. Colonial organisms were counted as one individual when colonies were clearly separated. These included poriferans, cnidarians (especially Hydrozoa), bryozoans, and tunicates. Sessile and semisessile forms were also used to estimate bottom cover. To do this, the image was projected onto a piece of paper marked with a grid of 100 points spaced at 5 cm intervals (55 x 55 cm). Each point contacting a specimen of a sessile or semi-sessile species was counted. In a few cases, a single point landed on a specimen overlapping another specimen. In such cases, the point was counted once for each specimen. Mobile animals, including ophiurids, asteroids, echinoids, and crustaceans, were not used as measurement of cover. Furthermore, by estimating the percentage of cover provided by each species, relative importance of specific taxa within the community was described. Dominance of one sessile taxon can be limiting to presence of other sessile taxa. Semi-sessile taxa are organisms that have the ability to move but do so rarely and/or do not move long distances. Good examples of semi-sessile taxa are tube-building polychaetes, crinoids, and some anemones.

In addition to organism identification, substrate type was determined by projecting the images onto the wall at actual size (0.83 m2) and measuring particles where possible. Bottom types were then determined based on the percentage of bottom covered by each type of substrate. Four grain sizes—mud, sand, pebbles, and rocks—were used as a basis for determination of bottom type. Where more than 50% of the photographed area was covered by a single bottom type the sample was labeled with that bottom type. In addition, if more than 10% of the photographed area was covered by a second bottom type the classification of bottom type for that photograph was recorded as the primary type followed by the secondary type (Tables 1&2). Stations with a primary and secondary type were referred to as areas of mixed bottom type.

2.3.2 JMFZ and Mohn Ridge samples

Digital video collected during three summers of sampling at the JMFZ and MR were written onto DVD for analysis and played from a DVD player to a 20" television. As with the photographic sample, videos were watched in their entirety prior to identification of organisms in order to assess them in terms of acceptability for the current study. Acceptability was first based on the presence of obvious geothermal vents in the video

because the cruises where the video was collected were intended to be investigations of such habitats. Using the time counter on the DVD player times were recorded where geothermal activity first appeared and where it was no longer in the frame. The other conditions determining acceptability were similar to those for the photographic sample. That is, clarity of image, appropriate lighting, and lack of obstruction of the seafloor. In addition, camera angle is extremely variable because the ROV is constantly moving in all directions in relation to the sea floor. So, the camera aspect was assessed prior to identification, to mark off sections of the video when camera angle in relation to the sea floor caused a loss of resolution needed for identification.

Once videos of acceptable quality were selected, identification began with description of the general bottom type observed during each dive. Next, each video was started at the beginning and, using the counter on the DVD player to measure time, every 30 seconds, the video was paused and the frozen image was analyzed. The identifications were compared to descriptions in the literature for accuracy. A list of species collected during the first series of ROV dives near Jan Mayen in 2005 had been compiled by the time this analysis commenced. This list proved to be most helpful in the identification of many species observed on the videos. Once a fauna list was compiled, all identifications were checked to verify previous records of those species in the region. The variable distance of the camera from the bottom and the low resolution of the image (with respect to that of the photographs from the GIF), only the biggest of epifauna could be identified. There was no indication of a known scale on the videos—such as the laser points that are often used on such video—so size was not used as a descriptive character for identification of organisms.

2.4 Statistical analysis

The software package Biodiversity Pro v. 2.00 (Natural History Museum, London and Scottish Association for Marine Science, Oban) was used to analyze diversity. Species diversity was examined using rarefaction (Hurlbert, 1971) and the Shannon diversity index H' log 10 base. Evenness was calculated using Shannon's J'. In addition, three other diversity indices were calculated using Primer 5 (v. 5.2). These three additional indices were Margalef's species diversity index (d), Fisher's (α) and Simpson's (λ '). A Bray-Curtis similarity index analysis was carried out and used as a distance matrix for a cluster analysis to show grouping of photographs based on community structure. This similarity index is used for marine samples because unlike other similarity tests, this one does not read absence as a sign of similarity. Instead, the Bray-Curtis method only uses abundances of species that are in both samples and those that are in only one in order to distinguish between the two distributions. In order to support conclusions about the grouping of stations by similarity or slides by bottom type, multidimensional scaling (MDS) was applied to the data using Primer 5 (v. 5.2). Furthermore, canonical correspondence analysis (CCA) was used to reveal the likely environmental causes of variation in community structure between stations. This was done with the R statistical computing environment version 2.7.0 and the Vegan software package version 1.13-0 (Jari Oaksanen, May 21, 2008).

3 Results

3.1 GIF Ridge

3.1.1 Present species and regional distribution

The regional pool from Icelandic waters included 118 separate taxa. Assignment of a conformis (cf) species or genus name was possible for 84 taxa from 68 families. In addition, there were 34 disparate taxa (mostly hydroids, mollusks, holothuroideans and nudibranchs) that could be identified only to the taxonomic level of class or order (see Appendix I). Almost half (16 of 34) of this latter group were found only at a single station and, of those, 14 were observed on only a single photograph each. These low density species were mostly mobile forms and the gastropods were at or near the minimal size limit for identification (~1 cm).

Species were not evenly spread across the entire region. Patchy distribution at the scale of seascape (the sampled area as a whole) was observed with the majority of species distributed into areas of concentration. Of the 84 identified species, there were 23 that were found only at single stations or were found in low density at many stations. Sixteen of these 23 were observed only at a single station and nine of the uncommon species were represented by a single individual in the entire sample. Only three of these nine species were represented by more than five individuals in the data set. First, the poriferan identified as cf. *Mycale* sp 2 had a density of 3.5 colonies/m2 in nine slides from S2. Second, seven specimens of cf. Sabellaria spinulosa appeared on a single slide at S8. Third, all but one slide from S5 showed the crinoid cf. *Antedon bifida*.

Table 3. List of species observed at a single station.

- S1 None
- S2 cf. Mycale sp 2, cf. Aureliania heterocera, cf. Bolocera tuediae, and cf. Myxicola infundibulum
- S3 None
- S4 cf. Nymphon gracile,
- S5 cf. Epizoanthus couchii, cf. Arcturus baffini, cf. Antedon bifida, cf. Gorgonocephalus eucnemis, and cf. Artediellus atlanticus
- S6 cf. Glypocephalus cynoglossus
- S7 cf. Munnopsis typica and cf. Ocnus lacteus
- S8 cf. Melonanchora elliptica, cf. Potamilla renniformis, and cf. Sabellaria spinulosa

Poriferans were abundant at S5 and S8—the stations on the eastern and western extremes of the sampled region—but not at stations in between. They were completely absent from

S3 and only three colonies (two cf. *Haliclona urceolus* and one cf. *Stylocordyla borealis*) were observed at S4. All species of Porifera identified in the study except cf. *Iophon* sp, cf. *Aplysilla sulfurea*, cf. *Melonanchora elliptica* and cf. *Mycale* sp 2 were present at station S1. This station showed the highest poriferan diversity (Shannon H' log base 10 = 1) in the study despite the fact that it was not the station with the highest poriferan abundance (50.7 colonies/m2, S5) nor was it the station of highest number of poriferan species (16 species, S8). No single species dominated the sponge community at S1 and evenness caused species richness to be high. The most common poriferan in the study was *Tetilla* sp 1 which was concentrated at S5 (17.2 colonies/m2) and S8 (9.8 colonies/m2). The only two identified poriferans that are encrusting forms were cf. *Aplysilla sulfurea* and cf. *Hymedesmia purpurtas*. The former was found mostly at S5 and S8 but was also present in small number at S6 and S7. Station S1 had the largest local population of cf. H. purpurtas (1.9 colonies/m2). The only other station where this species was found was S2.

The only taxon observed on nearly all photographs was Ophiuroidea. One species of this family, cf. *Ophiocten sericeum*, was observed on 56 of 80 slides and it was present at all sampling stations. In terms of number of observed specimens, this was the most abundant species in the study. While the density of this species averaged across all stations was 13.4 individuals/m2 (± 20.4), its density ranged from 46.7 individuals/m2 to 0.5 individuals/m2. The other two ophiuroids that were observed at all stations were cf. *Ophiura albida* (65% of slides) and cf. *Ophiothrix fragilis* (41% of slides). The next most abundant species of this family was cf. *Ophiocomina nigra* which was found at only half of the sampling stations but its density reached 26.2 indiv/m2 at S1. The second most abundant organism was the colonial tunicate cf. *Eudistoma vitreum* whose density ranged from 82.7 colonies/m2 at station S2 to 0.24 colonies/m2 at station S4. *E. vitreum* was only common at four of the sampled stations (S1, S2, S5 and S8) and was rare at two other stations (S4 and S7). Another tunicate, cf. *Synoicum pulmonaria*, was also common. This species had a density of 10.7 indiv./m2 at both S6 and S8. No tunicate was found at all stations so despite their great abundance at select stations the group cannot be considered regionally common.

Four bryozoans also showed very high abundance at specific stations. First, cf. *Cabarea ellisii* was present in high numbers (53.3 colonies/m2) at S8 and observed in all 10 photographs from that station. However, it was found on only 8 slides from the other five stations where it was observed and colonies were distributed in small numbers (density range: 0.1–1.1 colonies/m2) across stations S1, S2, S5, S6, and S7. Two other bryozoan species showed high density at only a single station. At S2 the most common bryozoan was cf. *Cellepora ramulosa* with a density of 17.0 colonies/m2, which population represented 87% of observed specimens of that species. The other, cf. *Eucratea loricata*, was most abundant (16.7 colonies/m2) at S7, whereas its density at the other six stations where it was observed ranged from 0.2–5.8 colonies/m2. The fourth common bryozoan species reached local populations of 40 or more (density: 4.8–6.7 colonies/m2) at stations S1, S5 and S8 which makes *Hornera lichenoides* the most common bryozoan species for the studied region.

Temperature, salinity and depth were measured at the time of sampling as environmental characteristics that could explain observed difference in assemblages between stations. The total variation in temperature over all stations was 1.5° C but five of the eight stations were within 0.5°C of each other. Despite this, the CCA suggested that of the measured variables, temperature explained the most variation. Salinity also varied extremely little

between stations with a total difference of 0.09 ppm and five stations of eight being within 0.02 ppm and it was calculated to be of negligible significance in describing the variation observed in megabenthic communities. The total range of depth (134 m) does not appear to be an important variable by itself but it does seem to play a role in combination with bottom type to explain some of the variation.

3.1.2 β-diversity and community analysis

In terms of species diversity and community structure, there was variation between sampling sites in the Icelandic data set. This was seen in the five diversity indices calculated (Table 4), rarefaction analysis, the Bray-Curtis similarity dendrogram, and the MDS analysis (Figs. 2, 3, & 4, respectively). The highest diversities were found at stations S5 and S8 but evenness of species composition was much higher at S5 than at S8 (Table 4). Species dominance was highest at stations S3 and S4 where diversity was lowest. These findings are in agreement with the Hurlbert rarefaction analysis, which showed far lower species richness at stations S3 and S4. In the areas of high diversity and evenness, the majority of the community was composed of Porifera, Echinodermata (especially Ophiuroidea), and Cnidaria. These stations had far less soft sediment bottom type than did the stations of low diversity, which were primarily mud or sand bottom with few stones or pebbles.

Table 4. Station average values of number of species (S), abundance (N), species diversity (d, H'), dominance (α , λ '), and evenness (J') for the Icelandic sample.

	S	N	d	H'(log10)	α	λ'	J'
S1	14.9	90.3	3.082	0.779	5.563	0.288	0.697
S2	19.7	187.6	3.600	0.899	5.748	0.201	0.701
S3	5.4	29.4	1.357	0.494	2.784	0.374	0.749
S4	5.7	25.1	1.504	0.544	2.658	0.358	0.733
S5	24.1	127.6	4.796	1.181	9.219	0.084	0.861
S6	7.6	25	2.142	0.712	5.678	0.213	0.831
S7	12.4	68.1	2.714	0.724	4.631	0.302	0.667
S8	24.6	155.2	4.686	1.072	8.364	0.157	0.771

Rarefaction analysis of the pooled data from eight sampling stations showed a marked difference between epibenthic megafaunal communities at stations with high habitat heterogeneity and those where habitat was more homogenous (Fig. 2, Table 5). Highest species richness was found in areas featuring hard substrate (stations S2, S5, S8) and lowest diversity was found on muddy bottom (stations S3 and S4). Rarefaction calculated that these latter two stations and station S6 will not show increase in species diversity as sample size increases past ES(100). However, the other stations were expected to increase to ES(240).

Table 5. Rarefaction results for expected numbers of species from two samples of different size.

	S1	S2	S3	S4	S5	S6	S7	S8
ES(100)	13.60	15.85	5.40	5.70	22.51	7.60	12.39	21.31
ES(240)	14.90	19.61	5.40	5.70	24.10	7.60	12.40	24.60

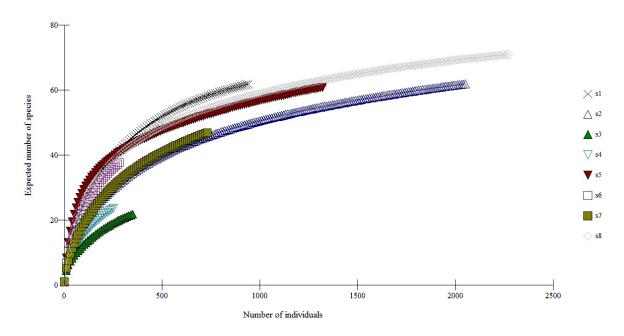


Figure 2. Rarefaction of pooled abundance data by station.

A cluster analysis divided the total data by means of calculated Bray-Curtis similarity indices applied to community structure (Fig. 3). Two of the eight stations, S3 and S4, were considerably different from the other six. These six stations were at least 50 % similar and were further divided into three groupings: S1 & S2, S5 & S8, and S6 & S7. The greatest similarity between community structures was found between stations S1 and S2 (63.9 %). The second most homogeneous group was composed of stations S5 and S8, which had a similarity of 63 %. The third group comprised stations S6 and S7, where community structures were 55.5% similar.

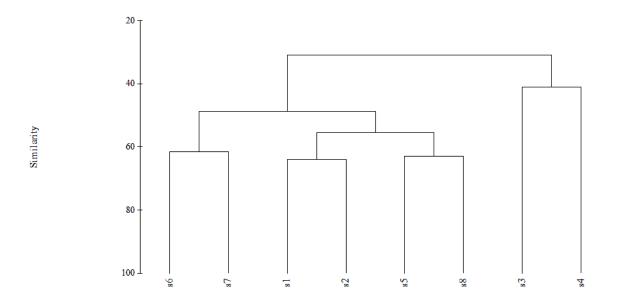


Figure 3. Cluster diagram of Bray-Curtis similarity indices for samples pooled by station.

Multidimensional Scaling illustrated the same pattern of relationship seen in the previous analyses where stations S3 and S4 were different from the other six stations (Fig. 4a). In the MDS plot, four stations are so close as to be unreadable. They are stations S1 sitting atop S2 and S5 sitting atop S8. In order to reduce the effect of the uniqueness of communities at stations S3 and S4, these two were removed from the ordination (Fig. 4b). Doing this illustrated that difference in community structure between stations followed the pattern described by the Bray-Curtis similarity index. Stations S5 and S8 had the most similar community composition followed by stations S1 and S2. Stations S6 and S7 were closer to each other than to either of the other two groups. Since bottom type varied somewhat within stations, data was then arranged by bottom type observed on each slide (Fig. 4c). A different pattern emerged here. The mud stations were still calculated to be very different from the other stations, but difference between the seven bottom types shows that bottom type is not the only variable that steers community structure.

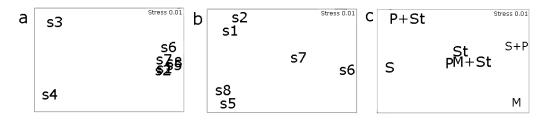


Figure 4 MDS plots of density data: a. density data from all photographs organized by station; b. density data omitting stations S3 and S4 to illustrate the relationship of the other six stations; c. density data organized by bottom type. (M: mud, S: sand, P: pebbles, St: stones).

The structure of the communities found at each station varied depending on the proportion represented by each phylum identified in the study (Figure 5). The two stations where the bottom consisted of mud (S3 and S4) featured communities where Porifera, Brachiopoda, and Tunicata were sparse and Annelida was common (3.9–8.6 indiv./m²). In these two stations, the majority of the emergent megafauna consisted of Ophiuroidea. This was also true in the community structure at station S1 where the primarily muddy bottom featured stones. However, the community at S6, a station with the same bottom type as S1, was not dominated by Ophiuroidea because of a high density of Tunicata (11.2 colonies/m²) and a higher density of Porifera (5.8 colonies/m²) than was found at S1, S3, or S4. A similar pattern of weaker proportional dominance of Ophiuroidea over other taxa was also observed at station S2 but it was due only to the density of Tunicata (86.5 colonies/m²) and not a high density of Porifera. The primary bottom type at S2 was sand but there was also a large number of pebbles. Station S7, the other station where the bottom type was sand and pebbles, showed a structure more like that of S3 and S4 except that at this station there was a moderate density of Bryozoa (19.2 colonies/m²). The last two stations are those that show the highest overall diversity. Station S5 is a rocky bottom site and proportional densities of Echinodermata, Annelida, and Cnidaria were rather similar, but at this station, Porifera represented a higher proportion of the community than other taxa. At station S8 a high density of Tunicata was present as well as strong representation of the other taxa common in the current study.

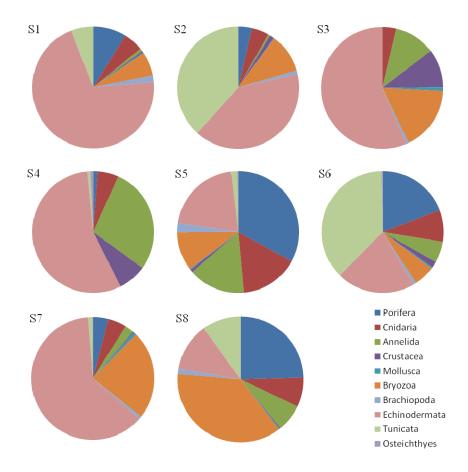


Figure 5. Proportion of community structure represented by densities of present phyla.

Species diversity and richness in areas where stones, gravel, or pebbles are present on a background of soft mud or sand (Tables 1, 3). At S6, a station where a background of mud featured scattered stones of varying sizes, present species were markedly different from soft-sediment epifaunal species found on the other two stations where the bottom was composed of mud alone (S3 and S4). The colonial tunicate Synoicum pulmonaria and two poriferans (Tetilla sp 1 and Aplysilla sulfurea) were observed. Greater abundance and diversity of hydroids and sponges were also recorded from station S6 than the mud bottom stations, though they were present at lower density than at stations where a larger proportion of the bottom was hard. This heightened diversity due to increased habitat heterogeneity was also observed at S7 where a background of sand was littered with pebbles and the bryozoan Eucratea loricata was present at high density. Station S2 had the highest diversity of all the stations with a mixed bottom composition (Table 1, 3). As was seen at S7, the community was dominated by species that require a hard surface for attachment. In this case, the tunicate Eudistoma vitreum and the bryozoan Cellepora ramulosa were extremely numerous. Also found in the sample were a large number of three identified species of ophiuroid (Ophiocten sericeum, Ophiura albida, and Ophiothrix fragilis) and one unidentified ophiuroid (Ophiuroidea sp 8).

Faunal communities at S5 and S8 were very different from those at other stations in that they contained a high abundance and diversity of poriferans, cnidarians, bryozoans and tunicates as well as the ubiquitous ophiuroids. Overall diversity at these two stations was higher than that of other stations and it was highest at S5. Evenness was also highest at S5 (Shannon J' = 0.86) but it was above 0.65 at all stations. The evenness at S8 was lower

than at S5 because of an extreme abundance of the bryozoans identified as *Cabarea ellisii*. Both Bray-Curtis similarity analysis and rarefaction showed difference and groupings of some of the stations.

The community structure between sites varied as well (Figure 5). Station S5 was the only station at which poriferans represented the majority of the population. This is the only station at which the bottom consisted of rocks with very little sediment. Station S8 also had a proportionally large population of poriferans, but there, the bryzoans were present in greater number. Porifera was absent only from a single station (S3), though it was a low-abundance taxon at S2, S4, and S7. Stations S2 and S7 have a mixed bottom type composed of sand with scattered pebbles. Stations S3 and S4, with their muddy bottom type, were scarcely populated by sponges.

Cnidaria held a constant proportion of the community across the entire GIF Ridge data set. The highest cnidarian abundance was found at station S5. This station had the lowest proportional abundance of anemones in relation to total local population of any station. The Octocorallia contributed the majority of cnidarians at this station. The proportion of anemones and hydroids found at stations S3 and S4 were quite different. These two sites varied very little in terms of measured abiotic characteristics of depth, salinity, temperature, or bottom type and even their geographical positions were not separated by a great distance (16.5 km).

3.1.3 Cover analysis

The amount of bottom cover accounted for by sessile and semi-sessile species also differed between stations (Table 6, Fig. 6). The stony bottom at station S5 had the highest percent cover (61 %) and the greatest range of percentages across the ten slides from a single station (15-61 %). The paucity of emergent fauna at stations S3 and S4 resulted in these two stations having by far lowest cover of the studied areas. At stations S3 and S4 no part of the bottom was covered by emergent fauna in 14 out of the combined total of 20 slides. On the slides from these stations where animals covered part of the bottom, the percentage covered ranged from 1-6 %. The taxa responsible for highest percentage of cover were usually the most abundant sessile taxa in the community at each station (Fig. 5, Table 6). At stations S5 and S8, where Echinodermata did not represent a proportional dominance of the community, the taxa responsible for the majority of bottom cover were also the more abundant taxa in community structure. This was the case at stations S5 and S8. Station S6 showed a different pattern between proportional importance in community structure and proportional importance in bottom cover. At this station, tunicates—which were responsible for the largest portion of animal abundance—were not important to bottom cover in relation to other taxa. This was due to the small size of individuals of the taxa in relation to that of other taxa.

The stations where percent cover varied most were stations S5 and S8. These stations were also the ones where the highest amount of bottom cover was reached. At all other stations, where cover was less, the variation between the amount of cover from one slide to the next was not high. This could be a result of habitat heterogeneity because that varies as well at these two stations.

Table 6. Percentage of cover on ten slides per sampling station including station averages used in discussion of cover and standard deviation. Photographs are labeled P1–P10 for each station.

	S1	S2	S3	S4	S5	S6	S7	S8
P1	4	10	3	0	38	2	2	14
P2	0	7	6	0	15	0	0	15
P3	5	4	1	0	26	1	3	37
P4	8	7	0	2	19	1	0	20
P5	1	8	0	0	28	9	1	9
P6	7	12	0	0	61	0	8	20
P7	4	6	0	1	39	7	3	41
P8	19	12	0	0	34	3	10	41
P9	2	5	1	0	31	3	7	11
P10	0	18	0	0	25	4	10	28
Average	5	8.9	1.1	0.3	31.6	3	4.4	23.6
St. dev.	5.348	3.986	1.868	0.640	12.200	2.828	3.774	11.698

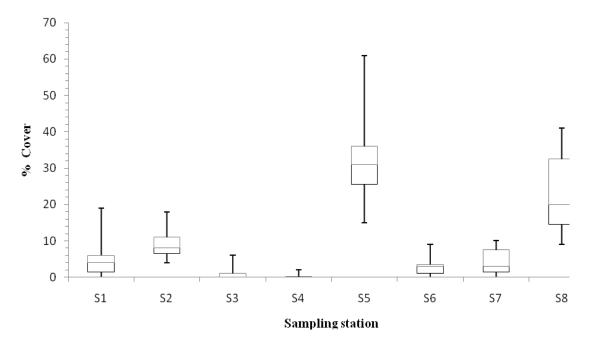


Figure 6. Boxplot of percentage cover per station. Range for each station is the range of cover indices on ten photographs. Error bars indicate highest and lowest cover indices.

The total amount of bottom covered was further divided to show which phyla were responsible for highest proportion of cover at each station. This revealed that the specific taxa causing cover in observed areas were variable between stations (Table 6). The Porifera were responsible for the majority of bottom cover at stations S1, S5, and S6. At station S2, the Tunicata were the most prevalent source of cover. At both S7 and S8, the Bryozoa were dominant in forming cover. This last taxon was also responsible for most of the sparse cover observed at station S3, the only station at which sponges did not provide

any bottom cover all. Crinoids accounted for a low proportion of the cover at station S3 despite the fact that the dominant phylum was Echinodermata. This was because the high density of ophiuroids in relation to other taxa.

Table 7. Average proportion of observed cover represented by each taxon per site.

	Porifera	Cnidaria	Polychaeta	Bryozoa	Brachiopoda	Crinoidea	Tunicata
S1	36.2	17.0	1.3	16.5	0.0	0.0	9.1
S2	2.9	9.9	0.6	25.8	1.4	0.0	59.4
S3	0.0	1.7	10.0	25.0	0.0	3.3	0.0
S4	10.0	10.0	0.0	0.0	0.0	0.0	0.0
S5	55.4	8.8	28.6	1.9	0.3	5.1	0.0
S 6	33.9	21.7	13.3	9.7	0.0	0.0	1.4
S7	8.5	14.7	10.0	44.6	1.3	1.0	0.0
S8	38.2	8.4	4.3	45.6	0.0	0.7	2.7

3.2 JMFZ and Mohn Ridge

3.2.1 Present species and regional distribution

The JMFZ and MR region sampled in the current study yielded 66 apparently disparate species (See Appendix II). Identification to genus or species level was possible for 47 of these. All species identified on the videos were present in both the Jan Mayen Fracture Zone area and the Mohn Ridge area. A highly patchy occurrence of emergent megabenthos was observed. Three distinct communities can be described because of the dominance of *Gorgonocephalus* spp., crinoidean species or anthozoan species each within patches where other species were present at very low abundance. These patches were clearly defined by the presence of hard substrate to support them. Diversity of the region was not calculated to be high and a wide range of Simpson's dominance index (λ '= 0.178–0.875) was calculated for the sample as a whole (Table 8).

Hexacorallia was the most common and abundant group. It was observed during all dives but one. The greatest abundance of individuals in the entire data set was comprised of Hexacorallia (1401 ind.), Porifera (962 ind.), Tunicata (927 ind.), and Crinoidea (656 ind.). The majority of hexacorals observed in the sample were of the species *Hormathia digitata* (860 ind.). This species was most often observed in dense colonies. Most of the species in these groups were not ubiquitous, rather they were observed on only a small number of the total dives. Seven species of fish were identified. One cartilaginous species (*Amblyraja hyperborea*) was observed on four dives. The other six species were bony fish (Osteichthyes). Of these, the two most common were *Lycodes* sp. (7 ind.) and *Gaidropsarus argentatus* (7 ind.). The other species were *Macrourus berglax*, *Rienhardtius hippoglossoides*, *Rhodichthys regina*, and *Paraliparis* sp. All fish were seen on or just above the seafloor.

Table 8. Average values for Abundance, species richness, and species diversity for dives from the Jan Mayen Fracture Zone and Mohn Ridge areas. Number of species (S), number of individuals (N), Margalef's diversity index (d), Fisher's diversity index(α), Shannon's diversity index (H'(log 10)), Simpson's index (dominance) (α), Pielou's evenness (J').

	Dive	S	N	d	α	H'(Log10)	λ'	J'
JMFZ	d1	3.3	8.5	1.246	2.837	0.402	0.298	0.863
	d2	3.3	15.1	0.953	1.690	0.381	0.439	0.806
	d3	2.2	15.7	0.664	2.005	0.188	0.666	0.619
	d4	2.8	10.1	0.946	2.089	0.265	0.569	0.739
	d5	1.7	4.7	0.613	1.258	0.135	0.690	0.654
	d6	1.2	2.2	1.329	3.133	0.155	0.295	0.855
	d7	3.4	12.7	1.049	2.061	0.366	0.470	0.711
	d8	2.3	8.9	1.262	3.280	0.260	0.330	0.787
	d9	1.9	7.4	0.552	1.053	0.180	0.599	0.765
	d10	2.8	21.3	0.596	0.925	0.297	0.566	0.717
	d11	4.3	35.5	1.191	1.686	0.338	0.499	0.618
	d12	2.0	6.0	0.808	1.414	0.191	0.539	0.715
Mohn Ridge	d13	0.7	1.6	0.419	0.828	0.038	0.744	0.847
	d14	1.3	2.5	0.180	0.995	0.061	0.875	0.811
	d15	5.0	23.4	1.353	2.265	0.506	0.330	0.792
	d16	10.3	70.1	2.224	3.531	0.840	0.178	0.834
	d17	1.3	6.3	0.177	0.541	0.057	0.880	0.709
	d18	0.9	2.4	0.417	1.144	0.054	0.738	0.778
	d19	3.2	6.3	1.508	4.070	0.375	0.264	0.858

3.2.2 B-diversity and community analysis

A Bray-Curtis similarity index used to create a dendrogram of similarity between dives showed a strong similarity (% similarity > 50%) between only 6 dives of the entire sample based on faunal composition (Figure 7). This was backed by a Simper analysis run on the data showing at least 81.3% dissimilarity between areas of different bottom types. Four dives were separated from the rest by similarity analysis. Dives D13, D14, D17, and D18 shared a very low similarity to all other dives but shared at least 43 % similarity with each other. Highest similarity was calculated to be between dives D2, D3, and D4.

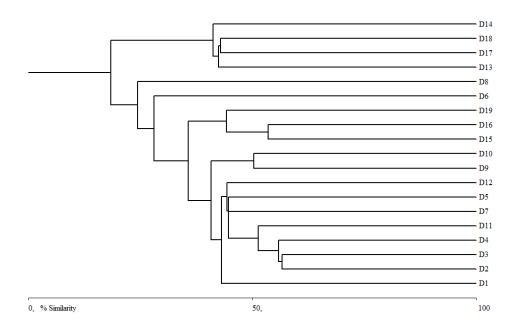


Figure 7. Dendrogram of Bray-Curtis similarity indices for the entire JMFZ--MR sample.

Rarefaction showed variation in the species richness between dives at the JMFZ–MR region (Fig. 8). This analysis indicated that there is probability of higher species diversity than was shown by the data. This is probably because of the low resolution of the video recordings. Multi-Dimensional Scaling (MDS) showed that more than half of the Mohn Ridge dives were significantly separated from those of the Jan Mayen Fracture Zone (Fig. 9). The other samples from the MR were not mixed with those from the JMFZ, indicating that the region is not homogeneous in terms of community composition. This variation was caused by depth at the Mohn Ridge and bottom type at the JMFZ. These variables were found to be the only ones to effect community structure. The small depth range of the sample from the JMFZ (530–800 m) reduced the importance of that variable at those dives and the bottom type variable had more effect. The greater depth range of the MR sample (895–2950 m) caused the influence of depth on the community composition to be magnified. Mutlidimensional scaling was also applied to the JMFZ data and the MR data independently but no pattern emerged. It resulted in all of the dives being superimposed over each other with almost no variation at all.

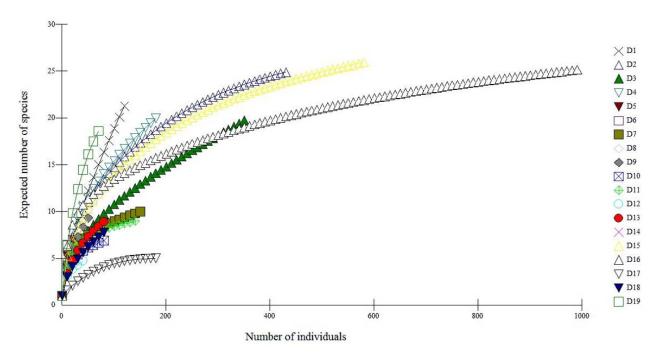


Figure 8. Rarefaction of dives (D#) from the JMFZ/MR region.

Two dives (D15 and D16) from the Mohn Ridge featured the highest abundance and diversity of sponges, though they were not the only videos of areas of hard bottom collected. These two dives also had the highest diversity of any in the region as a whole and among the other MR dives, as well. In addition, these sites had the highest average number of individuals, species, and the highest evenness. The diversity indices calculated for individual dives did not add up to a significant difference between the MR area and the JMFZ area.

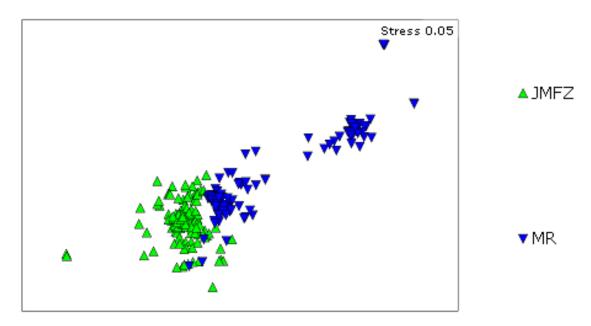


Figure 9. MDS grouping of JMFZ and MR frequency data by dive area. Very little variation is seen within the JMFZ sample and much more in the MR sample. The separation in the MR sample is caused by depth variation.

4 Discussion

4.1 Present species and regional distribution

4.1.1 GIF Ridge

Considering the novelty of the methods used herein, the results presented here are difficult to compare with examples from published literature. No other general surveys of megabenthos communities exist for this area at the depth sampled for this project. However, the number of identified taxa from the GIF Ridge (84) was not unusually high in comparison with studies of total megafauna from the North Atlantic (e.g. Jones et al. 2007a). Also, previous reports of similar numbers of identified species have been reported for individual taxa (e.g. Barthel & Tendal 1993, Brandt & Piepeburg 1994, Piepenburg & von Juterzenka 1994). Similar species diversities have been reported in studies from the Arctic (e.g. Mayer & Piepenburg 1996, Weslawski et al. 2003) and from the North Atlantic (e.g. Flach & Bruin 1999, Bett 2001, Starmans & Gutt 2002). Others have identified a lower number of species in a similar amount of sampling effort and using similar techniques (e.g. Sahade et al. 2004, Jones et al. 2007b). These last studies were strongly limited by the altitude (height from bottom) of the photographic equipment and considering that their size minimum for identification was > 5cm a great number of the smaller species identified herein would be omitted. All species identifications in the current paper have been compared with taxa that have been recently reported in other papers (e.g. Bamber & Thurston 1995, Hansson 1998a & b, Schuchert 2000, Schuchert 2001, Klitgaard & Tendal 2004). One difference in the current study is that this is only a full count of large epifauna and not a measure of the total presence of small (< 1 cm) nor infaunal forms. As a result, the observed community composition found in this research does not include the high diversity of polychaetes typically found in research on the sea floor below 200 m (e.g. Bett 2001). This reduction of the total contribution of polychaetes to community composition means that more emphasis is shifted to echinoderms (mostly ophiuroids), enidarians (mainly hydrozoans and hexacorals) or poriferans all three of which are often the second or third most important contributors to animal assemblages in other studies after polychaetes (e.g. Mayer & Piepenburg 1996, Jones et al. 2007b). The degree of variation in community composition between stations follows that shown by others such as Gage et al. (2000). That is, significant variation exists in the combination of species present at each sampling station.

As has been reported, 23 species were present either exclusively at specific stations or in low density across several stations. It has often been suggested that such species be omitted from analysis due to the small effect they have on the sample as a whole (e.g. Gray 2002, Fontana et al. 2008). However, there is contention on this point because of the possibility for rare species to step in an act as an ecological buffer to disturbance (e.g. Ellingsen et al. 2007, Hewitt et al. 2008). This belief is based on evidence that rare species are often taxa that fit ecologically functional roles that are already filled by one or more dominant species. In this way, they reflect the regional species pool and the potential for succession and expansion in the event of disturbance (Hewitt et al. 2008). One facet of functional diversity that has become known in the last decades is that functional groups are rarely filled by only one species or taxonomic group in marine benthic communities (Gray

1997, Loraeu et al. 2001, Ellingsen et al. 2007). This is referred to as functional redundancy. Such redundancy does not always mean an equal abundance of more than one species so dominance will sometimes occur—and that dominance can change because of disturbance. Most often, functional redundancy is viewed as a buffer to changes like physical disturbance and persistent alterations in physical oceanographic characteristics of a region. That is, when more than a small number of species hold roles in each necessary function in a given area there is less likelihood of total ecosystem collapse when change occurs. Since the ocean is a vast and dynamic environment, this allows the animal communities to survive even in the face of major changes. Ellingsen et al. (2007) linked redundancy to the commonly observed species curves that show a proportionally large number of rare species in most ecosystems analyzed (e.g. Magurran et al. 2003, Gray et al. 2005). They suggest that the preponderance of rare species in communities provides a source for opportunists with different qualities to fill functional roles when some sort of disturbance occurs and the previous species fulfilling that role decline in abundance. In this way, it seems that rare species may serve as a source for the increase of local diversity through migration and settlement (Gage 2004).

Many bryozoans and ophiuroids were left unidentified because they were too small for classification features to be identified. The Alcyoniidae and the Porifera are difficult to classify even when a specimen is available. Many individuals of these two groups proved impossible to classify. There were some slides showing obvious colonial encrusting organisms that were too small or ambiguous to assign to a phylum. In an ideal situation, physical samples of the organisms in the frame would be collected at the time of photographic sampling, but this would be complicated enough to render the method impractical. This is the major argument for the combination of photography with physical sampling from the study area. However, the advantages of photography outweigh the disadvantages. As pointed out by Schuchert (2000), the traditional sampling methods of grabs and towed gears fragment many species beyond recognition. This leaves gaps in our knowledge of the sea floor epifauna. Photography techniques cause extremely little disturbance of the bottom and return more complete information about the density of many of these fragile species that are often destroyed in the more traditional methods. In addition, photographs provide insight into the arrangement of animals within communities. Photography of the seafloor is also a blind sampling procedure, and sampling is not biased by the researcher. This helps to maintain a sampling regime free from human bias.

4.1.2 JMFZ and Mohn Ridge

The number of species identified in the current study is not unusually high for studies of benthic communities in such a large region and depth range (e.g. Jones et al. 2007a). Given the reported diversity of Arctic fauna in the benthic environment, it seems as though possibly more species should have been observed (Piepenburg 2005). There would likely have been many more species identified if not for the visual restrictions imposed by the lack of resolution needed to identify small forms. Birch (1981) noted that in marine fauna an increase in species diversity is often accompanied by a decrease in evenness. This was seen in the MR sample. In the estimation of species richness and evenness presented here (Table 9), evenness decreases in a few dives as species diversity rises. Such increases in dominance led to an obviously patchy distribution of epifauna. Patches were often surrounded by expanses of soft sediment where epifauna is rare. However, these community patches were species rich enough to raise

the diversity indices calculated for dives when taken as a whole. These patches were observed in most dives at both the JMFZ and the MR.

The area of the Jan Mayen Fracture Zone sampled was of relatively constant depth. This means that depth was less important in shaping community composition than it was on the Mohn Ridge. With that powerful variable gone, bottom type took over as the chief influence on the abundance and diversity of epifauna. Conversely, the Mohn Ridge sample traverses an incredibly wide depth range, much wider than that see at the JMFZ. This range of more than 2000 meters means that hydrography was probably variable between the shallowest dives and the deepest. At a depth of 3000 meters, water from the deep basin of the Greenland Sea is flowing close to the bottom (Hansen & Østerhus 2000). This water is cold and has a low salinity, both of which qualities can influence the composition of communities. Depth was seen to have a strong effect on the identified animal diversity of the Mohn Ridge sample (Fig. 10).

The most common hexacoral in the JMFZ and MR data sets, Hormathia digitata, was found in dense patches on exposed rock surfaces. In some of these patches, other species were found in extremely low abundance and the anemones clustered together, side by side. This brings up the question of how the patches form. H. digitata probably produces such tight colonies by cloning itself at a rapid rate. Once there are many anemones, other organisms have not the space required to settle and thrive. The other two patch-forming taxa—Gorgonocephalus sp and Crinoidea—are only semi-sessile and therefore, their aggregations may be expected to be much more mobile and short-lived. Schneider et al. (1987) found patchiness on the outer Grand Banks using photographic techniques. Their analysis indicated that mobility has a strong effect on the patchiness of species distribution and the scale at which that patchiness manifests. However, randomness in distribution was found to control half of the studied communities in epibenthos near the coast of northeast Greenland and on the Antarctic shelf (Gutt & Starmans, 2003). This unpredictability indicates that what may, at first, appear to be patchiness is perhaps random distribution being steered by ecological processes on the small scale. Furthermore, Parry et al. (2003) identified small-scale hydrography as a likely cause for observed patterns in distribution of sessile species in that such water movement close to the bottom determines how far planktonic larvae travel from the parent organism before they settle.

4.2 B-diversity and community analysis

4.2.1 GIF Ridge

The rarefaction performed seems to indicate a good deal of variation in the community compositions of the dives. Rarefaction is a highly contested method of analysis because of the heavy influence of community evenness on the analysis (Gray 2001) and it has been suggested that rarefaction cannot be used to compare samples of different size (Gray 2002). Despite this, it seems to have some validity for the current study because when compared to the other analyses performed herein it seems to provide similar results at low $ES_{(n)}$. It has been shown to be a versatile method with many uses, despite its pitfalls (e.g. Walker et al. 2008). Perhaps it is a better fit for the Icelandic sample within the current paper because of the equal size of the samples taken at each station for comparison.

The two dive sites where a high abundance and diversity of sponges were found both feature some hard substrate, but each to its own degree. Dive D15—the dive with the highest diversity overall and the highest abundance of sponges—was an area of muddy bottom that had also stones scattered about. Sponges were both attached to the stones and some species appeared to be growing in the fine sediment. The pattern of a higher overall diversity accompanying an abundance of sponges has been well documented (e.g. Klitgaard 1995, Mayer Piepenburg 1996, Rocha 2000, Hixon et al. 2007, Swain & Wulff 2007). This is also an area of mixed bottom types and as such, there are more ecological functions to fill. Habitat heterogeneity increases with an increase in three-dimensionality. Emergent fauna such as massive form sponges add to this heterogeneity (Ellingsen et al. 2007). Bulling et al. (2008) found that habitat heterogeneity of any kind effects benthic organisms strongly, although not always in the same way.

4.2.2 JMFZ and Mohn Ridge

The rarefaction performed seems to indicate a good deal of variation in the community compositions of the dives. Rarefaction is a highly contested method of analysis because of the heavy influence of community evenness on the analysis (Gray 2001) and it has been suggested that rarefaction cannot be used to compare samples of different size (Gray 2002). Despite this, it seems to have some validity for the current study because when compared to the other analyses performed herein it seems to provide similar results at low ES(n). It has been shown to be a versatile method with many uses, despite its pitfalls (e.g. Walker et al. 2008). Perhaps it is a better fit for the Icelandic sample within the current paper because of the equal size of the samples taken at each station for comparison.

The two dive sites where a high abundance and diversity of sponges were found both feature some hard substrate, but each to its own degree. Dive D15—the dive with the highest diversity overall and the highest abundance of sponges—was an area of muddy bottom that had also stones scattered about. Sponges were both attached to the stones and some species appeared to be growing in the fine sediment. The pattern of a higher overall diversity accompanying an abundance of sponges has been well documented (e.g. Klitgaard 1995, Mayer Piepenburg 1996, Rocha 2000, Hixon et al. 2007, Swain & Wulff 2007). This is also an area of mixed bottom types and as such, there are more ecological functions to fill. Habitat heterogeneity increases with an increase in three-dimensionality. Emergent fauna such as massive form sponges add to this heterogeneity (Ellingsen et al. 2007). Bulling et al. (2008) found that habitat heterogeneity of any kind effects benthic organisms strongly, although not always in the same way.

5 Concluding remarks

Most of the taxonomic classes analyzed in this paper are among those listed as suffering damage from fishing effort in general, and mobile fishing gears in particular, in other parts of the ocean (e.g. Kaiser et al. 2000, Rodrigues et al. 2001, Turner et al. 1999) The effects of fishing on the deep benthic communities of the sub-arctic can accordingly be expected to be devastating as they have been shown to be elsewhere. Turner et al. (1999) reported on some examples of areas in the South Pacific where bottom fishing removed poriferan. bryozoan, alcyonarian and polychaete assemblages that supported the very fish that were being sought. Further, the removal or damage of these groups was followed by decline in the fished stocks and a change in the dominant fish species in the areas under question. Poriferans, bryozoans, polychaetes, and to a lesser extent, alcyonarians have been shown to be important in bathyal waters around the Icelandic margin. The species that are deemed sensitive to these stresses are often responsible for the increased diversity in stations where soft sediments covered all or most of the bottom. The effect of trawling these areas has been likened to those of clear-cutting forests (Watling & Norse 1998) in which, the removal or destruction of the large emergent fauna greatly reduces the heterogeneity of the ecosystem and therefore the overall biodiversity of the area. In addition, there is a marked decrease in the abundance-biomass curves of large fauna in areas of frequent fishing activity (Kaiser et al. 2000). As fishing is practiced with greater intensity, the average sizes attained by fauna decrease because of the stress under which they live. However, the disturbance of trawled fishing gears, especially otter boards, is more than just the reduction of the biological quality of the ecosystem. Otter boards and other fishing gears towed on the bottom cause fine sediments to become suspended in the water column again. This causes clouds of silt that then settle elsewhere and can bury the hard surfaces we have shown to be influential in increasing biodiversity and habitat heterogeneity. In addition, these gears even out the surface of the bottom, removing rocks and leveling mounds, that otherwise influence water flow regimes just above the bottom as well as providing shelter and habitat for benthic species of all kinds. High fishing pressure disturbs large portions of the sea floor where trawls are repeatedly dragged across wide swaths of favored fishing grounds at short return intervals (Turner et al. 1999, Hixon & Tissot, 2007).

The understanding of marine ecological processes and their interrelatedness with animal life in the deep-sea should be a priority in provide researchers with an opportunity develop new understanding, technology, and methods that science has been lacking to date. Technology has suddenly provided us with an array of new equipment to delve the mysteries of this last earthly frontier in novel ways. We would be best advised to take this opportunity to expand our understanding of life around us before we disturb the nearly pristine natural condition in which much of the deep-sea exists at present.

References

- Abdo, D.A., Seager, J.W., Harvey, E.S., McDonald, J.I., Kendrick, G.A., Shortis, M.R., 2006. Efficiently measuring complex sessile epibenthic organisms using a novel photogrammetric technique. J. Exp. Mar. Biol. Ecol. 339, 120–133.
- Anonymous, 1992. Convention on Biological Diversity. United Nations Conference on Environment and Development. Rio de Janeiro.
- Ambrose Jr., W.G., Clough, L.M., Tilney, P.R., Beer, L., 2001. Role of echinoderms in benthic remineralization in the Chukchi Sea. Mar. Biol. 139, 937–949.
- Bamber, R.N., Thurston, M.H., 1995. The deep-water pycnogonids (Arthropoda: Pycnogonida) of the northeastern Atlantic Ocean. J. Linn. Soc. London, Zool. 115, 117–162.
- Barnes, D.K.A., Kaiser, S., Griffiths, H.J., Linse, K., 2009. Marine, intertidal, freshwater, and terrestrial biodiversity of an isolated polar archipelago. J. Biogeogr. 36, 756–769.
- Barthel, D., Tendal, O.S., 1993. The sponge association of the abyssal Norwegian–Greenland Sea: species composition, substrate relationships, and distribution. Sarsia. 78, 83–96.
- Bell, J.J., Barnes, D.K.A., 2003. Effect of disturbance on assemblages: an example using Porifera. Biol. Bull. 205, 144–159.
- Bett, B.J., 2001. UK Atlantic Margin environmental survey: introduction and overview of bathyal benthic ecology. Cont. Shelf Res. 21, 917–956.
- 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). J. Mar. Sys. 63, 35–48.
- Birch, D.W., 1981. Dominance in marine ecosystems. Am. Nat. 118, 262–274.
- Billett, D.SM., Lampitt, R.S., Rice, A.L., Mantoura, R.F.C., 1983. Seasonal sedimentation of phytoplankton to the deep sea benthos. Nature 302, 520–522.
- Blindheim, J., Rey, F., 2004. Water-mass formation and distribution in the Nordic Seas during the 1990's. ICES J. Mar. Sci. 61, 846–863.
- Bluhm, B.A., Macdonald, I.R., Debenham, C., Iken, K., 2005. Macro- and megabethnic communities in the high Arctic Canada Basin: initial findings. Polar Biol. 28, 218–231.
- Briggs, J.C., 2007. Marine longitudinal biodiversity: causes and conservation. Diversity Distrib. 13, 544–555.

- Bulling, M.A., Solan, M., Dyson, K.E., Hernandez-Milian, G., Luque, P., Pierce, G.J., Raffaelli,
 D., Paterson, D.M., White, P.C.L., 2008. Species effects on ecosystem processes are modified by faunal responses to habitat composition. Oecol. 158, 511–520.
- Buschbaum, C., Dittmann, S., Hong, J., Hwang, I., Strasser, M., Thiel, M., Valdivia, N., Yoon, S., Reise, K., 2009. Mytilid mussels: global habitat engineers in coastal sediments. Helgol. Mar. Res. 63, 47–58.
- Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. Mar. Ecol. Prog. Ser. 92, 205–219.
- Clausen, C., 2004. Gastrotricha from the Faroe Bank. Sarsia 89, 423–458.
- Dinmore, T.A., Duplisea, D.E., Rackham, B.D., Maxwell, D.L., Jennings, S., 2003. Impact of large-scale area closure on patters of fishing disturbance and the consequences for benthic communities. ICES J. Mar. Sci. 60, 371–380.
- Dijkstra, H.H., Warén, A., Guðmundsson, G., 2009. Pectinoidea (Mollusca: Bivalvia) from Iceland. Mar. Biol. Res. 5, 207–243.
- Dewdney, A.K., 2000. A dynamical model of communities and a new species-abundance distributuion. Biol. Bull. 198, 152–165.
- Ellingsen, K.E., Hewitt, J.E., Thrush, S.F., 2007. Rare species, habitat diversity and functional redundancy in marine benthos. J. Sea Res. 58, 291–301.
- Flach, E., de Bruin, W., 1999. Diversity patterns in macrobenthos across a continental slope in the NE Atlantic. J. Sea Res. 42, 303–323.
- Fontana, G., Ugland, K.I., Gray, J.S., Willis, T.J., Abbiati, M., 2008. Influence of rare species on beta diversity estimates in marine benthic assemblages. J. Exp. Mar. Biol. Ecol. 366, 104–108.
- Gage, J.D., 2001. Deep-sea benthic community and environmental impact assessment at the Atlantic Frontier. Cont. Shelf Res. 21, 957–986.
- Gage, J.D., 2004. Diversity in deep-sea benthic macrofauna: the importance of local ecology, the larger scale, history and the Antarctic. Deep Sea Res. Part II 51, 1689–1708.
- Gage, J.D., Lamont, P.A., Kroeger, K., Paterson, G.J.L., Gonzales Vecino, J.L., 2000. Patterns in deep-sea macrobenthos at the continental margin: standing crop, diversity and faunal change on the continental slope off Scotland. 440, 261–271.
- Galparsoro, I., Borja, Á., Bald, j., Liria, P., Chust, G., 2009. Predicting suitable habitat for the European lobster (Homarus gammarus), on the Basque continental shelf (Bay of Biscay), using Ecological-Niche Factor Analysis. Ecol. Modell. 220, 556–567.
- Gotto, R.V., 1957. The biology of a commensal copepod, Ascidicola rosea Thorell, in the ascidian Corella parollelogramma (Müller). J. Mar. Biol. Ass. U.K. 36, 286–290.

- Gray, J.S., 1997. Marine biodiversity: patterns, threats and conservation needs. Biodiversity and Cons. 6, 153–175.
- Gray, J.S., 2001. Marine diversity: the paradigms in patterns of species richness examined. Sci. Mar. 65, 41–56.
- Gray, J.S., 2002. Species richness of marine soft sediments. Mar. Ecol. Prog. Ser. 244, 285–297.
- Gray, J.S., Bjørgsæter, A., Ugland, K.I., 2005. The impact of rare species on natural assemblages. J. Anim. Ecol. 74, 1131–1139.
- Gutt, J., Starmans, A., 2003. Patchiness of the megabenthos at small scales: ecological conclusions by examples from polar shelves. Polar Biol. 36, 276–278.
- Hansen, B., Østerhus, S. 2000. North Atlantic—Nordic Seas exchanges. Prog. Oceanogr. 45, 109–208.
- Hansson, H.G. (Comp.), 1998a. NEAT (Northeast Atlantic Taxa): Scandanavian Chordata Check-List. Internet PDF Ed., Aug. 1998. [http://www.tmbl.gu.se].
- Hansson, H.G. (Comp.), 1998b. NEAT (Northeast Atlantic Taxa): Scandanavian Echinodermata Check-List. Internet PDF Ed., Aug. 1998. [http://www.tmbl.gu.se].
- Hewitt, J.E., Thrush, S.F., Dayton, P.D., 2008. Habitat variation, species diversity and ecological functioning in a marine system. J. Exp. Mar. Biol. Ecol. 366, 116–122.
- Hillebrand, H., 2004. On the generality of the latitudinal diversity gradient. Am. Nat. 163, 192–211.
- Hirose, E., 2000. Diet of a notodelphyid copepod inhabiting in an algal-bearing didemnid ascidean Diplosoma virens. Zool. Sci. 17, 833–838.
- Hixon, M.A., Tissot, B.N., 2007. Comparison of trawled vs untrawled areas of mud seafloor assemblages of fishes and macroinvertebrates at Coquille Bank, Oregon. J. Exp. Mar. Biol. Ecol. 344, 23–34.
- Ho, J., Conradi, M., Lopez-González, P.J., 1998. A new family of cyclopoid copepods (Fratiidae) symbiotic in the ascidian (Clavellina dellavallei) from Cádiz, Spain. J. Zool., Lond. 246, 39–48.
- Johnson, N.A., Campbell, J.W., Moore, T.S., Rex, M.A., Etter, R.J., McClain, C.R., Dowell, M.D., 2007. The relationship between the standing stock of deep-sea macrobenthos and surface production in the western North Atlantic. Deep Sea Res. 54, 1350–1360.
- Jones, D.O.B., Bett, B., Flewellen, C., Conquer, M., 2005. Seabed photography from an autonomous underwater vehicle. J. Mar. Sci. Environ. No. C3, 29–36.
- Jones, D.O.B., Bett, B., Tylor, P., 2007a. Megabenthic ecology of the Faroe–Shetland channel: a photographic study. Deep Sea Res. 54, 1111–1128.

- Jones, D.O.B., Bett, B., Tylor, P., 2007b. Depth-related changes in the arctic epibenthic megafaunal assemblages of Kangerdlusssuaq, East Greenland. Mar. Biol. Res. 3, 191–204.
- Jones, D.O.B., Wigham, B.D., Hudson, I.R., Bett, B.J., 2007c. Anthropogenic disturbance of deep-sea megabenthic assemblages: a study with remotely operated vehicles in the Faroe–Shetland Channel, NE Atlantic. Mar. Biol. 151, 1731–1741.
- Jónsson, S., Valdimarsson, H., 2005. The flow of Atlantic water to the North Icelandic Shelf and it's relation to the drift of cod larvae. ICES J. Mar. Sci. 62, 1350–1359.
- Kaiser, M.J., Ramsay, K., Richardson, C.A., Spence, F.E., Brand, A.R., 2000. Chronic fishing disturbance has changed shelf sea benthic community structure. J. Anim. Ecol. 69, 494–503.
- Klitgaard, A.B, 1995. The fauna associated with outer shelf and upper slope sponges Porifera, (Demospongia) at the Faeroe Islands, northeastern Atlantic. Sarsia 80, pp. 1-22.
- Klitgaard, A.B., Tendal, O.S., 2004. Distribution and species composition of mass occurrences of larg-sized sponges in the northeast Atlantic. Prog. Oceanogr. 61, 57–98.
- Leonard, G.H., Clarck, R.P., 1993. Point quadrat versus video transect estimates of the cover of benthic red algae. Mar. Ecol. Prog. Ser. 101, 203–208.
- Leujak, W., Ormond, R.F.G., 2007. Comparative accuracy and efficiency of six coral community survey methods. J. Exp. Mar. Biol. Ecol. 351, 168–187.
- Lindholm, J.B., Auster, P.J., Ruth, M., Kaufman, L., 2001. Modeling the effects of fishing and implications for the design of marine protected areas: juvenile fish responses to variations in seafloor habitat. Conserv. Biol. 15, 424–437.
- Lobo, J.M., Favila, M.E., 1999. Different ways of constructing octaves and their consequences on the prevalence of the bimodal species abundance distribution. Oikos 87, 321–326.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808.
- Macpherson, E., 2003. Species range size distributions for some marine taxa in the Atlantic Ocean. Effect of latitude and depth. J. Linn. Soc. London, Biol. 80, 437–455.
- Magurran, A.E., Henderson, P.A., 2003. Exlaining the excess of rare species in natural species abundance distributions. Nature 422, 714–716.
- Maldonando, M., Young, C., 1996. Bathymetric patterns of sponge distribution on the Bahamian slope. Deep Sea Res. Part I 43, 897–915.
- Margalef, R., 1963. On certain unifying principles in ecology. Am. Nat. 97, 357–374.

- Mayer, M., Peipenburg, D., 1996. Epibenthic community patterns on the continental slope off East Greenland at 75°N. Mar. Ecol. Prog. Ser. 143, 151–164.
- McClanahan, T.R., Sala, E., 1997. A Mediterranean rocky-bottom ecosystem fisheries model. Ecol. Model. 104, 145–164.
- Morato, T., Watson, R., Pitcher, T.J., Pauly, D., 2006. Fishing down the deep. Fish and Fisheries 7, 24–34.
- Moore, J.A., Vecchione, M., Collette, B.B., Gibbons, R., Hartel, K.E., 2004. Selected fauna of Bear Seamount (New England Seamount Chain), and the presence of "natural invader" species. Arch. Fish. Mar. Res. 51, 241–250.
- Mortensen, P.B., Buhl-Mortensen, L., 2004. Distribution of deep-water gorgonian corals in relation to benthic habitat features in the Northeast Channel (Atlantic Canada). Mar. Biol. 144, 1223–1238.
- Mumby, P.J., 2001. Beta and habitat diversity in marine systems: a new approach to measurement, scaling and interpretation. Oecol. 128, 274–280.
- Ojeda, G.Y., Gayes, P.T., Van Dolah, R.F., Schwab, W.C., 2004. Spatially quantitative seafloor habitat mapping: example from the northern South Carolina inner continental shelf. Estuarine Coastal Shelf Sci.59, 399–416.
- Parry, D.M., Kendall, M.A., Pilgrim, D.A., Jones, M.B., 2003. Identification of patch structure within marine benthic landscapes using a remotely operated vehicle. L. Exp. Mar. Biol. Ecol. 285–286, 497–511.
- Pech, D., Condal, A.R., Bourget, E., Ardisson, P., 2004. Abundance estimation of rocky shore invertebrates at small spatial scale by high-resolution digital photography and digital image analysis. J. Exp. Mar. Biol. Ecol. 299, 185–199.
- Piepenburg, D., 2005. Recent research on Arctic benthos: common notions need to be revised. Polar Biol. 28, 733–755.
- Piepenburg, D., von Juterzenka, K., 1994. Abundance, biomass and spatial distribution of brittle stars (Echinodermata: Ophiuroidea) on the Kolbeinsey Ridge north of Iceland. Polar Biol. 14, 185–194.
- Puce, S., Calcinai, B., Bavestrello, G., Cerrano, C., Gravili, C., Boero, F., 2005. Hydrozoa (Cnidaria) symbiotic with Porifera: a review. Mar. Ecol. 26, 73–81.
- Rabaut, M., Vincx, M., Degraer, S., 2009. Do Lanice conchilega (sandmason) aggregations classify as reefs? Quantifying habitat modifying effects. Helgol. Mar. Res. 63, 37–46.
- Rhoads, D.C., Young, D.K., 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts II. Reworking by Molpadia oolitica (Holothuroidea). Mar. Biol. 11, 255–261.
- Ringvold, H., 1999. Starfishes (Echinodermata, Asteroidea) new for the Faroe Islands collected by "BIOFAR". Sarsia 84, 469–472.

- Rocha, L.A., Rosa, I.L., Feitoza, B.M., 2000. Sponge-dwelling fishes of northern Brazil. Environ. Biol. Fishes 59, 453–458.
- Ross SW, Quattrini AM, 2007. The fish fauna associated with deep coral banks off the southeastern United States. Deep-Sea Res. (1 Oceanogr. Res. Pap.) 54, 975–1007.
- Ross, S.W., Quattrini, A.M., 2009. Deep-sea reef fish assemblage patterns on the Blake Plateau (Western North Atlantic Ocean). Mar. Ecol. 30, 74–92.
- Rudels, B., Fahrbach, E., Meincke, J., Budéus, G., Eriksson, P., 2002. The East Greenland Current and its contribution to the Denmark Strait overflow. ICES J. Mar. Sci. 59, 1133–1154.
- Sahade, R., Stellfeldt, A., Tatián, M., Laudien, J., 2004. Macro-epibenthic communities and diversity of Arctic Kongsfjorden, Svalbard, in relation to depth and substrate. Publication of the Alfred Wegner Institute for Polar and Marine Research, ePIC Repository. Bremerhaven, Germany.
- Santini, D.B., Dauvin, J., 2008. Contribution to knowledge of the genus Haploops, a new location for Haploops lodo (Crustacea: Amphipoda: Ampeliscidae) from the bathyal North Atlantic Ocean with a complement to the description of the species. J. Nat. Hist. 42, 1065–1077.
- Schander, C., Rapp, H.T., Bakken, T., Berge, J., Cochrane, S., Kongsrud, J.A., Oug, E., Byrkjedal, I., Cedhagen, T., Fosshagen, A., Larsen, K., Obst, M., Pleijel, F., Stöhs, S., Todt, C., Warén, A., Hadler-Jacobsen, S., Keuning, R., Mikkelsen, N.T., Heggøy, K.K., Torseth, I., Pedersen, R.B. The fauna of the hydrothermal vents on the Mohn Ridge (North Atlantic). In preparation.
- Schneider, D.C., Gagnon, J.M., Gilkinson, K.D., 1987. Patchiness on the outer Grand banks of Newfoundland. Mar. Ecol. Prog. Ser. 39, 1–13.
- Schuchert, P., 2000. Hydrozoa (Cnidaria) of Iceland collected by the BIOICE programme. Sarsia 85, 411–438.
- Schuchert, P., 2001. Hydroids of Greenland and Iceland (Cnidaria, Hydrozoa). Meddelelser om Grønland, Bioscience 53. Danish Polar Centre, Coppenhagen, 184 pp.
- Schuchert, P., 2005. Taxonomic revision and systematic notes on some Halecium species (Cnidaira, Hydrozoa). J. Nat. Hist. 39, 607–639.
- Seiderer, L.J., Newell, R.C., 1999. Analysis of the relationship between sediment compostion and benthic community structure in coastal deposits: implications for marine aggregate dredging. ICES J. Mar. Sci. 56, 757–765.
- Serrano, A., Preciado, I., 2007. Environmental factors structuring polychaete communities in shallow rocky habitats: role of physical stress versus habitat complexity. Helgol. Mar. Res. 61, 17–29.

- Shumway, C.A., Hoffman, H.A., Dobberfuhl, A.P., 2007. Quantifying habitat complexity in aquatic ecosystems. Freshwat. Biol. 52, 1065–1076.
- Sigurðsson, Th., Kristinsson, K., Rätz, H-J., Nedreaas, K.H., Melnikov, S.P., Reiner, J., 2006. The fishery for pelagic redfish (Sebastes mentella) in the Irminger Sea and adjacent waters. ICES J. Mar. Sci. 63, 725–736.
- Solan, M., Germano, J.D., Rhoads, D.C., Smith, C., Michaud, E., Parry, D., Wenzhöfer, F., Kennedy, B., Henriques, C., Battle, E., Carey, D., Iocco, L., Valente, R., Watson, J., Rosenberg, R., 2003. Towards a greater understanding of pattern, scale and process in marine benthic systems: a picture is worth a thousand worms. J. Exp. Mar. Biol. Ecol. 285–286, 313–338.
- Søiland, H., Prater, M.D., Rossby, T. 2008. Rigid topographic of currents in the Nordic Seas. J. Geophys. Res. 35, L18607, DOI: 10.1029/2008GL034846.
- Stål, J., Paulsen, S., Pihl, L., Rönbäk, P., Söderqvist, T., Wennhage, H., 2008. Caostal habitat support to fish and fisheries in Sweden: integrating ecosystem functions into fisheries management. Ocean Coast. Manage. 51, 594–600.
- Stelzenmüller, V., Rogers, S.I., Mills, C.M., 2008. Spatio-temporal patterns of fishing pressure on UK marine landscapes, and their implications for spatial planning and management. ICES J. Mar. Sci. 65, 1081–1091.
- Svavarsson, J., 1997. Diversity of isopods (Crustacea): new data from the Arctic and Atlantic Oceans. Biodiversity Conserv. 6, 1571–1579.
- Swain, T.D., Wulff, J.L., 2007. Diversity and specificity of Caribbean sponge-zoanthid symbioses: a foundation for understanding the adaptive significance of symbioses and generating hypotheses about higher-order systematics. Biol. J. Linn. Soc. 92, 695–711.
- Terlizzi, A., Anderson, M.J., Bevilacqua, S., Fraschetti, S., Wlodarska-Kwalczuk, M., Ellingsen, K.E., 2009. Beta-diversity and taxonomic sufficiency: Do higher-level taxa reflect heterogeneity in species composition? Diversity Distrib. 15, 450–458.
- Thomas, J.D., Klebba, K.N., 2007. New species and host associations of commensal leucothid amphipods from coral reefs in Florida and Belize (Crustacea: amphipoda). Zootaxa 1494, 1–44.
- Turner, S.J., Thrush, S.F., Hewitt, J.E., Cummings, V.J., Funnell, G., 1999. Fishing impacts and the degradation or loss of habitat structure. Fisheries Management Ecol. 6, 401–420.
- Voultsiadou, E., Pyrounaki, M., Chintiroglou, 2007. The habitat engineering tunicate Microcosmus sabatieri Roule, 1885 and its associated peracarid epifauna. Estuar. Coast. Shelf Sci. 74, 197–204.
- Walker, S.C., Poos, M.S., Jackson, D.A., 2008. Functional rarefaction: estimating functional diversity from field data. Oikos 117, 286–296.

- Weisshappel, J.B.F., Svavarsson, J., 1998. Benthic amphipods (Crustacea: Malacostraca) in Icelandic waters: diversity in relation to faunal patterns from shallow to intermediate deep Arctic and North Atlantic Oceans. Mar. Biol. 131, 133–143.
- Weslavski, J.M., Wlodarska-Kowalczuk, M., Legezynska, J., 2003. Occurrence of soft bottom macrofauna along the depth gradient in High Arctic, 79° N. Polish Pol. Res. 24, 73–88.
- Wilhm, J.L., 1970. Range of diversity index in benthic macroinvertebrate populations. J. Water Pollut. Control Fed. 42, 221–224.
- Zajac, R.N., 2008. Macrobenthic biodiversity and sea floor landscape structure. J. Exp. Mar. Biol. Ecol. 366, 198–203.

Appendix I

Table 9. Species identifications for the BIOICE sample. All identifications are conformis (cf.) names as physical specimens were not available for concrete identifications.

Phylum (no. spp)	Genus /species	Authority	Phylum (no. spp)	Species	Authority
Porifera (20)	Tetilla sp. 1	Sollas, 1886	Arthropoda (10)	Arcturus baffini	Sabine, 1824
	Tetilla sp. 2	Sollas, 1886		Munnopsis typica	M. Sars, 1861
	Haliclona urceola	Rathke & Vahl, 1806		Unident. Amphipoda sp. 1	
	Haliclona sp. 2	Grant, 1836		Unident. Amphipoda sp. 2	
	Haliclona sp. 3	Grant, 1836		Unident. Amphipoda sp. 3	
	Grantia compressa	Fabricius, 1780		Sclerocrangon sp.	
	Stylocordyla borealis	Loven, 1868		Pandalus borealis	Krøyer, 1838
	Mycale sp. 1	Gray, 1867		Pycnogonum crassirostrum	Sars, 1888
	Mycale sp. 2	Gray, 1867		Nymphon gracile	Leach, 1814
	Phakellia sp.	Bowerbank, 1862		Nymphon brevirostre	Hodge, 1863
	Polymastia sp. 1	Bowerbank, 1864	Mollusca (9)	Unident. Nudibranchia sp. 1	C ,
	Polymastia sp. 2	Bowerbank, 1864		Unident. Nudibranchia sp. 2	
	Antho dichotoma	Linnaeus, 1767		Unident. Nudibranchia sp. 3	
	Iophon sp	Gray, 1867		Unident. Gastropoda sp.	
	Aplysilla sulfurea Schulze, 1878			Unident. Gastropoda sp. 2.	
	Hymedesmia Boerbank, 1866 paupertas			Unident. Gastropoda sp.	
	Tedania sp	Gray, 1867		Unident. Gastropoda sp. 4	
	Ciocalypta penicillus	Bowerbank, 1862		Unident. Gastropoda sp. 5	
	Tethya aurantium	Pallas, 1766		Unident. Gastropoda sp. 6	
	Melonanchora elliptica	Carter, 1874	Bryozoa (7)	Porella compressa	J. Sowerby, 1805
Cnidaria (28)	Corymorpha glacialis	Sars, 1859		Eucratea loricata	Linnaeus, 1758
` ′	Nemertesia ramosa	Lamark, 1816		Hornera lichenoides	Linnaeus, 1758
	Nemertesia antennina	Linnaeus, 1758		Reteporella beaniana	King, 1846
	Halecium halecium	Linnaeus, 1758		Caberea ellisii	Flemming, 1814
	Thuiaria articulata	Pallas, 1766		Cellepora ramulosa	Linnaeus, 1767
	Unident. Hydro. sp. 6			Bryozoa sp. 7	
	Unident. Hydro. sp. 7		Brachiopoda (2)	Terebratulina retusa	Linnaeus, 1758
	Unident. Hydro. sp. 8			Unident. Articulata sp. 2	
	Unident. Hydro. sp. 9		Echinodermata (23)	Heliometra glacialis	Owen, 1833 ex Leach MS
	Unident. Hydro. sp. 10		(-)	Antedon bifida	Pennant, 1777
	Unident. Hydro. sp.			Antedon petasus	Düben & Koren, 1846
	Unident. Hydro. sp. 12			Henricia sanguinolenta	O.F. Müller, 1776

Cnidaria (cont)	Drifa glomerata	Verrill, 1869	Echinodermata (cont)	Crossaster papposus	Linnaeus, 1776
` /	Unident. Alcyoniidae sp. 2		(cont)	Stichastrella rosea	O.F. Müller, 1776
	Unident. Alcyoniidae sp. 3			Pteraster militaris	O.F. Müller, 1776
	Ceratocaulon wandeli	Jungerson, 1892		Freyella elegans	Verrill, 1874
	Pennatula phosphorea	Linnaeus, 1758		Ophiocten sericeum	Forbes, 1852
	Virgularia mirabilis	Müller, 1776		Ophiura albida	Forbes, 1839
	Ceriathus lloydii	Gosse, 1859		Ophiopleura borealis	Danielssen & Koren, 1877
	Sagartia ornata	Holdsworth, 1855		Ophiothrix fragilis	Abildgaard, 1789
	Protanthea simplex	Carlgren, 1891		Ophiocomina nigra	Abildgaard, in O.F. Müller, 1789
	Capnea sanguinea	Forbes, 1841		Gorgonocephalus eucnemis	Müller & Troschel, 1842
	Bolocera tuediae	Johnston, 1832		Unident. Ophiu. sp. 7	
	Urticina felina	Linnaeus, 1767		Unident. Ophiu. sp. 8	
	Epizoanthus couchii	Johnston in Couch, 1844		Unident. Ophiu. sp. 9	
	Hormathia digitata	Müller, 1776		Echinus esculentus	Linnaeus, 1758
	Unident. Hexacorallia sp.5			Ocnus lacteus	Forbes & Goodsir, 1839
	Unident. Hexacorallia sp. 6			Unident. Holothu. sp. 2	
Annelida (10)	Myxicola infundibulum	Renier, 1804		Unident. Holothu. sp. 3	
, ,	Potamilla reniformis	Malmgren, 1966		Unident. Holothu. sp. 4	
	Sabella crassicornis	Sars, 1851		Unident. Holothu. sp. 5	
	Sabellaria spinulosa	Leuckart, 1849	Tunicata (6)	Eudistoma vitreum	Caullery, 1908
	Sabella penicillus	Linnaeus, 1767		Pycnoclavella aurilucens	Garstang, 1891
	Protula tubularia	Montagu, 1803		Didemnum albidum	Verrill, 1871
	Unident. Polych. sp. 7			Synoicum pulmonaria	Ellis & Solander, 1786
	Unident. Polych. sp. 8			Ciona intestinalis	Linnaeus, 1758
	Unident. Polych. sp. 9			Botryllus schlosseri	Pallas, 1766
	Unident. Polych. sp. 10		Osteichthyes (3)	Glyptocephalus cynoglossus	Linnaeus, 1758
				Artediellus atlanticus Lycodes sp. 1	Jordan & Evermann, 1898

Appendix II

Table 10. Species identified from the Jan Mayen Fracture Zone and Mohn Ridge dive videos. All identifications are conformis (cf.) names as physical specimens were not available for concrete identifications.

Phylum (no. spp.)	Species	Authority	Phylum (no. spp.)	Species	Authority
Porifera (18)	Haliclona sp. 1	Grant, 1836	Crustacea (5)	Pandalus sp. 1	Leach, 1815
	Haliclona sp. 2	Grant, 1836		Lebbeus polaris	Sabine, 1824
	Haliclona sp. 3	Grant, 1836		Decapoda sp.	
	Myxilla sp.			Colossendeis	Sabine, 1824
	Tethya aurantum	Pallas, 1766	Bryozoa (4)	<i>proboscidea</i> Bryozoa sp. 1	
	Stylocordyla borealis	Loven, 1868		Bryozoa sp. 2	
	Phakellia sp.	Bowerbank, 1862		Hornera lichenoides	Linnaeus, 1758
	Tetilla sp.	Sollas, 1886		Reteporella beaniana	King, 1846
	Polymastia sp. 1	Bowerbank, 1864	Echinodermata (15)	Heliometra glacialis	Owen, 1833 ex Leach MS
	Polymastia sp. 2	Bowerbank, 1864	(15)	Antedon petasus	Düben & Koren, 1846
	Aplysia sulfurea	Schulze, 1878		Antedon bifida	Pennant, 1777
	Leucandra sp. 1	Haeckel, 1872		Pteraster sp.	Müller & Troschel, 1842
	Por sp.11			Astropecten sp.	Gray, 1840
	Por sp.12			Hymenaster sp.	Thomsen, 1873
	Por sp.13			Crossaster papposus	Linnaeus, 1776
	Por sp.14			Ophiu sp. 1	
	Cladorhiza sp.	Sars, 1872		Ophiu sp. 2	
Cnidaria (12)	Hydro sp. 1			Ophiu sp. 3	
	Corymorpha groenlandica	Allman, 1876		Ophiu sp. 4	
	Tubularia indivisa	Linnaeus, 1758		Ophiu sp. 5	
	Gersemia sp. 1	Marenzeller, 1877		Gorgonochephalus eucnemis	Müller & Troschel, 1842
	Gersemia sp. 2	Marenzeller, 1877		Gorgonocephalus sp. 2	Leach, 1815
	Umbellula encrinus	Linnaeus, 1758		Echinoidea sp. 1	
	Urticina felina	Linnaeus, 1767	Tunicata (3)	Ascidea sp. 1	
	Hormathia digitata	Müller, 1776		Ascidea sp. 2	
	Hexa sp. 3			Ascidea sp. 3	
	Hexa sp. 4		Chondrichthyes	Amblyraja hyperborea	Collett, 1879
	Hexa sp. 5		Osteichthyes	Macrourus berglax	Lacepède, 1801
	Cerianthus sp.	Delle Chiaje, 1830	(6)	Reinhardtius hippoglossoides	Walbaum, 1792
Annelida (4)	Sabella sp. 1	Linnaeus, 1767		Rhodichthys regina	Collett, 1879
	Sabella sp. 2	Linnaeus, 1767		Paraliparis sp.	Collett, 1878
	Serpulida sp.	Rafinesque, 1815		Lycodes sp. 1	
	Nothria conchylega	Sars, 1835		Gaidropsarus argentatus	Reinhardt, 1837