Benthic community mapping in the northern Dreki area, Iceland

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Abstract

The deep Arctic seafloor supports a wide diversity of benthic megafauna that provide important ecosystem services. However, deep-sea Arctic environments are increasingly under threat due to climate change and ocean acidification as well as the ongoing expansion of human activities such as fishing, shipping, and hydrocarbon production into deeper and higher-latitude waters. There is thus a growing need for baseline information on megafauna community composition and distribution, without which assessment of impacts is virtually impossible. This study reviewed the available information on deep-sea megafauna communities in the Greenland-Iceland-Norwegian (GIN) Seas. An in-depth review of 12 studies documented a diverse array of benthic communities and revealed large regional variations in the quantity and quality of information. No information was available for the northern Dreki area in the Icelandic EEZ despite interest in hydrocarbon exploration in this area. This study modelled the distribution of communities at a 10,500 km^2 study site located within the northern Dreki area. Acoustic and benthic surveys were carried out at this site in 2008. The benthic data were analysed using multivariate methods, resulting in the identification of five megafauna communities. Random forest was used to model the relationship between communities and variables derived from the acoustic survey data, including depth and backscatter, which enabled the generation of a full-coverage map of predicted community distribution. While this map indicates that the impacts of hydrocarbon operations could greatly alter community structure in the northern Dreki area, further studies using more comprehensive datasets are required to confirm these findings.

Útdráttur

Hafsbotninn á norðlægum hafsvæðum einkennist af fjölskrúðugu lífríki stórvaxinna botndýra. En þessi norðlægu svæði eru undir auknu álagi af völdum hnattrænnar hlýnunar og súrnun sjávar, sem og auknum athöfnum mannsins, svo sem af völdum veiða, skipaflutninga og olíuvinnslu, oft á miklu dýpi. Í ljósi þessa er því rík nauðsyn að afla grunngagna um samfélagsgerðir botndýra og útbreiðslu þeirra, en án slíkra gagna er ómögulegt að meta áhrif af völdum mannsins á lífríki hafsbotnsins. Í þessari rannsókn voru teknar saman birtar upplýsingar um djúpsjávarbotndýr og samfélög sem finnast á grænlenska, íslenska og norska hafsvæðinu. Þetta yfirlit byggði á upplýsingum úr 12 greinum, sem sýndi að á þessu svæði væri fjölskrúðugt dýralíf en jafnfram að það væri mikill svæðisbundinn breytileiki í magni og gæðum gagnanna. Árið 2008 var landslag hafsbotnsins sem og lífríkið á Drekasvæðinu kannað í tveimur rannsóknaleiðöngrum Hafrannsóknastofnunar. Gögn úr þessum leiðöngrum voru notuð hér í þessu verkefni til að kortleggja útbreiðslu botndýrasamfélaga á Drekasvæðinu, innan svæðis sem er 10,500 km2. Með fjölþátta aðferðum voru þannig skilgreind fimm samfélög botndýra á svæðinu. "Random forest" líkani var beitt til að kanna sambönd á milli margvíslegra umhverfisþátta svo sem dýpis og botnhörku og þess lífríkis sem fannst á svæðinu en þannig var mögulegt að yfirfæra þessi fimm botndýrasamfélög á allt svæðið. Niðurstöður gefa til kynna að áhrif olíuvinnslu á svæðinu geta haft töluverð áhrif á lífríki botnsins en þörf er á frekari úrvinnslu annarra gagna sem eru fyrir hendi til að geta metið ítarlegar áhættuna af olíuvinnslunni.

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1 Benthic megafauna communities in the deep GIN Seas

1.1 Introduction

The deep waters of the Greenland-Iceland-Norwegian (GIN) Seas form a dynamic and topographically complex ocean region, encompassing steep slopes, extensive ridge systems, and deep basins (Drange et al., 2005). Similar to other Arctic and sub-Arctic areas, the GIN Seas are characterised by large seasonal variations in solar radiation and primary production and very low water temperatures (Piepenburg, 2006). Contradicting traditional notions of the scarcity or non-existence of life in seemingly inhospitable deep and high latitude seafloor environments (Jobstvogt et al., 2014), it is now well established that the deep Arctic seafloor supports a wide diversity of benthic fauna. However, Arctic deep-sea communities are increasingly under threat due to growing pressures from human activities.

The Arctic has warmed at almost double the global average rate over the past century (Trenberth et al., 2007), and the latest IPCC report predicts with very high confidence that it will continue to warm faster than the rest of the world (Collins et al., 2013). Recent research suggests that increases in atmospheric and surface ocean temperatures may have unexpectedly large impacts on deep-sea ecosystems due to the disruption of benthic-pelagic coupling mechanisms (K. L. Smith et al., 2009). Furthermore, a series of extreme sea ice minima over the past decade and an all-time summer minimum in 2012 indicate that Arctic sea ice loss is accelerating, with rates of decline approaching 13% per decade (NSIDC, 2016; Stroeve et al., 2012). As sea ice retreats, human activities such as fishing, shipping, tourism, and hydrocarbon extraction are expanding northward into previously ice-covered areas (Jørgensen et al., 2016). The northward expansion of fishing is further motivated by the climate change induced migration of commercial species (e.g., Drinkwater, 2005; Jørgensen et al., 2016). Human activities are also expanding into deeper waters due to the depletion of land-based and shallow-water resources and the development of new technologies, e.g., offshore hydrocarbon technology (Benn et al., 2010).

Examples of such expansion in the GIN Seas are abundant. The first major deep (> 400 m) longline and bottom trawl fisheries in the GIN Seas were established in the late 1960s and 1970s due to the declining catches of traditional near-shore fisheries (Gordon, 2003). Bottom trawling is known to be a particularly destructive fishing method with impacts including alterations to seafloor morphology, sediment resuspension, and benthos mortality (Pusceddu et al., 2014). Benn et al. (2010) found that bottom trawling had the greatest footprint of various human activities on the deep Northeast Atlantic seafloor in 2005. It is not known whether this applies specifically to the GIN Seas because none of the countries surrounding the GIN Seas supplied fishing data for the study. However, activities certainly affecting the deep GIN Seas according to Benn et al. (2010) include the dumping of chemical weapons at two sites prior to the introduction of the London Protocol regulating marine dumping in 1996 and Norwegian offshore hydrocarbon operations. The primary concerns associated with

hydrocarbon operations are accidental oil spillage and the discharge of drilling waste, both of which can reduce species diversity and abundances (Blackburn et al., 2014; Ellis, Fraser, & Russell, 2012). Hydrocarbon operations are currently confined to relatively shallow areas of the Norwegian shelf; however, hydrocarbon exploration may begin in 2022 at depths of ~750-1500 m in the northern Dreki area, located at the northeast border of the Icelandic Exclusive Economic Zone (Orkustofnun, 2016). Considering that the likelihood of accidents increases by 8.5% with each 30 m of added depth (Muehlenbachs, Cohen, & Gerarden, 2013), hydrocarbon operations in the northern Dreki area pose a significant new risk to GIN Seas ecosystems. Another emerging concern is marine litter. From 2002 to 2011, litter at one station at 2500 m depth at the HAUSGARTEN observatory to the west of Svalbard unexpectedly increased from 3635 to 7710 items km^{-2} (Bergmann & Klages, 2012). Increased shipping activity due to retreating sea ice was cited as a likely cause. Given these pressures, it is not surprising that Halpern and colleagues rated the cumulative human impact in most areas of the deep GIN Seas as medium to medium high (Halpern et al., 2008).

Deep-sea ecosystems may be especially vulnerable to the loss of biodiversity commonly associated with human impacts due to the slow metabolism and growth rates of deep-sea fauna (Montagna et al., 2013). It is thought that loss of biodiversity in deep-sea ecosystems could be accompanied by an exponential decline in ecosystem function (Danovaro et al., 2008). At stake are unique benthic communities that provide many crucial ecosystem services (Armstrong et al., 2012). This review focuses on epibenthic megafauna communities. Epibenthic megafauna (henceforth referred to as megafauna) are commonly defined as organisms living on the seafloor that are big enough to be seen in photographs and/or are larger than 1-2 cm in size (Taylor et al., 2016). Although relatively low in abundance compared to meiofauna and macrofauna, megafaunal organisms often make up a considerable proportion of benthic biomass, and they play an important role in marine ecosystem function (Piepenburg & Schmid, 1996; Soltwedel et al., 2009). Many megafauna are ecosystem engineers that enhance habitat heterogeneity (Taylor et al., 2016). For instance, vagile megafauna (e.g., gastropods, isopods) create burrows, mounds, and Lebensspuren (traces), and sessile megafauna (e.g., sponges, corals) form complex three-dimensional structures (L. Buhl-Mortensen et al., 2010; Soltwedel et al., 2009). Megafauna are also involved in important carbon cycle processes such as oxygenation, bioturbation, and remineralisation (Taylor et al., 2016).

Despite their importance, knowledge on the composition and distribution of deep-sea megafauna communities is scarce due to the practical difficulties and high costs associated with deep-sea surveys. This is especially the case for high latitude regions, where remoteness, seasonal sea-ice cover, and hostile weather conditions present additional barriers to research (Jørgensen et al., 2016). Given the dearth of knowledge about Arctic deep-sea megafauna communities in general, this study aims to assess the information available for deep-sea megafauna communities in the GIN Seas and identify research priorities. Specifically, the study will establish how much research has been carried out and evaluate geographic and bathymetric coverage, as well as provide a brief overview of the methods used and their challenges. Furthermore, a description of what is known about deep-sea megafauna communities focusing on key species, interregional similarities and differences, and drivers of community composition will be presented. Finally, future research priorities will be identified.

1.2 Methods

1.2.1 Study site

The GIN Seas are defined here as the region north of the Greenland-Scotland Ridge, south of the Central Arctic Ocean, and west of the Barents Sea (Figure 1.1). They cover an area of approximately 2.5 million km^2 and are a dynamic, diverse, and topographically complex region (Drange et al., 2005). Submarine ridges divide the GIN Seas into the Greenland, Norwegian, Lofoten, and Boreas Basins, which are ~3200-3600 m deep (Korablev, Smirnov, & Baranova, 2014). A maximum depth of ~5400 m occurs in a rift valley in the 440 km wide Fram Strait (OSPAR Commission, 2000). The Fram Strait has a sill depth of 2600 m and constitutes the primary connection between the GIN Seas and the Central Arctic Ocean (Blindheim & Østerhus, 2005; OSPAR Commission, 2000). The relatively shallow Greenland-Scotland Ridge, with a maximum sill depth of 850 m, prevents deep Atlantic waters from flowing into the GIN Seas (Guijarro Garcia et al., 2007). Hence, all deep waters in the GIN Seas were formed either in the Central Arctic Ocean or in the GIN Seas themselves (Guijarro Garcia et al., 2007; OSPAR Commission, 2000). Deep water formation in the GIN Seas plays an important role in global ocean circulation and contributes to the complex systems of horizontal and vertical currents present in the deep GIN Seas (Gamiz-Fortis & Sutton, 2007; Guijarro Garcia et al., 2006; see OSPAR Commission (2000) for a figure showing deep water circulation). In the winter, the northern and western areas of the GIN Seas are covered to a varying degree by sea ice, while the region is almost entirely ice-free in the summer (Blindheim & Østerhus, 2005; Drange et al., 2005). Fine-grained sediments such as silt and clay predominate in the basins of the GIN Seas, whereas continental margins are generally characterised by coarser sediments such as sand (Guijarro Garcia et al., 2007; OSPAR Commission, 2000).

1.2.2 Literature search

Using Web of Science, Google Scholar, and Google, a search was conducted for peer-reviewed and grey literature on deep-sea epibenthic megafauna communities in the GIN Seas. Search terms consisted of combinations of the words "megafauna", "benthic fauna", "communities", and "deep-sea" in conjunction with the names of countries/regions bordering or within the GIN Seas, i.e., Iceland, Greenland, Svalbard, Norway, Faroe Islands, and Jan Mayen. Due to the focus on deep-sea megafauna communities, the literature identified is by no means an exhaustive account of all benthic fauna research carried out in this region. Studies on meiofauna and macrofauna were excluded. Furthermore, a large number of studies on single taxa, e.g., isopods (Brix & Svavarsson, 2010), were excluded, leaving only those that investigate megafauna communities in their entirety. Studies without any stations deeper than 500 m were also discarded. Although a water depth of 500 m is to some extent an arbitrary cut-off point, it corresponds remarkably well to the shelf break in most regions of the GIN Seas, and it has been considered appropriate in other deep-sea reviews (e.g., Bluhm et al., 2011).

A total of 12 studies were identified that fit the above criteria (Table 1.1). Also, five additional studies were identified that investigate benthic megafauna communities at cold seeps, hot vents, and mud volcanoes in the GIN Seas (Gebruk et al., 2003; Pedersen et al., 2010; Rybakova Goroslavskaya et al., 2013; Schander et al., 2010; Vanreusel et al., 2009).

These five studies were considered beyond the scope of this review and are not included in Table 1.1, however, the approximate locations of their respective study sites are indicated by yellow stars on Figure 1.2. The open-source geographic information system QGIS (QGIS Development Team, 2016) was used to create Figures 1.1 and 1.2.
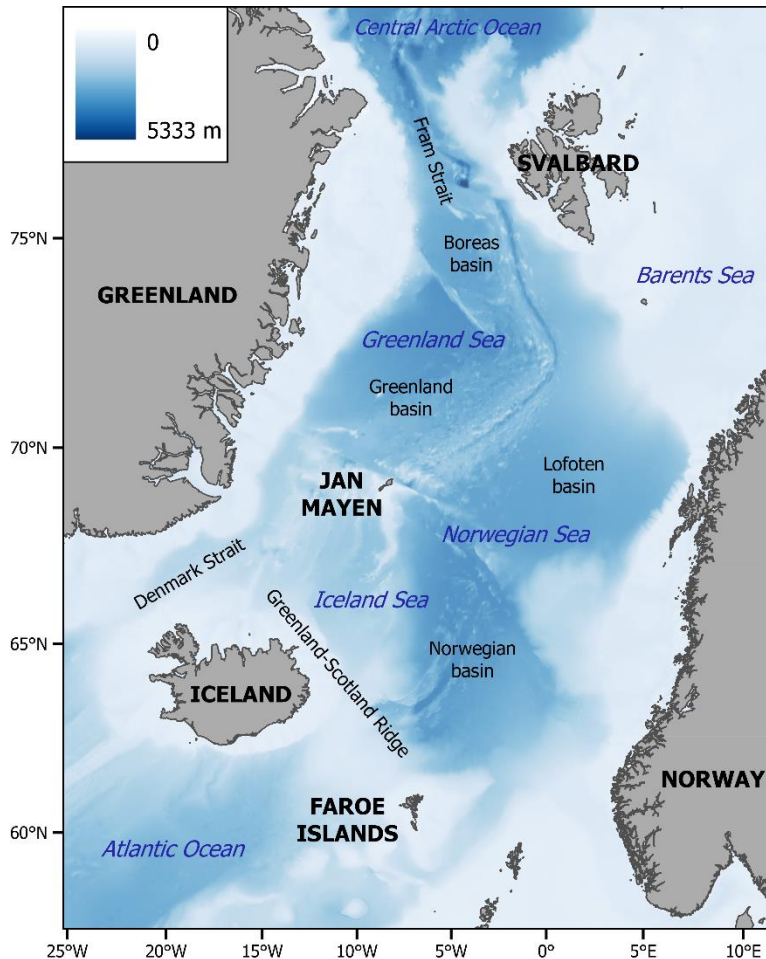
Figure 1.1 Map of the Greenland-Iceland-Norwegian (GIN) Seas. Features referred to in the text are labelled. Bathymetry was extracted from the GEBCO (General Bathymetric Chart of the Oceans) 30 arc-second global grid dataset (The GEBCO_2014 Grid, version 20150318, www.gebco.net).

1.2.3 Communities

'Community' is used to represent terms such as assemblage, biotope, habitat, nature type, and faunistic zone that are mentioned in the studies reviewed. An overview of the information on the deep-sea communities identified or described in each study is displayed in Table 1.2. Deep-sea communities were defined as those mainly or entirely occurring at depths > 500 m. The results of the Deep Basin and Rocky Reef studies (Dahl et al., 1976; Meyer, Soltwedel, & Bergmann, 2014) could not be effectively shown in Table 1.2 and are therefore briefly described in Section 1.3.4.

4

This review compares communities with regards to dominant, discriminator, typical, and characteristic taxa (hereafter jointly referred to as defining taxa) usually identified by the authors or in a few cases inferred from lists of species abundances presented in the studies. Dominance is usually assessed in terms of taxa abundance per unit area, while discriminator taxa are those that contribute most to differences between communities and are usually identified using statistical analyses. Taxa can evidently be both dominant and discriminator. Furthermore, taxa are sometimes described as typical or characteristic without further clarification (e.g., Elvenes et al., 2014). Given that all of these terms can have very different meanings, efforts were made in Table 1.2 to label taxa accordingly.

1.3 Results

1.3.1 Amount of research

An extensive literature search identified 12 megafauna community studies carried out in the deep GIN Seas (Table 1.1). The countries or regions in which most research has been conducted are Norway (Elvenes et al., 2014; Holte et al., 2015), Svalbard (Meyer, Soltwedel, & Bergmann, 2014; Soltwedel et al., 2009; Taylor et al., 2016), and Greenland (Henrich et al., 1992; Mayer & Piepenburg, 1996; Piepenburg & Schmid, 1996), with three studies apiece. Little research exists on the deep-sea megafauna communities around Iceland and Jan Mayen, which are represented by studies from Meißner et al. (2014) and P. Buhl-Mortensen (2012), respectively. Dahl and colleagues' 1976 Deep Basins study is the only one to investigate megafauna communities in multiple regions within the GIN Seas. Most of the research was carried out within the last two decades, with the notable exceptions of the Deep Basins study (Dahl et al., 1976) and of the studies from Greenland, where the most recent sampling occurred in 1994.

1.3.2 Geographic and bathymetric coverage

Aside from certain research hotspots (e.g., offshore Norway), research on benthic megafauna communities in the GIN Seas is rather scarce (Figure 1.2). There are a total of 328 sampling stations in the deep GIN Seas, 262 of which are located in offshore Norway. The geographic coverage of stations is particularly low in Icelandic (4 stations) and Faroese (0 stations) waters and in the central areas of the GIN Seas. There are only four stations in the high seas (waters outside territorial jurisdiction), and all are from the Deep Basins study, which was conducted 40 years ago (Dahl et al., 1976). The only seamount in the GIN Seas that has been investigated with regards to benthic megafauna is Vesterisbanken Seamount, which was sampled in 1990 (Henrich et al., 1992). However, one recent study predicts that there could be as many as 65 seamounts in the GIN Seas (Morato et al., 2013).

Overall, the sampling stations cover most of the depth range of the deep GIN Seas including the maximum depth of ~5400 m, however, some depths are much better represented than others. Stations at depths of 500 - <1000 m, 1000 - <2000 m, 2000 - <3000 m and 3000+ m number 183, 99, 32, and 14, respectively. This shows that sampling effort is much higher in shallower waters.

Table 1.1 Overview of deep-sea megafauna community studies in the GIN Seas. Studies are grouped by country/region. The main sampling gear for data collection is highlighted using bold typeface if applicable. Type of analysis refers to the analysis used for community identification. Environmental variables are written in black typeface if statistical methods were used to test their importance, and in grey typeface otherwise. Biogenic habitat variables were excluded. Variables identified as being the most important drivers of community composition are underlined and bold typeface is used to indicate the single most important driver if applicable. Abbreviations: AFDW (ash-free dry weight), CPE (chloroplastic pigment equivalents: chlorophyll a plus phaeopigments), PL (phospholipids), PP (particulate proteins), FDA (bacterial enzymatic turnover rates).

Country/ region	Reference(s)	Sampling month(s)	Sampling year(s)	Study area	Depth range (m)	No. stations (>500 m)	Camera	Trawl	Sled	Grab	Corer	Other	Type of analysis	Environmental variables
Greenland	Henrich et al., 1992	Jun, Jul	1990	Vesterisbanken Seamount	133-3175	Unknown	X			X	X		Descriptive	Depth
	Mayer & Piepenburg, 1996	Jul	1994	East Greenland 75° N	190-2800	8 (6)	X	X					Multivariate	Depth (correlated with temperature), sediment type (no. and size of stones), sponge spicules, **temperature**, salinity, Phaeopigment, Chlorophyll *a*
	Piepenburg & Schmid, 1996	Jun, Jul, Aug	1985, 1990, 1993	Northeast Greenland	40-770	54 (4)	X	X					Multivariate	Depth
Iceland	Meißner et al., 2014	Aug, Sep	2011	Around Iceland	119-2750	5 (4)	X		X	X	X		Descriptive	Depth, sediment type, sediment grain size, sediment water contents, sediment sorting, total organic content
Jan Mayen	Buhl-Mortensen, 2012	Oct	2011	Jan Mayen Ridge	388-1574	23 (22)	X			X			Multivariate	Depth, slope, **latitude**, longitude
Norway	Holte et al., 2015 (See also Elvenes et al., 2012; Elvenes et al., 2014)	2006-2011	Lofoten, Vesterålen & Troms	70-2700	449 (164)	X	X	X	X			Multivariate, predictive	Depth, backscatter, terrain variables, latitude, sediment grain size, sedimentary environment, landscape
	Holte et al, 2015	2006-2011	Tromsøflaket/ Eggakanten	150-1000	312 (88)	X	X	X	X	X		Multivariate, predictive	Depth, backscatter, terrain variables, sediment grain size, landscape, temperature, salinity, current speed

Table 1.1 cont.

	Reference	Month	Year	Location	Depth (m)	Stations (n)								Analysis	Environmental variables
	Holte et al., 2015		2006-2011	Mid-Norway	38-1500	176 (10)			X	X	X	X		Multivariate, predictive	Unknown, probably similar to Elvenes et al., 2014
Svalbard	Soltwedel et al., 2009	Aug	1997, 2002	HAUSGARTEN: Longitudinal gradient	1200-5500	5 (5)	X	X			X	X		Multivariate	Depth, slope, sediment grain size, sediment water contents, hard substrata, AFDW, CPE, PL, PP, FDA, bacterial numbers, bacterial biomass, meiofauna
	Taylor et al., 2016	Jul	2011	HAUSGARTEN: Latitudinal gradient	2351-2788	3 (3)	X	X			X			Multivariate	Sediment water contents, CPE, PL, PP, sea ice concentration, depth, dropstones, pebbles, anthropogenic litter
	Meyer et al., 2014	Jul	2012	HAUSGARTEN: Rocky reef	1796-2373	1 (1)	X				X			Multivariate	Depth, hard substrata, dropstones
Multiple	Dahl et al., 1976	Jul, Aug	1975	Deep basins of GIN Seas	2465-3718	11 (11)	X	X			X	X		Descriptive	Depth, organic carbon, organic nitrogen

1.3.3 Overview of methods

Sampling

The number of sampling stations and their distribution differ according to the primary objectives of each study (Figure 1.2). Studies from Norway and Northeast Greenland have the highest number of sampling stations (Table 1.1), and they aimed to investigate megafauna communities over broad areas. The Northeast Greenland study site was set up to study the Northeast Water (NEW) polynya, with particular emphasis on benthic-pelagic coupling mechanisms in ice-covered ecosystems (Piepenburg & Schmid, 1996). The MAREANO programme is tasked with conducting seabed mapping in the Norwegian Exclusive Economic Zone (EEZ), and has carried out an extensive sampling campaign, with sampling stations numbering more than 1000 (L. Buhl-Mortensen, Buhl-Mortensen, Dolan, & Holte, 2015; Elvenes et al., 2014; Holte et al., 2015). In contrast, the study sites at East Greenland 75° N, HAUSGARTEN (Lon. gradient), and HAUSGARTEN (Lat. gradient) all consist of small numbers of stations (≤ 8) arranged linearly, and were designed to investigate latitudinal, bathymetric, and climatic effects on benthic community composition (Mayer & Piepenburg, 1996; Soltwedel et al., 2009; Taylor et al., 2016). For example, the HAUSGARTEN (Lat. gradient) study incorporates three stations with varying degrees of annual sea-ice cover in order to investigate the effects of sea ice on fauna composition (Taylor et al., 2016). The Around Iceland and Deep Basins studies also have small numbers of stations, but these stations are very widely spaced (Dahl et al., 1976; Meißner et al., 2014). Sampling stations in the remaining studies are concentrated on three 'special' or anomalous features: Vesterisbanken Seamount, the Jan Mayen Ridge, and a deep-water rocky reef within the HAUSGARTEN observatory (P. Buhl-Mortensen, 2012; Henrich et al., 1992; Meyer, Soltwedel, & Bergmann, 2014).

All studies except Meyer and colleagues' 2014 Rocky Reef study use multiple types of sampling gear (Table 1.1). The majority of studies use video and/or photo cameras as their main sampling gear for data collection. Other gears such as trawls and sleds are usually used to provide physical samples of fauna to aid with taxonomic identification. The Deep Basins study is an exception, since most of the data used in the analysis were obtained using beam trawl, epibenthic sled, and Reineck corer (Dahl et al., 1976).

Data analysis

Studies can be divided into three broad groups according to the type of analysis conducted (Table 1.1). The two oldest studies (Deep Basins and Vesterisbanken Seamount) and the study on the seas around Iceland are all relatively simplistic. Henrich et al. (1992) use photo and video transects from Vesterisbanken Seamount to identify benthic communities on a visual basis and provide very detailed qualitative descriptions of substrates and communities. Meißner et al. (2014) also provide qualitative descriptions, albeit very brief, of typical sediments and fauna observed at single widely-spaced stations in the seas surrounding Iceland. Dahl et al. (1976) focus on comparing faunal densities and the relative dominance of different phyla in different basins and at different depths in the GIN Seas.

The remaining nine studies are all quantitative and use multivariate analysis. In the East Greenland 75° N, Northeast Greenland, Jan Mayen, and Norway studies, communities are identified by grouping stations with similar faunal composition using multivariate techniques such as cluster analysis and ordination (Elvenes et al., 2014; Holte et al., 2015; Mayer & Piepenburg, 1996; Piepenburg & Schmid, 1996). In contrast, the HAUSGARTEN

(Lon. gradient), HAUSGARTEN (Lat. gradient), and Rocky Reef studies analyse very small numbers of single stations and, in the case of the latter two studies, test for differences between the single stations (and/or transect segments within the single stations) that would entail their classification as separate communities (Meyer, Soltwedel, & Bergmann, 2014; Soltwedel et al., 2009; Taylor et al., 2016). These three studies from HAUSGARTEN are notable for their detailed analysis: They provide full taxa lists, report taxa densities at each station, compute diversity indices, and discuss the faunal composition of stations with regards to feeding groups. Such ecological detail is moderate in the East Greenland 75° N and Northeast Greenland studies (Mayer & Piepenburg, 1996; Piepenburg & Schmid, 1996), and almost entirely lacking in the Norway and Jan Mayen studies, where the focus is squarely on community identification and/or mapping (P. Buhl-Mortensen, 2012; Elvenes et al., 2014; Holte et al., 2015).
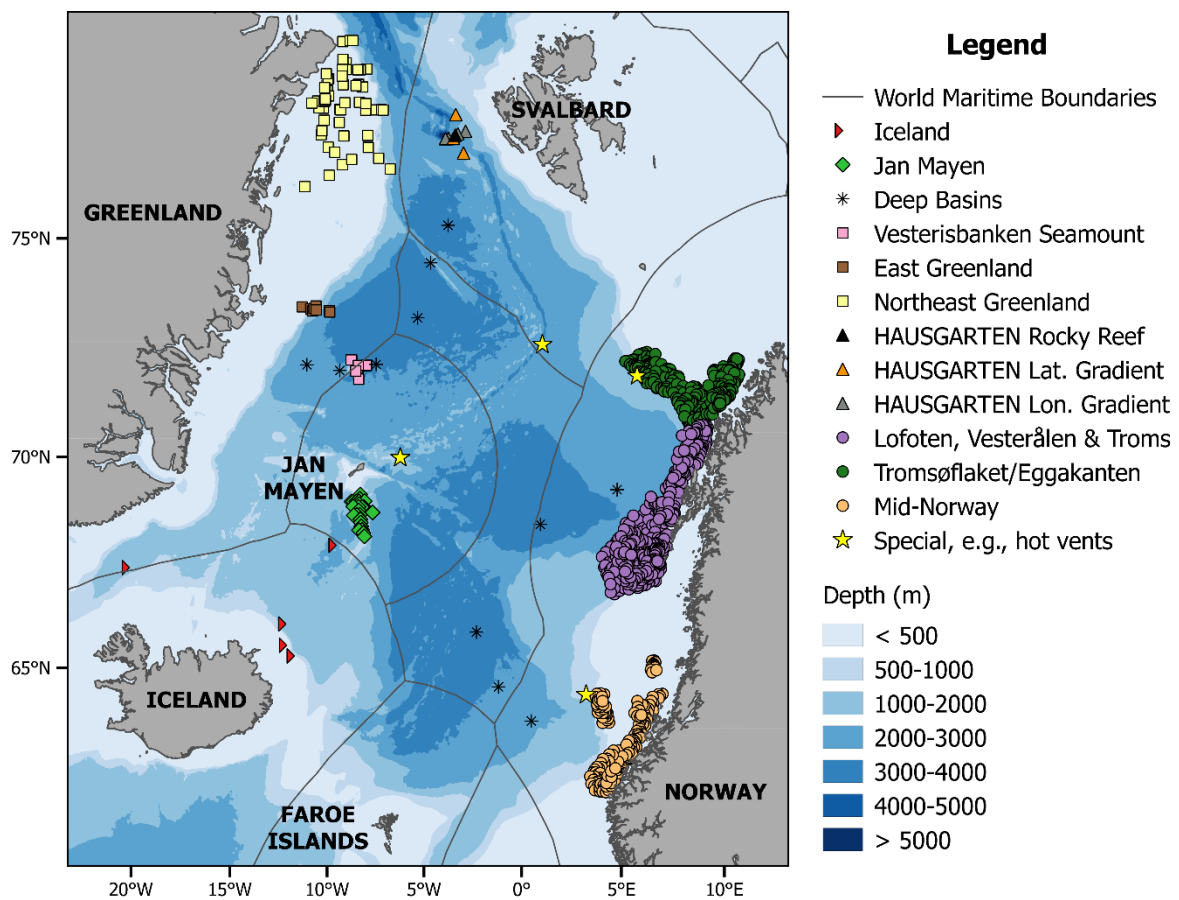
Figure 1.2 Map of the Greenland-Iceland-Norwegian (GIN) Seas with coloured symbols (except yellow stars) showing approximate location of benthic megafauna sampling stations from the studies in Table 1.1. Stations both shallower and deeper than 500 m are shown. Yellow stars indicate the approximate locations of study sites from studies on cold seeps, hot vents, and mud volcanoes (Gebruk et al., 2003; Pedersen et al., 2010; Rybakova Goroslavskaya et al., 2013; Schander et al., 2010; Vanreusel et al., 2009). Bathymetry was extracted from the GEBCO (General Bathymetric Chart of the Oceans) 30 arc-second global grid dataset (The GEBCO_2014 Grid, version 20150318, www.gebco.net).

The three Norway studies differ from all others in that they include a predictive as well as a multivariate element (Elvenes et al., 2014; Holte et al., 2015). These studies used multivariate analysis to identify biological communities, i.e., groups of samples with similar faunal composition, and to identify the most important environmental predictor variables. They then used Maximum Entropy Modelling, a machine-learning technique (Phillips et al., 2006), to assess the relationships between the communities and the predictor variables and predict community distribution for the entire study site. The studies generated full-coverage community distribution maps, with each pixel assigned a colour according to which community is most likely to be present.

Environmental predictor variables

Benthic community composition is potentially influenced by numerous environmental variables comprising characteristics of both the underlying seafloor and the overlying water column (Brown et al., 2011). Most of the studies under review measure and/or obtain information on environmental variables and, following identification or description of benthic communities, discuss or test which of these variables are likely to be important drivers of community composition. A wide range of biotic and abiotic variables (> 30 variables in total) are incorporated in the studies. Depth is measured by all studies, and variables relating to sediment characteristics (e.g., grain size) are also very common. Less common variables include food availability variables (e.g., phaeopigment concentration), which are incorporated in five studies (Dahl et al., 1976; Mayer & Piepenburg, 1996; Meißner, Brenke, & Svavarsson, 2014; Soltwedel et al., 2009; Taylor et al., 2016), and oceanographic variables (e.g., temperature), which are included in only three studies (Elvenes et al., 2014; Holte et al., 2015; Mayer & Piepenburg, 1996; Taylor et al., 2016). Some variables are very study-specific, such as coverage of sponge spicule mats at the East Greenland 75° N study site (Mayer & Piepenburg, 1996). The studies from Norway are the only ones to incorporate variables derived from acoustic survey data, including backscatter and terrain variables (Elvenes et al., 2014; Holte et al., 2015). Key terrain variables include aspect (the direction that the seafloor is facing) and slope.

Six of the studies under review investigate the relationships between environmental variables and community composition using statistical methods (P. Buhl-Mortensen, 2012; Elvenes et al., 2014; Holte et al., 2015; Mayer & Piepenburg, 1996; Soltwedel et al., 2009; Taylor et al., 2016). The most common method is BIOENV (Clarke & Ainsworth, 1993), used in two studies (Mayer & Piepenburg, 1996; Soltwedel et al., 2009), and other methods include forward selection and correlation with ordination axes.

Challenges

One of the main methodological challenges encountered in the studies is species identification. The taxonomic resolution to which fauna are identified is dependent on the expertise of the research team in question. Furthermore, identifying species in photographs and videos is often difficult or impossible. This is exemplified by the Northeast Greenland study (Piepenburg & Schmid, 1996), where 200 megafauna species were identified in trawl catches, but only ten were identified in photographs. Many studies address these problems by using a mixture of species, higher taxa (e.g., genera, families), and morphotypes (e.g., 'small round sponge') in their analysis. This makes sense in practical terms, but there are obvious drawbacks. For example, the use of higher taxa could create artificial similarities between stations (Bluhm et al., 2011). Time and manpower are further limiting factors mentioned in several studies. For instance, photo transects from the HAUSGARTEN (Lon.

gradient) study covered an average distance of 3.5 km, but detailed analysis was restricted to 0.3-0.7 km sections of each transect due to the time-consuming and labour-intensive nature of image analysis (Soltwedel et al., 2009). As camera technology develops and ever larger numbers of ever higher quality photographs are taken, the magnitude of this problem will increase.

One potential solution to these issues is semi-automated image analysis. Schoening et al. (2012) successfully used semi-automated techniques to determine the approximate densities of a small number of relatively easily recognisable megafauna species in seafloor photographs; however, they did not fare so well with less recognisable species. Another solution is to involve the public in identifying better-known species. For example, a recent Zooniverse citizen science project called 'Seafloor Explorer' asked participants to identify species and substrate types in ~250,000 seafloor images (www.seafloorexplorer.org). All identification is now complete, but results have not yet been published. It is also possible that environmental DNA will be used to help identify some of the better-known megafauna species in coming years. Pawlowski et al. (2011) performed environmental DNA analysis on sediment samples from the deep Arctic Ocean and found the DNA of benthic organisms such as Echinodermata and Cnidaria. Although these new techniques are promising, it is unlikely that they will fully replace expert interpretation in the near future.

1.3.4 Communities

Data

Table 1.2 displays the 34 deep sea communities identified or described in the studies. This table documents a diverse array of communities located on the upper, mid, and lower continental slope, as well as on the deep-sea plain and on underwater elevations (Jan Mayen Ridge and Vesterisbanken Seamount). Sediments range from volcanic foundation to mud, and defining taxa incorporate a large number of different organisms, ranging from small, motile fauna such as crustaceans, to large, sessile fauna such as soft corals. The results of the Deep Basin and Rocky Reef studies (Dahl et al., 1976; Meyer, Soltwedel, & Bergmann, 2014) could not be effectively shown in Table 1.2 and are therefore briefly described here.

Dahl et al. (1976) described the faunal composition of the deep basins of the GIN Seas using samples collected from 11 widely-spaced stations at 2465-3718 m depth located in the Greenland (5), Norwegian (3), Lofoten (2), and Spitsbergen (1) Basins. Only higher taxa were discussed with the exception of a few easily identifiable species; however, some interesting general trends were observed. In terms of number of individuals per hectare, the most numerous taxa in the beam trawl samples in descending order were Holothuroidea, Polychaeta, Bivalvia, Actiniaria, Amphipoda, and Pycnogonida. Asteroidea and Crinoidea were comparatively rare, and Ophiuroidea were very rare (only 16 individuals in 16 hauls). Holothuroidea were extremely dominant at 4 stations, constituting 76-96% of the individuals collected, with *Elpidia glacialis* by far the most abundant species. Porifera were not quantified, but were collected in 'fairly large quantities', particularly in the Greenland basin. Overall faunal densities estimated from beam trawl samples ranged from 0.48 to 3.17 ind. m^{-2} (mean: 1.32 ind. m^{-2}). The faunal densities in the Norwegian and Lofoten Basins were generally much lower than at similar depths in the Greenland Basin for the beam trawl, epibenthic sled, and box corer sampling. Moreover, faunal density was generally high in the Greenland Basin, particularly at the two deepest stations (mean depths: 3570 m and 3709 m;

beam trawl faunal densities: 2.4 and 3.1 ind. m^{-2}, respectively), which may be due to higher organic matter input through vertical convection.

Meyer, Soltwedel, & Bergmann (2014) investigated megafauna communities on a steep rocky reef at 1796-2373 m depth on the continental slope to the west of Svalbard. Their data consisted of a 3.8 km photo transect incorporating a longitudinal segment of the reef as well as the abyssal plain immediately below and above the reef. For analysis, the transect was split up into six segments that differed in terms of hard substratum cover and slope. The relatively flat abyssal plain segments were characterised by soft sediments and the presence of occasional dropstones. Average hard-substratum cover within the reef segments ranged from 28% at the deepest segment to 91% at the eastern summit. All six transect segments were dominated by Porifera, which accounted for 55-75% of individuals on abyssal plain segments and for 80-95% of individuals on reef segments. Overall, 17 of the 60 identified taxa were more abundant on the reef than the abyssal plain and attained their highest abundances on the eastern summit, including *Bathyphellia margaritacea* (Actiniaria), *Bythocaris leucopis* (Decapoda), Pennatulacea, *Polymastia* sp. (Heteroscleromorpha), *Tentorium semisuberites* (Demospongiae), and many sponge morphotypes. Several sponge morphotypes were exclusively present on the eastern summit, while *Saduria megalura* (Isopoda), *Neohela lamia* (Amphipoda), *Bathycrinus carpenterii* (Crinoidea) and *Ophiostriatus striatus* (Ophiuroidea) were mostly or exclusively found on the abyssal plain. Taxa numbers and densities were on average highest on the eastern summit of the reef (26.7 ± 0.9 taxa m^{-2}, 418.1 ± 49.6 ind. m^{-2}), and were much lower on the abyssal plain (18.1 ± 1.4 taxa m^{-2}, 29.4 ± 4.3 ind. m^{-2}). The dominance of sessile suspension feeders on the reef in general and in particular on the rocky eastern summit, which faces into the current, is likely a consequence of higher food availability due to faster bottom currents.

Comparability

Comparing communities identified or described in different studies is difficult due to differences in methodology (see Section 1.3.3) and reporting. The amount of information provided by each study varies considerably, as evident in Table 1.2. Figures such as number of stations per community, species richness, and number of individuals per m^2 are not always reported. Methodological factors affecting comparability are numerous and include sampling month and year, sampling effort, sampling gear, sample size, taxonomic resolution, statistical methods, methods used to select the defining taxa of each community (see Section 1.2.3), and methods used to describe or measure sediment characteristics. One of the most notable factors is taxonomic resolution. Due to the use of different gears (e.g., cameras with different resolution), the differing expertise of each research team, and the differing amount of time available, the taxonomic resolution achieved in the studies varies. For example, the defining taxa identified in different studies include *Gersemia rubiformis*, *Gersemia*, Alcyonacea, and even Anthozoa. These four taxa may represent the same species, four different species, or any combination thereof. These differences in taxonomic resolution could result in actual similarities between communities being obscured and false ones being created (Bluhm et al., 2011). Of the 77 defining taxa identified in the studies under review, there are 24 species, 26 genera, 5 families/superfamilies, 7 orders, 7 classes, 3 phyla, and 5 morphotypes. Comparability would be greatly improved if more taxa were identified to species level or if taxa were identified to the same level regardless of the study.

It is arguable that between-study comparability is also notably affected by the month and year in which sampling took place, which varies considerably between studies (Table 1.1).

Table 1.2 Overview of deep-sea megafauna communities identified or described by the studies in Table 1.1. The information presented is copied (denoted by text in quotation marks) or adapted from the studies. Defining taxa are marked as dominant (dom.), discriminator (dis.), typical (typ.) and/or characteristic (char.). Dominance is usually assessed in terms of taxa abundance per unit area, while discriminator taxa are those that contribute most to differences between communities and are usually identified using statistical analyses. Taxa are sometimes described as typical or characteristic without further clarification.

Study area	Deep-sea communities/ samples	Depth (m)	No. stat. taxa	No. taxa	No. ind. (m-2)	Sediments/terrain	Defining taxa	Study quotes
Vesterisbanken Seamount (Henrich et al., 1992)	"Sponge-crinoid mounds"	750-1075				"Dominated by lava rocks, partly covered by a thin layer of sandy mud within small depressions"; steep slopes	**Typ.:** *Schaudinnia* (Hexactinellida), *Clathria* (Poecilosclerida), *Heliometra glacialis* (Crinoidea)	*Schaudinnia* and *Clathria* settle on pillow lava blocks. *H. glacialis* often fixes its roots on *Schaudinnia*. Worm tubes common within small depressions.
	"Bryozoan thickets"	1008-1137				"Volcanic foundation"	**Dom.:** *Idmidronea atlantica* (Bryozoa), *Phidolopora elongata* (Bryozoa)	Bryozoans "associated with thin and transparent blue ascidians". "Small Actiniaria are relatively common."
	"Bathycrinus community"	1532-1600				"Muddy soft bottoms" with "sparse small rock fragments"	**Char.:** Sessile crinoids (*Bathycrinus carpenterii*), Octocorallia, Actiniaria	Small rock fragments have a "low abundance fixosessile benthos".
	Small sponge mounds I	1600-1655				Mud to sandy mud, local "volcanoclastic mass flows with sharp-edged lava blocks", some lava fragments and lapilli	**Char.:** *Hyalonema* (Hexactinellida), *Cladorhiza* (Poecilosclerida), *Thenea* sp. (Tetractinellida), *Schaudinnia* (Hexactinellida), *Scyphidium* (Hexactinellida)	Sponge mounds found on "rough lava block or pillow surface". Most abundant bryozoans are *Palmicellaria skenei* and *Phidolopora elongata*.
	Small sponge mounds II	1655-2063				Mud to sandy mud, "local volcanoclastic mass flows with sharp-edged lava blocks", some lava fragments and lapilli	**Dis.:** *Caulophacus arcticus* (Hexactinellida). **Char.:** *Hyalonema* (Hexactinellida), *Cladorhiza* (Poecilosclerida), *Thenea* sp. (Tetractinellida), *Schaudinnia* (Hexactinellida), *Scyphidium* (Hexactinellida) *Heliometra glacialis* (Crinoidea)	Sponge mounds found on "rough lava block or pillow surface". *C. arcticus* commonly grow on *Thenea*.
	"Abyssal plain facies"	>2000				"Fine-grained sediments"	**Char.:** *Thenea abyssorum* (Tetractinellida), Foraminifera, Calcarea	Calcarea sponges attached to Foraminifera "islands". Mean of 20-30 *T. abyssorum* specimens collected on surface of each 0.5 m2 box core.

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Table 1.2 cont.

Region	Station	Depth (m)	n			Sediment	Fauna	Comments
East Greenland 75° N (Mayer & Piepenburg, 1996)	"Upper slope"	760-800	3	28-30	28.6-41.3	Mosaic of soft bottom (sandy clay) and "dense sponge spicule mats", many small stones	**Dis.:** *Isidella lofotensis* (Alcyonacea), *Lissendendoryx complicata* (Poecilosclerida). **Typ.:** *Idmidronea atlantica* (Bryozoa), Vase-shaped Porifera, *Latrunculia* sp. (Poecilosclerida)	Spicule mats "colonized by a high-diversity octocoral-sponge assemblage'. Sponges dominant in general.
	"Lower slope"	1400-2780	3	12-15	14.4-22.1	Sandy clay and many small stones at shallowest station (1400 m); clay and no stones at two deepest stations (2640, 2780 m)	**Dis.:** *Bathycrinus* sp. (Crinoidea), *Elpidia glacialis* (Holothuroidea), *Polymastia* sp. (Demospongiae)	Shallowest station (1400 m) distinct from other two (2640, 2780 m) and dominated by *Polymastia* sp. (due to presence of stones); echinoderms dominant at deeper stations.
Northeast Greenland (Piepenburg & Schmid, 1996)	"Deep"	380-770	4	2-5 (med: 2)	0.2-2.2 (med: 0.4)	Very fine sediments, no stones	**Dom:** *Ophiacantha bidentata* (Ophiuroidea)	Epibenthic fauna "poor in every respect".
Around Iceland (Meißner et al., 2014)	1-30 ("Iceland Sea, close to the Icelandic shelf")	631	1			"(slightly gravelly) muddy sand". 35% mud, 61% sand, 4% gravel	**Typ.:** Alcyonacea, Euphausiacea, Chaetognatha	"Diverse and abundant macrofauna". "High abundance of soft corals". "Abundant macrofauna swimming above seafloor."
	1-21 ("Denmark Strait, North, deep waters")	1243	1			"(slightly gravelly) sandy mud". 61% mud, 36% sand, 3% gravel. Some stones	**Typ.:** Porifera, *Umbellula encrinus* (Pennatulacea), *Ophiopleura borealis* (Ophiuroidea), Sabellidae (Sedentaria), Pantopoda (Pycnogonida)	"Diverse macrofauna". "Dropstones carried diverse, sessile epibenthic fauna" (e.g. Crinoidea, Anthozoa, Porifera).
	1-27 ("Iceland and Norwegian Seas, deep waters")	1579	1			"(slightly gravelly) sandy mud". 71% mud, 29% sand, <1% gravel. No stones	**Typ.:** Cephalopoda, Euphausiacea, Polychaeta tubes	
	1-22 ("Iceland and Norwegian Seas, deep waters")	2160	1			"(slightly gravelly) sandy mud". 57% mud, 42% sand, 1% gravel. No stones	**Typ.:** *Kolga hyalina* (Holothuroidea), Sabellidae (Sedentaria), Actiniaria, Euphausiacea	"Many holothurians". Dense Holothuroidea aggregations may be linked to high total organic content of deep Iceland/Norwegian seas.
Jan Mayen Ridge (Buhl-Mortensen, 2012)	A	400-700 (670)	8	28 (mean)		Mixed clay-mud; 4 stations with scattered stones	**"Dom.:** Antedonoidea (Crinoidea), Ophiuroidea, *Gorgonocephalus* sp. (Ophiuroidea), Actinaria Indet., *Gersemia rubiformis* (Alcyonacea), Cerianthidae (Ceriantharia). **Typ.:** *Pontaster tenuispinus* (Asteroidea)"	Scattered stones often colonized by sessile fauna. Crinoids rarely observed in such dense and dominant colonies.

Table 1.2 cont.

Region	Zone	Depth (m)	n	Mean	Habitat	Dominant / Typical taxa	Remarks
	B	700-800 (749)	5	33 (mean)	Mixed clay-mud; 2 stations with scattered stones, 1 with scattered stones and consolidated sediments	**Dom.:** Antedonoidea (Crinoidea), Ophiuroidea, *Gorgonacephalus* sp. (Ophiuroidea), *Stylocordyla borealis* (Demospongiae), Cerianthidae (Ceriantharia). **Typ.:** *Bathybiaster* sp. (Asteroidea), *Virgularia* sp. (Pennatulacea)"	Scattered stones often colonized by sessile fauna. Consolidated sediments colonized by a large variety of sessile fauna. Crinoids rarely observed in such dense and dominant colonies.
	D	800-1000 (915)	8	27 (mean)	Mixed clay-mud; 2 stations with scattered stones	"**Dom.:** Ophiuroidea, agglutinated Foraminifera, *Jasmineira* sp. (Sedentaria). **Typ.:** *Bythocaris* sp. (Decapoda), Pycnogonida Indet."	Scattered stones often colonized by sessile fauna.
	C	1300-1600 (1447)	2	18 (mean)	Mixed clay-mud; 1 station with scattered stones	"**Dom.:** Ophiuroidea, Cerianthidae (Ceriantharia), agglutinated Foraminifera. **Typ.:** *Neohela* sp."	Scattered stones often colonized by sessile fauna.
Lofoten, Vesterålen & Troms (Holte et al., 2015)	A	500-800			"Coarse bottom" "Upper steep continental slope"	**Typ.:** "*Drifa glomerata* (Alcyonacea), *Gorgonocephalus eucnemis* (Ophiuroidea)"	See also Elvenes et al., 2012; Elvenes et al., 2014.
	B	700-1000			"Mixed sediments" "Mid continental slope with canyons"	**Typ.:** "*Chondrocladia* (Poecilosclerida), *Lucernaria* (Stauromedusae), Pycnogonida, *Umbellula* (Pennatulacea), *Ophiopleura* (Ophiuroidea)"	
	C	1000-1500			"Mud and mixed sediments" "Mid continental slope/ Faunal transition zone"	**Typ.:** "Nemertea pink, Actiniaria small pink, Hexactinellida bush, *Bythocaris* (Decapoda)"	
	D	1200-2000			"Mixed sediments" "Lower continental slope"	**Typ.:** "*Conocrinus/Bathycrinus* (Crinoidea), *Hymenaster* (Asteroidea), *Caulophacus* (Hexactinellida)"	
	E	2000-2700			"Mud" "Deep-sea plain"	**Typ.:** "*Elpidia glacialis* (Holothuroidea), *Kolga hyalina* (Holothuroidea), *Bathycrinus carpenterii* (Crinoidea), *Bythocaris* (Decapoda), *Pourtalesia* (Echinoidea)"	

Table 1.2 cont.

Site (reference)	Station	Depth (m)				Sediment / slope parameters	Substrate & habitat description	Dominant / typical fauna	Notes
Tromsøflaket/ Eggakanten (Holte et al., 2015)	VI	400–1000					"Mixed gravelly muddy sand" "Steep parts of upper slope and canyon"	**Typ.:** "Broccoli corals, Pennatulacea, Zoanthidae (Zoantharia), *Drifa glomerata* (Alcyonacea), *Gorgonocephalus eucnemis* (Ophiuroidea), *Gersemia* sp. (Alcyonacea)"	
	VII	500–700					"Gravelly sandy sediments" "Lower slope with canyons"	**Typ.:** "Broccoli corals, *Chondrocladia gigantea* (Poecilosclerida), *Gorgonocephalus eucnemis* (Ophiuroidea)"	
	VIII	700–1000					"Mixed sandy muddy sediments" "Smooth lower slope"	**Typ.:** "Small crustaceans, Sabellidae (Sedentaria), *Cleippides* (Amphipoda)"	
Mid-Norway (Holte et al., 2015)	B5	650–1500					"Mixed soft and gravelly" "Continental slope"	**Char.:** "*Gersemia rubiformis* (Alcyonacea), *Gorgonocephalus* sp. (Ophiuroidea), *Bythocaris* sp. (Decapoda), *Cerianthus vogti* (Ceriantharia), *Drifa glomerata* (Alcyonacea)"	
HAUSGARTEN Ion. gradient (Soltwedel et al., 2009)	Transect A	1313–1316 (1315)	1	12	31 ± 6 (mean)	Median grain size (Φ): 6.8 / Hard substrata (%): <1 / Slope inclination (deg): 0.2		**Dom.:** *Ophiocten gracilis* (Ophiuroidea), Amphipoda	Mean densities (ind.m-2): *O. gracilis* 16.8 ± 3.7, Amphipoda 14.1 ± 4.6. *O. gracilis* (54%) and Amphipoda (45%) account for 99% of organisms. Average sediments Transects A–D: "26% sand, 49% silt, 25% clay".
	Transect B	1642–1688 (1665)	1	27	38 ± 10 (mean)	Median grain size (Φ): 6.7 / Hard substrata (%): <1 / Slope inclination (deg): 4.4		**Dom.:** Amphipoda	Mean Amphipoda density: 37.0 ± 17.3 ind.m-2. Amphipoda account for 96% of organisms.
	Transect C	2609–2629 (2619)	1	22	12 ± 1 (mean)	Median grain size (Φ): 6.3 / Hard substrata (%): 13 / Slope inclination (deg): 1.9		**Dom.:** *Kolga hyalina* (Holothuroidea), Anthozoa	Mean densities (ind.m-2): Holothuroidea 4.1 ± 2.7, *K. hyalina* 3.8 ± 2.8, *Elpidia heckeri* 0.3 ± 0.4. Holothuroidea account for 34% of organisms, Anthozoa for 25%. Conspicuous dropstones.
	Transect D	2965–3043 (3004)	1	19	11 ± 2 (mean)	Median grain size (Φ): 6.4 / Hard substrata (%): <1 / Slope inclination (deg): 14.6		**Dom.:** *Bathycrinus carpenterii* (Crinoidea), Anthozoa	Mean *B. carpenterii* density: 5.2 ± 2.8 ind.m-2. *B. carpenterii* account for 47% of organisms, Anthozoa for 19%,

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Table 1.2 cont.

Transect E	5333-5404 (5369)	1	4	35 ± 12 (mean)	Median grain size (Φ): 8.0 Hard substrata (%): <1 Slope inclination (deg): 1.6	Dom.: *Elpidia heckeri* (Holothuroidea)	Mean *E. heckeri* density: 29.8 ± 7.4 ind.m-2. *E. heckeri* account for 85% of organisms. Sediments at Transect E: "1% sand, 48% silt, 51% clay."
HAUSGARTEN lat. gradient (Taylor et al., 2016) S3	2351-2366	1	24	18.3 ± 0.4 (mean)	(Drop)stone: 0.1/m-2 Shell: 0.1/m-2 Pebble: 1.0/m-2	**Dis.:** *Gersemia fruticosa* (Alcyonacea), *Elpidia heckeri* (Holothuroidea). **Dom.:** Small round Porifera, Isopoda, cf. *Bathyphellia margaritacea* (Actiniaria)	Mean densities (ind.m-2): *G. fruticosa* 0.8 ± 0.1, *E. heckeri* 0.8 ± 0.1, small round Porifera 6.4 ± 0.2, Isopoda 4.7 ± 0.2, *B. margaritacea* 2.0 ± 0.1.
HG-IV	2407-2639	1	27	11.2 ± 0.3 (mean)	(Drop)stone: 0.1/m-2 Shell: 0.2/m-2 Pebble: 3.8/m-2	**Dis./dom.:** *Bathycrinus carpenterii* (Crinoidea). **Dom.:** Small round Porifera, cf. *Bathyphellia margaritacea* (Actiniaria)	Mean densities (ind.m-2): *B. carpenterii* Porifera, 1.8 ± 0.1, small round Porifera 3.1 ± 0.2, cf. *B. margaritacea* 2.5 ± 0.1. Species composition of start and end of transect is significantly different.
N3	2663-2788	1	23	26.7 ± 0.6 (mean)	(Drop)stone: 0.1/m-2 Shell: 0.9/m-2 Pebble: 17.1/m-2	**Dis./dom.:** *Kolga hyalina* (Holothuroidea), *Bathycrinus carpenterii* (Crinoidea), *Mohnia* spp. (Gastropoda). **Dom.:** Small round Porifera	Mean densities (ind.m-2): *K. hyalina* 4.5 ± 0.1, *B. carpenterii* 4.1 ± 0.1, *Mohnia* spp. 3.9 ± 0.2, small round Porifera 6.8 ± 0.3.

Mayer and Piepenburg (1996) acknowledge that their data, which was collected over a two-week period in July, might not be representative of the entire summer due to fluctuations over the summer period. There is little mention of seasonality or interannual variation in the other studies. Time-series studies of deep-sea megafauna communities are rare, and the only location in the GIN Seas where such studies have been conducted is the HAUSGARTEN observatory to the west of Svalbard. Meyer, Bergmann, & Soltwedel (2013) demonstrated that average megafauna density at a HAUSGARTEN station at ~1300 m depth was significantly higher in 2012 (54.9 ind.m^{-2}), than in 2002 (19.7 ind.m^{-2}) or 2007 (17.2 ind.m^{-2}). Bergmann, Soltwedel, & Klages (2011) also observed changes in faunal density at a HAUSGARTEN station at ~2500 m depth. These changes were not consistent across species, with different species reaching maximum density in different years. For example, the proportion of suspension feeders ranged from 72% in 2004 to 92% in 2007 (Soltwedel et al., 2015). These results indicate that community composition and overall megafauna abundance may be less stable than commonly assumed, and that currently most benthic community studies are providing a snapshot of community composition at a particular location in a particular year and season. It is essential that long-term monitoring studies are conducted in more locations in the deep GIN Seas in order to investigate whether the variability observed at HAUSGARTEN occurs elsewhere as well as to detect potential broad-scale interregional changes arising from pressures such as climate change. Well-established shallow-water programs such as the Pacific Reef Assessment and Monitoring Program (www.pifsc.noaa.gov/cred/pacific_ramp.php), which monitors benthic organisms and oceanographic conditions at over 50 Pacific locations, could provide useful inspiration.

Defining taxa

Many of the studies identify defining taxa for each of the communities identified or described. These vary in number; for example, some of the communities in Table 1.2 are dominated to a large extent by one taxa, and thus only one defining taxa is identified. This is exemplified by the HAUSGARTEN (Lon. gradient) transects, where Amphipoda accounted for 96% of individuals at Transect B, and *Elpidia heckeri* for 85% at Transect E. Overall, 77 different taxa were identified as defining taxa. These include species, phyla, and all taxonomic levels in between, as well as several morphotypes, e.g., 'vase-shaped Porifera'. Due to variations in taxonomic resolution between studies, there is probably considerable overlap between taxa, e.g., *Bathycrinus* and *Bathycrinus carpenterii* are likely to represent the same species. The 77 defining taxa mainly belong to the phyla Porifera (26%), Echinodermata (25%), and Cnidaria (25%). This is likely in part because members of these phyla are often relatively large and easy to discern in seafloor photographs. Most of the rest of the taxa belong to Arthropoda (12%) and Annelida (4%). The most common genera identified as defining taxa were all echinoderms: *Bathycrinus* (5 studies), *Elpidia* (4), *Gersemia* (4), *Gorgonocephalus* (4), and *Kolga* (4). This is in line with the observation that echinoderms tend to dominate the megafauna in soft sediment environments such as those found in much of the deep sea (Bluhm et al., 2011). Most of these echinoderms are known to be abundant pan-Arctic endemics (Mironov, Dilman, & Krylova, 2013).

Recurrence

It is very difficult to determine whether the same or similar communities recur in different studies and different areas of the GIN Seas due to comparability issues, including unreported figures and variability in taxonomic resolution and selection criteria of the defining taxa. Where species richness and number of individuals are reported, they tend to be on the same

order of magnitude across studies and in different areas (Table 1.2). Furthermore, many fauna are a defining taxa for communities in multiple regions. For example, *Bathycrinus* is a defining taxa for communities at Vesterisbanken Seamount; East Greenland 75° N; Lofoten, Vesterålen & Troms; HAUSGARTEN (Lon. Gradient); and HAUSGARTEN (Lat. Gradient). Moreover, the communities for which *Bathycrinus* is a defining taxa tend to be deep (> 1500 m) and to occupy soft sediments such as mud and clay. However, when all of the defining taxa for each community containing *Bathycrinus* are examined, it is clear that these communities share very little in common.

Despite the aforementioned comparability issues, pairs of communities were compared according to the defining taxa listed in Table 1.2. The distinctions between dominant, discriminator, typical, and characteristic species (see Section 1.2.3) were ignored for the purpose of simplification, and taxonomic levels were relaxed (e.g., *Bathycrinus* and *Bathycrinus carpenterii* were viewed as equivalent). Between-study pairwise comparisons of communities revealed that no two communities of the 34 deep sea communities described by the studies identify the same defining taxa. 13 pairs of communities have two defining taxa in common, and four pairs of communities have three defining taxa in common. For example, Iceland's I-21 transect in the Denmark Strait (1240 m) and Norway's Biotope B at Lofoten, Vesterålen & Troms (700-1000 m) both identify *Ophiopleura* (Ophiuroidea), *Umbellula* (Pennatulacea), and Pycnogonida as defining taxa (Elvenes et al., 2014; Holte et al., 2015; Meißner, Brenke, & Svavarsson, 2014). From this analysis, it is clear that the 34 communities in Table 1.2 are generally rather diverse (at least in terms of defining taxa), but whether this is due to artificial differences arising from comparability issues or to actual diversity is unknown. It would hardly be surprising if a large number of significantly different megafauna communities existed in the GIN Seas considering that environmental conditions in Arctic regions are very heterogeneous, with factors such as sea-ice cover, seafloor composition, and biogeographical history differing greatly among regions (Piepenburg, 2006). Interestingly, however, almost a third of the 17 pairs of communities having two or three taxa in common are pairs made up of a community from the Jan Mayen study and a community from one of the Norway studies, despite the fact that these study sites are geographically far apart. The Jan Mayen and Norway studies were carried out by the same research institute, and the methods used were very similar. This indicates that standardisation of investigators and methodology could have a large impact on the similarity of the communities identified in different areas.

Environmental predictor variables

The environmental variables identified as the most important drivers of community composition vary among studies (Table 1.1). One variable that is regarded as particularly important in the studies is depth. The distribution of most deep-sea fauna is limited to certain predictable depth ranges (Howell, 2010), and this is evident in Table 1.2. For instance, ophiuroids are very often one of the defining taxa in communities shallower than 1600 m, but never dominate deeper communities, while the opposite is true for holothuroids, which are very often a defining taxa in deeper communities (> 1400 m). The depth ranges of communities identified through the grouping of samples with similar fauna composition using multivariate analysis also tend to indicate that depth is an important factor: Within studies, the depth ranges of the communities at East Greenland 75° N (Mayer & Piepenburg, 1996); Jan Mayen Ridge (P. Buhl-Mortensen, 2012); and Lofoten, Vesterålen & Troms (Elvenes et al., 2014; Holte et al., 2015) hardly overlap or do not overlap at all, suggesting that the communities are restricted to certain depths. The Tromsøflaket/Eggakanten study

(Holte et al., 2015) provides the sole counterexample; the overlapping depth ranges of the communities identified at this study site indicate that other variables are exerting a greater influence than depth. The communities described in the qualitative Vesterisbanken Seamount study (Henrich et al., 1992) and the HAUSGARTEN (Lon. gradient) study (Soltwedel et al., 2009), which investigates single samples along a bathymetric gradient, also point to a pronounced depth zonation. Significant changes in community composition and decreases in abundance and biomass with increasing depth are trends very commonly observed on the continental margins of the Arctic and world oceans (Bluhm et al., 2011; Piepenburg, 2006). However, the cause of depth zonation is much debated. Depth itself does not affect community composition; it is a proxy for other variables that affect biological processes, and, by extension, species distribution (ICES, 2014). Depth zonation has been attributed to many different variables including temperature, currents, sediment characteristics, and food availability (Soltwedel et al., 2009).

Two of the six studies that test statistically for the importance of environmental variables identify variables associated with sediment characteristics (no./size of stones and backscatter) as being particularly important drivers of community composition (Elvenes et al., 2014; Mayer & Piepenburg, 1996). The importance of dropstones and pebbles, which increase habitat heterogeneity and provide important habitat for certain sessile invertebrates, is also mentioned by six out of twelve studies (P. Buhl-Mortensen, 2012; Mayer & Piepenburg, 1996; Meißner, Brenke, & Svavarsson, 2014; Meyer, Soltwedel, & Bergmann, 2014; Soltwedel et al., 2009; Taylor et al., 2016). Furthermore, within studies, there is usually at least some difference in sediment characteristics between the communities identified. Specific communities tend to be associated with certain substrates (Howell, 2010), and this is most apparent in the differences between the communities occurring at hard bottom and soft bottom study sites. It is clear that the communities found at the Rocky Reef (Meyer, Soltwedel, & Bergmann, 2014), on parts of Vesterisbanken Seamount (Henrich et al., 1992), and on sponge spicule mats at East Greenland 75° N (Mayer & Piepenburg, 1996) are entirely different (at least in terms of defining taxa) to those found on soft sediments. The vast majority of defining taxa in these communities are sessile suspension-feeding organisms in the phyla Porifera and Bryozoa. This difference in community composition is likely not only due to sediment characteristics, but also to altered hydrodynamic conditions such as increased current speed, particularly at Vesterisbanken Seamount. Meyer, Soltwedel, & Bergmann (2014) describe hard-bottom habitats as anomalies in the deep sea; indeed, rocky substrates are thought to cover less than 4% of the deep sea floor (Glover & Smith, 2003). Considering the large differences between soft and hard sediment deep sea habitats, and the comparative rarity of and high faunal densities at the latter, deep-sea hard-sediment habitats are an important target for conservation efforts.

1.4 Recommendations

In light of the information gained from this review, four main recommendations are identified. The first is that more deep-sea benthic megafauna studies are conducted in the GIN Seas, particularly at depths > 2000 m and in areas where stations are few or non-existent, such as the high seas and the deep areas of the Icelandic and Faroese EEZs north of the Greenland-Scotland Ridge. Currently, there are large regional variations in the quantity and quality of available information on deep-sea megafauna communities. For example, there are 262 sampling stations in offshore Norway and only four in offshore Iceland.

Furthermore, while a large proportion (> 1/3) of the deep GIN Seas has depths > 3000 m, only 4% of the stations identified in the present study are located at such depths. Prioritising the largest knowledge gaps would help to ensure that baseline information is available for as many different locations and depths within the GIN Seas as is possible, which would improve scientific understanding of community variability and distribution in this highly heterogeneous ocean region and also allow for better assessment of the broad-scale and depth-dependent impact of diffuse pressures such as ocean acidification. However, in an era of unprecedented human-induced changes in the Arctic, high priority should also be accorded to those areas that are most likely to be affected by human activities in the near future. This is because it is virtually impossible to accurately monitor and assess the ecological impacts of activities such as shipping and hydrocarbon operations in the absence of comprehensive baseline data.

The second recommendation is to conduct up-to-date seamount studies in the GIN Seas. Seamounts are often described as biodiversity hotspots that have elevated levels of endemism and act as stepping stones for species dispersal (e.g., Davies et al., 2015), although these assertions are increasingly disputed (e.g., Clark et al., 2010). It is possible that as many as 65 seamounts exist in the GIN Seas (Morato et al., 2013), but only one seamount (Vesterisbanken) has been subject to biological research. While very thorough descriptions of communities are provided, the research on Vesterisbanken Seamount is of a qualitative nature and was conducted in 1990 using much more rudimentary technologies than those available today (Henrich et al., 1992). Modern, quantitative seamount studies in the GIN Seas are an exciting prospect as they would provide an Arctic perspective on fundamental questions in seamount research, e.g., whether or not seamounts have higher biodiversity and endemicity levels than the adjacent continental slope. As well as sampling new seamounts, revisiting Vesterisbanken Seamount and resampling the large variety of interesting habitats discovered by Henrich et al. (1992) could be a worthwhile exercise. This would allow any environmental and community changes that have occurred over the past 25 years to be documented.

Thirdly, it is recommended that benthic community mapping efforts in the GIN Seas are increased. Benthic community mapping is represented in this review by three studies from Norway (Elvenes et al., 2014; Holte et al., 2015). These studies are the only megafauna community mapping studies to have been conducted not only in the GIN Seas, but also in the entire Arctic. Benthic habitat mapping is defined by Brown et al. (2011) as 'the use of spatially continuous environmental data sets to represent and predict biological patterns on the seafloor'. Using habitat mapping techniques, point or transect observations can be used to predict community distribution over large swathes of seafloor. Among other advantages, the full-coverage, simplified depictions of biological patterns supplied by the resulting maps provide policy-makers and marine managers with the means to make informed decisions, thereby helping to safeguard marine biodiversity. For example, habitat maps produced by the Norwegian seabed mapping programme MAREANO have played an important role in the decision to prevent the reopening of certain ecologically sensitive areas to the petroleum industry (L. Buhl-Mortensen, Buhl-Mortensen, Dolan, & Holte, 2015). Ideally, continuous map layers depicting the distribution of biological communities on the one hand and human impacts on the other would be produced for the entirety of the GIN Seas, allowing potential conflicts to be assessed. Presently, however, this is an unrealistic goal due to practical and technological constraints. It is therefore important, as mentioned in the first recommendation, that habitat mapping sites are selected in such a manner that not only

maximises the amount of locations and depths represented, but also prioritises those areas that are most likely to be affected by human activities in the near future.

Finally, this study joins others in recommending that collaborative interregional studies using standardised methodologies are conducted, and that communication between research teams in different countries and regions is increased in a general effort to standardise methodologies (Bluhm et al., 2011; Piepenburg, 2006; Piepenburg et al., 2011). This study has shown that it is currently very difficult to compare communities identified in different studies due to inconsistent reporting and methodology. Knowledge on how communities are distributed throughout the GIN Seas and whether the same or similar communities recur in different regions is essential for marine ecosystem management, e.g., Marine Protected Area design. Collaboration is especially encouraged with regards to taxonomic identification, since it is imperative that more taxa are identified to species level. A centralised online platform where Arctic and sub-Arctic taxonomic expertise can be amassed and shared would be very helpful in this regard.

2 Benthic community mapping in the northern Dreki area

2.1 Introduction

Human activities such as commercial fishing, waste dumping, mining, and hydrocarbon extraction can damage benthic ecosystems and decrease benthic biodiversity (Brown et al., 2011). The intensity and geographic extent of these activities are increasing, and no area of the ocean is entirely unaffected by human actions (Halpern et al., 2008). Damage includes major ecosystem-wide regime shifts such as coral degradation and reconfiguration of food webs (Rocha et al., 2015). In this context, comprehensive information on the composition and spatial distribution of benthic communities is critical for assessing the consequences of human activities, managing marine resources sustainably, and protecting ecologically sensitive areas (Brown et al., 2011; Holmes et al., 2008).

However, compared to terrestrial environments, scientific understanding of marine environments is poor due to the practical difficulties and high costs associated with surveying the seafloor (Lecours et al., 2015). While reasonably high-resolution elevation data exist for the entire terrestrial surface, only around 10% of the seafloor has been mapped at a comparable resolution (L. Buhl-Mortensen, Buhl-Mortensen, Dolan, & Gonzalez-Mirelis, 2015). Furthermore, knowledge on benthic community distribution at scales suitable for marine management is very limited. Studies of benthic communities traditionally consist of detailed descriptions and analyses of point or transect samples collected using gears such as trawls, corers, and cameras. The total area of seabed sampled is usually very small due to the limitations presented by such gears, and the spatial extent and broad-scale distribution of marine benthic communities remain poorly known (Brown et al., 2011).

Since the late 1990s, our ability to characterise the distribution of benthic communities has been revolutionised by the increasing availability and affordability of high-resolution acoustic survey technologies (Brown et al., 2011). These technologies have led to the development of benthic habitat mapping, defined by (Brown et al., 2011) as 'the use of spatially continuous environmental data sets to represent and predict biological patterns on the seafloor'. Using habitat mapping techniques, point or transect observations can be used to predict community distribution over large swathes of seafloor. Among other advantages, the full-coverage, simplified depictions of biological patterns supplied by the resulting maps provide policy-makers and marine managers with the means to make informed decisions, thereby helping to safeguard marine biodiversity. For example, habitat maps produced by the Norwegian seabed mapping programme MAREANO have played an important role in the decision to prevent the reopening of certain ecologically sensitive areas to the petroleum industry (L. Buhl-Mortensen, Buhl-Mortensen, Dolan, & Holte, 2015).

The combination of disparate data sets from disciplines such as marine biology, geology, and oceanography is central to habitat mapping (Brown et al., 2011, Smith et al., 2015). Most

habitat maps are generated using two main types of data: continuous coverage environmental data, often consisting of acoustic survey data, and point or transect coverage biological sample data. There are two main approaches to habitat mapping. The traditional top-down approach has the defining characteristic that environmental data are grouped into spatial units prior to the integration of biological data (Brown, Sameoto, & Smith, 2012). Abiotic characteristics therefore form the basis of the resulting habitat map. The more recent bottom-up approach, on the other hand, is based on biotic characteristics, with biological data used to guide the grouping of environmental data (Brown, Sameoto, & Smith, 2012). Benthic communities are identified based on similarity between biological samples, and statistical relationships between communities and environmental variables are used to delineate habitats (J. Smith et al., 2015). Comparative studies reveal that the boundaries, composition, and number of the resulting habitats can differ substantially according to the approach adopted, and that the preferred approach depends on the characteristics and objectives of individual studies (LaFrance et al., 2014; Shumchenia & King, 2010; J. Smith et al., 2015). The top-down approach is generally better at generating full-coverage maps with distinct boundaries between habitats (LaFrance et al., 2014). However, it makes the assumption that distinct geological regions contain distinct biological communities, which has often proven untrue (e.g., J. Smith et al., 2015). In comparison to the top-down approach, the bottom-up approach tends to produce higher within-habitat biological similarity and between-habitat biological dissimilarity, to distinguish habitat characteristics on a finer scale, and to better capture the non-discrete nature of habitats (LaFrance et al., 2014; Shumchenia & King, 2010; J. Smith et al., 2015).

Benthic habitat mapping is an umbrella term that encompasses abiotic surrogate mapping, single species habitat mapping, and benthic community mapping (Brown et al., 2011). Community-level mapping can be advantageous for datasets containing large numbers of species, particularly if many of the species occur only rarely (Ferrier & Guisan, 2006). While single species mapping produces a series of maps and often excludes species with low occurrences for statistical reasons, community mapping synthesises information on all species into one readily interpretable map (Ferrier & Guisan, 2006; Puls et al., 2012). Benthic community mapping has been carried out in a wide range of geographic locations over the past two decades, however, the total area of seafloor mapped is still very small, and some biogeographic regions and depths are less well represented than others. One poorly represented region is the Arctic, where Norway is the only country to have conducted benthic community mapping, albeit over a large area ($> 100,000$ km^2) of Norwegian territorial waters (L. Buhl-Mortensen, Buhl-Mortensen, Dolan, & Holte, 2015). Due to practical and financial considerations, worldwide benthic community mapping efforts have largely focused on coastal and near-coastal regions, with the majority of study sites having a maximum depth of < 500 m. As technological developments allow human activities to expand into deeper and more remote waters (Ramirez-Llodra et al., 2011), there is an increasing need for benthic community mapping in offshore areas in order to ensure sustainable resource use.

One such offshore area is the northern Dreki area, located in Arctic waters at the northeast border of the Icelandic Exclusive Economic Zone (EEZ). Interest in hydrocarbon production in this area has increased the need for baseline knowledge on benthic communities. In 2007, the Icelandic Ministry of Industry issued a proposal describing a plan to offer licenses for the commercial exploration of oil and gas in the northern Dreki area. Information on benthic fauna in the accompanying strategic environmental assessment (SEA) consists of a single sentence: 'A few samples of benthic organisms have been taken in the Dreki area and these

show enormous variations in species composition mainly according to substrate type' (Ministry of Industry, 2007). The document also lists the potential 'impact factors' of different phases of hydrocarbon operations (e.g., 'acute pollution incidents – well blowout, ship damage') and evaluates their severity with regards to benthic fauna on a four-point scale. However, this is a very general assessment that could apply to almost any marine hydrocarbon operation, and no specifics are provided as to the potential effects of hydrocarbon operations on deep and high latitude seafloor environments.

The Ministry of Industry proposal was written prior to the Deepwater Horizon hydrocarbon spill in the Gulf of Mexico in 2010. This spill was unprecedented in scale and depth, with approximately 5 million barrels of oil and gas released from a depth of 1500 m (Fisher, Demopoulos, et al., 2014; Fisher, Hsing, et al., 2014). The spill proved so difficult to contain due to its deep location that oil and gas were released for 87 days before the well was finally capped, and permanent sealing of the well was not completed for a further two months (Gohlke et al., 2011; Joye, 2015). However, recent research indicates that hydrocarbons continued to leak for at least another 1 year and 10 months after the capping of the well (Kolian et al., 2015). These severe difficulties were encountered despite the proximity of the well to the continental USA, which begs the question as to how long would be required to contain a similar spill in the remote northern Dreki area. One of the main messages arising from the literature on the consequences of the Deepwater Horizon spill is that accurate assessment of impacts is virtually impossible in the absence of comprehensive environmental baseline data (e.g., Joye, 2015). Despite these recent, high-profile, and very relevant events, three exploration licenses were granted for the northern Dreki area in 2013/2014 (Manning, 2015) in the absence of basic information on benthic community composition and distribution and on the potential impacts of hydrocarbon operations on this deep-water, high latitude environment. Two of the licenses have since been relinquished because seismic measurements have shown that it is unlikely that there is recoverable oil in the license areas (Manning, 2015), but the third license is still active, and exploratory drilling is expected to begin as early as 2022 (Orkustofnun, 2016).

Given the dearth of information on deep-sea benthic communities, this study modelled the distribution of benthic communities at a study site within the northern Dreki area. The study site had an area of 10,500 km^2 and depths ranging from 756-2167 m. Since the primary aim was to generate the most ecologically realistic community map possible, a bottom-up approach was used. The resulting benthic community map is the first to be produced in Icelandic waters. A short summary of literature relating to the potential effects of hydrocarbon operations on Arctic deep-sea communities is also provided, and findings are briefly discussed in relation to the benthic community map.

2.2 Methods

2.2.1 Study site

The study site has an area of 10,500 km^2 and is located at the northeast border of the Icelandic EEZ, within the northern Dreki area (~43,000 km^2) on the Jan Mayen Ridge (Figure 2.1) (Ministry of Industry, 2007). Acoustic and benthic surveys were carried out at this site in 2008 due to plans to offer licenses for hydrocarbon exploration and production. Knowledge on the sediments and oceanography in the study site is limited. Data from two moorings at

1007 m and 2029 m depth indicate that bottom currents are relatively weak (Mork et al., 2014). Bottom temperature ranges from -0.87 to -0.56°C according to data from the World Ocean Atlas (Locarnini et al., 2013). The study site lies just beyond the maximum sea-ice extent (SAGEX, 2006).
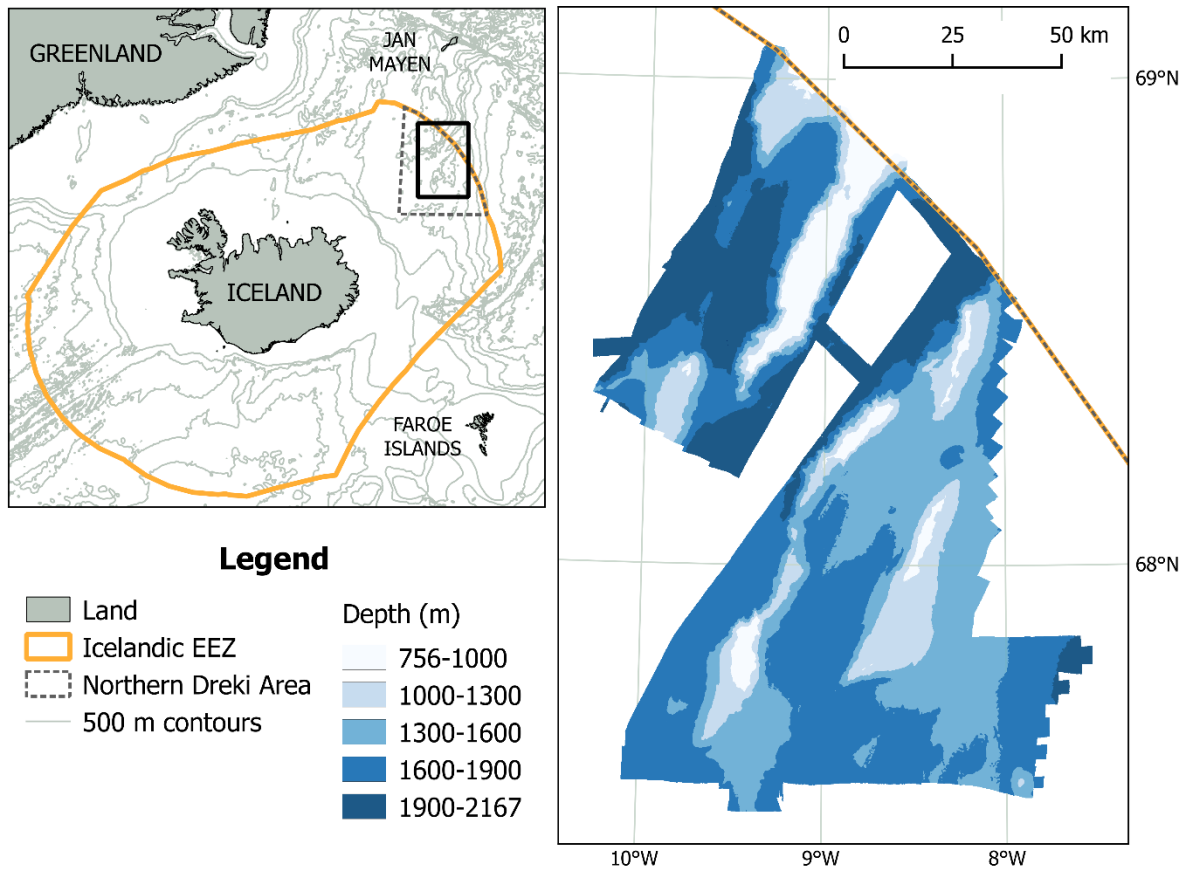

Figure 2.1 Overview of the study site in the northern Dreki area, Iceland. Left panel: geographical location of the study site. Right panel: depths shown in blue indicate the extent of the acoustic survey and thus of the study site.

2.2.2 Data collection and preparation

Multibeam data

Multibeam echosounder data were collected by the Marine Research Institute (MRI) of Iceland in June 2008 using research vessel R/V Árni Fridriksson, which was equipped with a Kongsberg-Simrad EM300 (30 Khz) multibeam system. The system is hull mounted and has 135 (2*2 degrees) beams with an angular coverage sector of up to 150°. A Seapath 200 position and motion sensor was used for navigational purposes. Sound velocity corrections were made using a Sea-Bird SBE911 CTD. The survey covered an area of 10,500 km^2 and was designed to encompass potential hydrocarbon development sites. The focus was therefore on ridge areas where potential hydrocarbon prospects are located, and the central basin was excluded. Data processing was carried out using CARIS HIPS & SIPS hydrographic processing software. Bathymetry and backscatter data were gridded at a

resolution of 50 m. The bathymetry raster was used to generate a suite of terrain variables including slope, northness, eastness, topographic position index (TPI), terrain ruggedness index (TRI), and roughness (Figure 2.2).
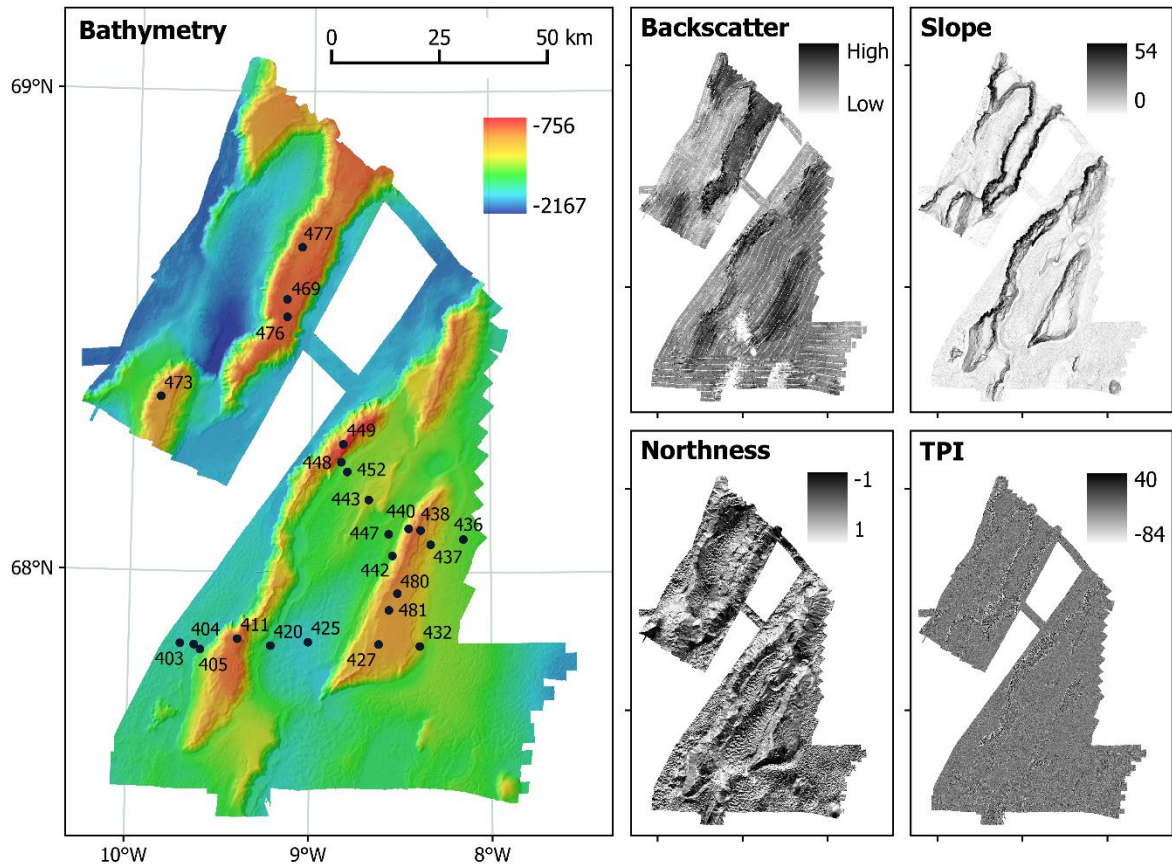
Figure 2.2 Selected data layers derived from multibeam data of the northern Dreki area study site: bathymetry (shown as colour shaded relief), backscatter, and examples of terrain variables (slope, northness, and TPI). All layers are at 50 m resolution. Locations of Agassiz trawl samples (n=24) are indicated by black points on the bathymetry map. The numbers next to the points are the sample numbers.

Benthic sampling

In August 2008, bottom samples were collected at 65 sampling stations within the multibeam survey area. These data were not specifically collected for predictive habitat mapping purposes; the primary aim of the cruise was to describe the benthos in the northern Dreki area in order to provide baseline information before the onset of hydrocarbon exploration. The data therefore differ from those commonly used in benthic habitat mapping studies in several regards. First, the sampling stations are not randomly distributed across the study site because, similarly to the multibeam survey, sampling effort was higher on the ridges due to their status as potential hydrocarbon development sites. Second, while most benthic habitat mapping studies use data from one type of gear in their main analysis, the samples in the present study were collected using five different types of gear (with no single gear type accorded particular priority): Agassiz trawl (24 samples), RP sledge (17 samples), underwater camera (12 samples), triangle dredge (8 samples), and Sneli sledge (4 samples).

Each sample represents a single sampling station. The gear deployed at each station depended on the seabed characteristics. For example, the triangle dredge was used on rough seabed because it is better able to withstand heavy impact, while the Agassiz trawl and RP sledge were generally used on softer sediments. This means that the samples collected using one type of gear may not provide representative biological information on the full range of bottom types present in the study site. Due to this concern, as well as the relatively low number of samples collected with each type of gear, data from multiple gear types would ideally be used in the analysis. However, this is challenging because different gears sample different fractions of the benthos due to the fact that they are often employed on different types of seabed, as well as their different sizes, efficiency, and species selectivity. For example, the Agassiz trawl tends to collect larger taxa, while the RP sledge is designed to collect the suprabenthos. Unsurprisingly, preliminary ordination analysis of the Agassiz trawl, RP sledge, and triangle dredge data revealed that samples collected with the same type of gear tend to cluster together, preventing identification of biological communities. For this reason, only data from the Agassiz trawl were used, as it is the gear with the largest number of samples.

The Agassiz trawl was deployed at 24 locations in water depths ranging from 758 to 1862 m using a wire length of around twice the water depth (Figure 2.2). It was towed for approximately 40 minutes at speeds varying from 0.8 to 1.4 knots, depending on weather conditions. Trawled distance over the seafloor ranged from 630 to 2370 m. The approximate position of each transect was later calculated using the layback equation supplied by MESH (Curtis & Coggan, 2006). Samples were rinsed if necessary, and their volumes were recorded. All visible fauna were plucked from the samples, sorted into high taxonomic groups, and fixed in 4-6% formaldehyde solution. In the laboratory, all specimens were identified to the lowest possible taxonomic level, and their abundances were recorded. Agassiz trawls have a large mesh size (typically ~2 cm) and are thus intended for collecting megafauna. However, the mesh often becomes clogged with megafauna and/or sediment, resulting in the collection of smaller organisms (e.g., Nematoda, Copepoda, Osctracoda). These fauna cannot be representatively sampled with an Agassiz trawl and were therefore removed from the data. Potentially non-benthic fauna (e.g., Euphausiacea, Cephalopoda, Chaetognatha) were also excluded.

2.2.3 Data analysis

Community identification

A 200 m buffer was drawn around the track of each of the 24 Agassiz trawls in order to account for uncertainty in the position of the gear on the seafloor. The mean values for depth, backscatter, and terrain variables were calculated within each buffer. Pearson correlation analysis revealed that slope, TRI, and roughness were highly correlated, and TRI and roughness were therefore excluded from further analyses.

Multivariate analysis was used to evaluate species abundance data obtained from the 24 Agassiz trawl samples. A bottom-up approach was employed, which first required the identification of biological communities, i.e., groups of samples with similar faunal composition. Non-metric multidimensional scaling (NMDS) (Kruskal, 1964) and cluster analysis were performed on fourth-root transformed species abundances using a) a chord distance matrix (Orloci, 1967) and b) a Bray-Curtis dissimilarity matrix (Bray & Curtis, 1957). Multiple cluster analysis methods were tested, including hierarchical methods such

as complete-linkage (Fager, 1957), group-average (Rohlf, 1963), and Ward's minimum variance (Ward, 1963) and non-hierarchical methods such as k-means partitioning (Macqueen, 1967), partitioning around medoids (Kaufmann & Rousseeuw, 1987), and model-based clustering (Banfield & Raftery, 1993). The resulting sample classifications were compared with each other and with the NMDS. An Analysis of Similarity (ANOSIM) (Clarke, 1993) was also performed on the environmental variables in order to test for significant differences in environmental characteristics between the sample groupings in each classification, since the aim was to identify discrete biological communities occupying distinct physical environments (J. Smith et al., 2015). Identical classifications were generated by complete-linkage clustering, Ward's minimum variance clustering, and k-means partitioning (no. groups = 5) using a chord distance matrix. This classification was selected because it contained groups of samples often occurring in other classifications, corresponded well with the NMDS, and gave a high ANOSIM global R value (R = 0.59, p = 0.001) in comparison with other classifications.

Community characteristics

The sample groupings, i.e., communities, determined by the Ward/complete-linkage/k-means classification were summarised according to their biological and environmental characteristics. Taxa richness was calculated as the mean number of taxa in the samples making up each community. Similarity percentage analysis (SIMPER) (Clarke, 1993) was used to assess within-community similarity and between-community dissimilarity and to identify the taxa that contribute most to both parameters. For each community, mean values for depth, backscatter, and slope were calculated, and box plots showing the median and range of these variables were generated. Arrows generated using the R function envfit in the package vegan (Oksanen et al., 2015; R Core Team, 2015) were added to the NMDS to show the correlation between environmental variables and the NMDS axes, with the length of the arrows representing the strength of the correlation (Dolan et al., 2009).

Predictive modelling

The next step in the bottom-up approach was to use statistical relationships between identified communities and environmental variables to delineate habitats. Modelling was conducted using random forest (Breiman, 2001), an ensemble technique that works by building a large number of decision trees and then synthesizing their results using a voting process (Bučas et al., 2013; Che Hasan et al., 2014). Random forest differs from standard decision tree methods in that the data at each node are split using the best environmental predictor variable among a random subset of variables, rather than among all variables (Che Hasan, Ierodiaconou, & Laurenson, 2012; Robert et al., 2016). This keeps bias low and allows the relative importance of each variable to be estimated (Che Hasan et al., 2014; Gonzalez-Mirelis & Lindegarth, 2012). Since a bootstrap sample of the training data is used to build each tree, out-of-bag (OOB) classification error is also estimated (Gonzalez-Mirelis & Lindegarth, 2012; Lucieer et al., 2012). Random forest has performed well in comparisons of supervised learning methods and has been successfully used in benthic habitat mapping applications (e.g., Bučas et al., 2013; Che Hasan, Ierodiaconou, & Monk, 2012). The random forest modelling was conducted using the package 'randomForest' (Liaw & Wiener, 2002) in the statistical environment R (R Core Team, 2015). The number of classification trees to grow (ntree) was set to 1000, and all other parameters were set to default. Training data consisted of the environmental data and the Ward/complete-linkage/k-means classification. The random forest model generated from the training data was used in conjunction with the

depth, backscatter, and terrain variable rasters to predict community distribution at unsampled locations. Since the Agassiz trawl transects were rather long (max: 2370 m), the resolution of the rasters was decreased from 50 m to 500 m prior to the prediction in order to reduce the discrepancy between the resolution of the environmental and biological data. A 3x3 pixel 'moving window' calculating modal values was used to simplify the predicted community map by reducing local variations in community prediction (Dolan et al., 2009).

Software

All data preparation and analysis except for SIMPER was carried out in the open-source statistical environment R (R Core Team, 2015). The following packages were used: cluster (Maechler et al., 2015), dplyr (Wickham & Francois, 2015), HDclassif (Bergé, Bouveyron & Girard, 2012), maptools (Bivand & Lewin-Koh, 2016), mclust (Fraley & Raftery, 2002), randomForest (Liaw & Wiener, 2002), raster (Hijmans, 2015), reshape (Wickham, 2007), rgdal (Bivand, Keitt, & Rowlingson, 2015), rgeos (Bivand & Rundel, 2016), sp (Pebesma & Bivand, 2005), and vegan (Oksanen et al., 2015). SIMPER was performed using PRIMER 6 (Clarke & Gorley, 2006). The open-source geographic information system QGIS (QGIS Development Team, 2016) was used to explore and visualise the data and to create Figures 2.1, 2.2, 2.4, and 2.6.

2.3 Results

2.3.1 Multibeam data

The bathymetry data reveal a complex bottom topography (Figure 2.2). The study site is characterised by multiple large ridges running in the NE-SW direction, which are separated by broad, deep basins. Several of the ridges form wide plateaus. Water depths range from 756 m on the shallow northern section of the central ridge to 2167 m in the deepest basin to the northwest of the study site. Groups of pockmarks are present in several shallow and mid-depth locations, and iceberg ploughmarks are common on the ridges. The backscatter data reveal that substrates are relatively homogeneous. Backscatter intensity ranges from -3 to -41 decibels (dB), but over 99% of values fall between -20 and -35 dB. This indicates that soft, muddy substrates predominate in the study site (J. Smith et al., 2015). The ridges generally have higher backscatter intensity values and therefore harder substrates than the basins, with the highest values found on the steepest slopes. Areas of particularly low backscatter intensity are found in the basins to the south of the study site. Seafloor photographs taken during the cruise support these observations. The vast majority of photographs show soft sediments, but some photographs taken on the ridges and ridge slopes reveal the presence of apparently extensive gravelly or rocky areas. Secondary data layers derived from the bathymetry data help to further characterise the study site. For example, slope calculations indicate that some of the ridge slopes are steep (maximum slope 54°), while others incline more gradually, such as the eastern slope of the southeast ridge.

2.3.2 Community identification

The 24 Agassiz trawl samples contained a total of ~40,000 individuals. Overall, 115 taxa were identified, of which 32 were identified to species, 14 to genus, 45 to family, and 24 to higher taxonomic levels. The two-dimensional NMDS ordination of the 24 samples had a

reasonable stress value and showed that samples tended to form groups (Figure 2.3). However, these groups were not very distinct, and it was not obvious to which groups some of the samples belonged. Ward/complete-linkage/k-means cluster analysis was therefore used to classify the samples into five groups, i.e., communities, that were environmentally distinct (ANOSIM global R = 0.59, p = 0.001) and that corresponded well to perceived groupings on the NMDS. Groups consisted of two to nine samples. The spatial distribution of the classified samples is displayed in Figure 2.4.
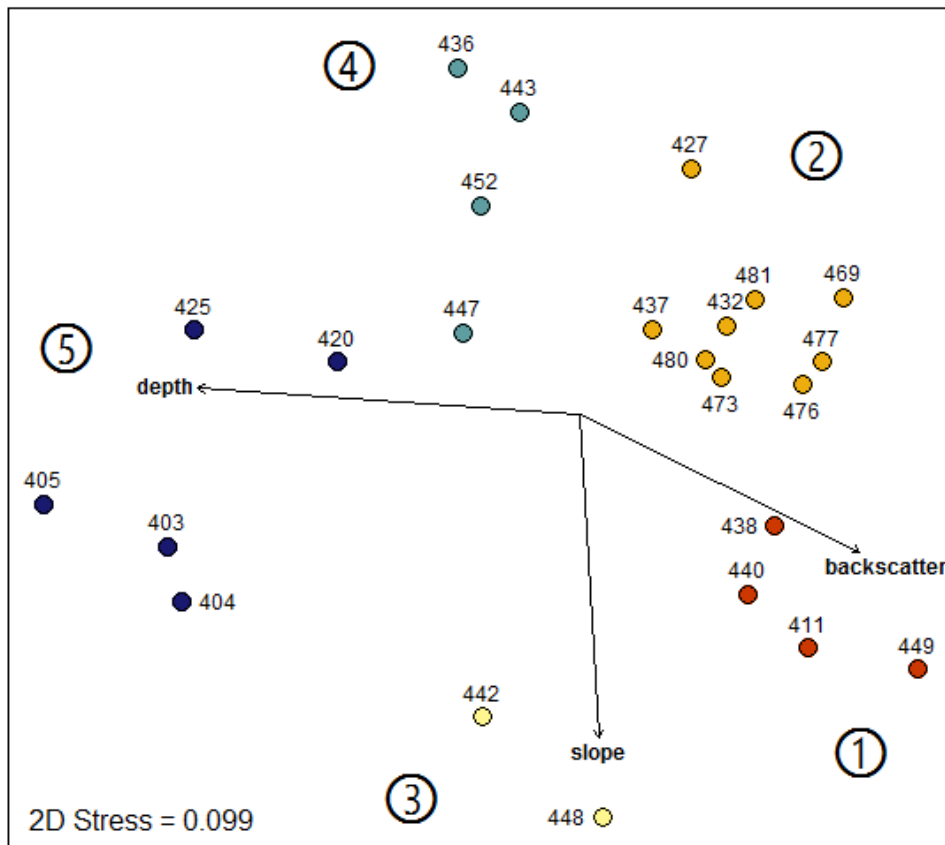

Figure 2.3 NMDS ordination of fourth-root transformed species abundance data derived from Agassiz trawl samples (n=24). The number above each point is the sample number and corresponds to the numbering in Figure 2.2. Points are coloured according to the community classification determined by Ward/complete-linkage/k-means cluster analysis. Communities are numbered from 1 to 5 using large circled numbers. Arrows generated using envfit depict the relationship between environmental variables and the NMDS axes, with the length of the arrows indicating the strength of the correlation (Dolan et al., 2009). Only environmental variables with significant relationships to the NMDS axes are displayed on the plot.

2.3.3 Community characteristics

The biological and environmental characteristics of the five identified communities are summarised in Table 2.1 and Figure 2.5. Within-community similarity ranged from 56.8 to 67.4%, and averaged 63.9%. This is well reflected by the spacing of samples on the NMDS and indicates an overall moderate to low level of variation in fauna composition between the

samples within each community (J. Smith et al., 2015). The taxa cumulatively contributing 50% to within-community similarity for each community (hereafter referred to as 'typical taxa') are listed in Table 2.1. Between-community dissimilarity was moderate to low, ranging from 40.9 to 61.9%, and averaging 51.5% (Table 2.2). This indicates that the identified communities are not particularly discrete. The envfit analysis showed that depth, backscatter, and slope were significantly correlated with the NMDS ordination axes (Table 2.3). R^2 values indicated that depth ($R^2 = 0.91$, p = 0.001) was the most important driver of community composition, which is shown by its long arrow on the NMDS (Figure 2.3).
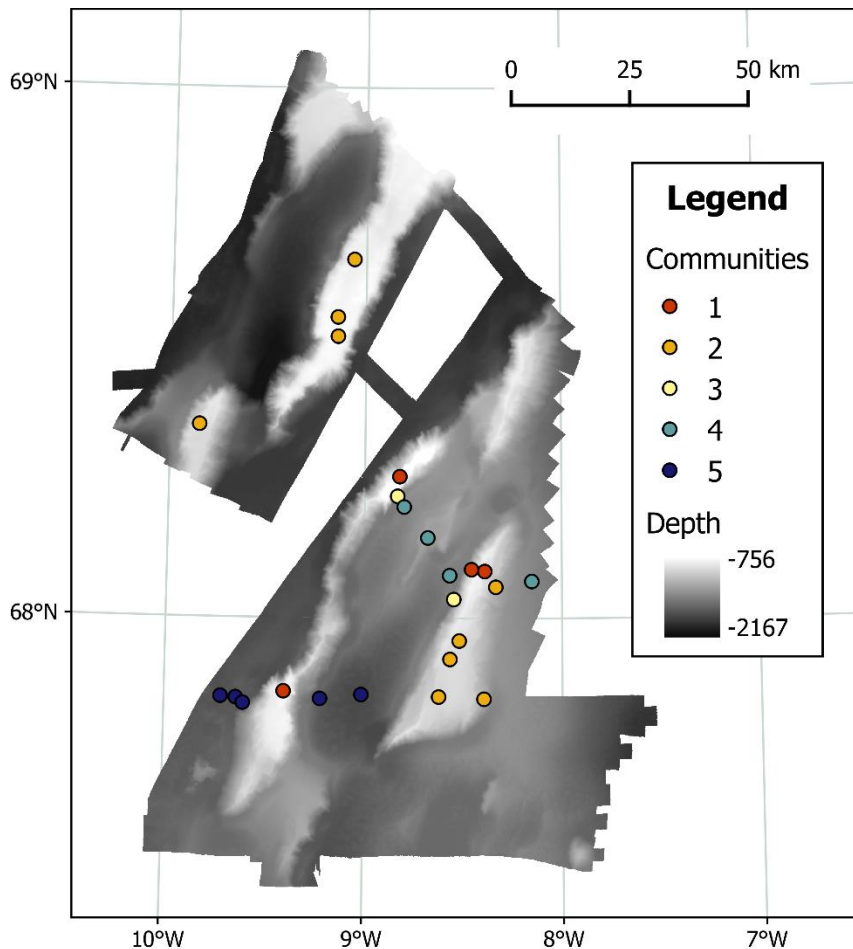
Figure 2.4 Spatial distribution of classified Agassiz trawl samples (n=24) shown on a black-and-white bathymetry map of the northern Dreki area study site.

2.3.4 Prediction

The random forest model had an estimated OOB classification error of 25%. Classification error was lowest for communities 2 and 5 (0%), moderate for communities 1 and 4 (50%), and highest for community 3 (100%). Analysis of variable contribution ranked depth as the most important variable, followed by backscatter, slope, TPI, eastness, and northness. The model was successfully applied to the environmental rasters in order to generate a full-coverage map of predicted community distribution for the study site (Figure 2.6). Each pixel on the map was assigned a colour according to which of the five communities was most

likely to be present. Community 5 was predicted to be the most common community, covering 53% (5806 km^2) of the study site (Table 2.1). In contrast, community 3 was predicted to cover only 4% (395 km^2) of the study site. The community map documents a clear distinction between ridge and basin, with communities 1 and 2 and communities 4 and 5 almost exclusively present on the ridges and in the basins, respectively.

Table 2.1 Summary of the environmental and biological characteristics of communities 1-5. Communities are arranged in order of increasing depth. Mean values are given for depth, backscatter, slope, and taxa richness. Area refers to the area of each community on the predicted community map (Figure 2.6). Average within-community similarity and taxa contributing most to average within-community similarity were determined using SIMPER analysis. The higher the average similarity (%), the more similar the samples within the community are. Taxa cumulatively contributing 50% to average within-community similarity are listed, and figures in brackets show the percentage contribution of each individual taxa. The top five contributing taxa for each community are highlighted in bold.

Community	No. samples	Depth (m)	Backsc. (dB)	Slope (°)	Area (km2)	Taxa richness	Average similarity (%)	Taxa contributing most to average similarity
1	4	943	-26.2	5.8	786	39.0	67.1	**Alcyonacea (6.87)**, **Zoantharia (4.75)**, **Calliopiidae (4.49)**, **Onuphidae (4.46)**, **Terebellomorpha (4.43)**, *Bathyarca frielei* (4.40), Bryozoa (4.28), Ascidiacea (4.12), *Pontaster* (4.03), *Bythocaris gracilis* (3.80), *Nymphon hirtum* (3.80), Porifera (3.61)
2	9	1065	-26.1	1.9	1525	51.9	67.4	***Nymphon* sp. (5.25)**, **Oweniidae (5.23)**, ***Nymphon hirtum* (4.74)**, ***Pontaster* (4.33)**, ***Ophiocten gracilis* (4.31)**, Aphroditidae (4.18), Terebellomorpha (3.70), *Bythocaris gracilis* (3.28), *Ophiopleura borealis* (3.18), Porifera (3.13), Calliopiidae (3.09), Onuphidae (2.93), *Bathybiaster vexillifer* (2.64)
3	2	1465	-25.6	14.5	395	26.5	56.8	**Porifera (12.61)**, **Ascidiacea (7.50)**, ***Bythocaris gracilis* (7.33)**, **Calliopiidae (6.82)**, **Aphroditidae (6.60)**, *Nymphon* sp. (6.40), Crinoidea (5.18)
4	4	1495	-27.8	1.4	2413	40.5	62.9	**Oweniidae (9.31)**, ***Nymphon* sp. (5.98)**, ***Ophiocten gracilis* (5.75)**, **Aphroditidae (5.32)**, ***Bathybiaster vexillifer* (5.03)**, Terebellomorpha (4.76), *Nymphon hirtum* (4.55), Porifera (4.24), *Ophiopleura borealis* (3.89), Cirripedia (3.87)
5	5	1785	-29.4	2.2	5806	26.2	65.0	***Elpidia* sp. (11.09)**, **Actiniaria (8.28)**, **Oweniidae (8.12)**, **Aphroditidae (7.07)**, **Calliopiidae (6.55)**, *Bathybiaster vexillifer* (6.49), *Bythocaris gracilis* (5.97)

2.4 Discussion

2.4.1 Community identification

This study has integrated acoustic and biological datasets using a bottom-up approach to create a full-coverage benthic community map of a deep-water Arctic study site. Data not originally intended for predictive habitat mapping were repurposed. This led to challenges, particularly during the community identification stage. Non-metric multidimensional scaling (NMDS) was used in conjunction with cluster analysis to identify communities. Different types of association measure and cluster analysis produced different sample groupings, as would be expected. Due to the low number of samples, minor changes in sample groupings

had large impacts on community characteristics (e.g., mean depth, typical taxa) and on community boundaries in the predicted community map. For example, samples 420 and 425 were placed in community 4 rather than community 5 by some classifications, which increased the area of community 4 on the predicted map from 2413 to 6448 km^2 and reduced that of community 5 from 5806 to 1862 km^2. As a further example, some classifications identified the samples on the northernmost ridge (samples 469, 477, and 476) as a separate community, which is interesting because the northernmost ridge is the only one that is directly connected to the main Jan Mayen Ridge. This indicates that connectivity may affect community composition in the northern Dreki area. Since there is no foolproof objective means of determining the optimal association measure, cluster analysis method, or number of groups, it is necessary to rely on comparisons of classifications with each other and with the NMDS and on ANOSIM results in order to choose a classification. The reliability of the predicted map must therefore be considered in the context of the inherent instability and uncertainty arising from a small sample size.
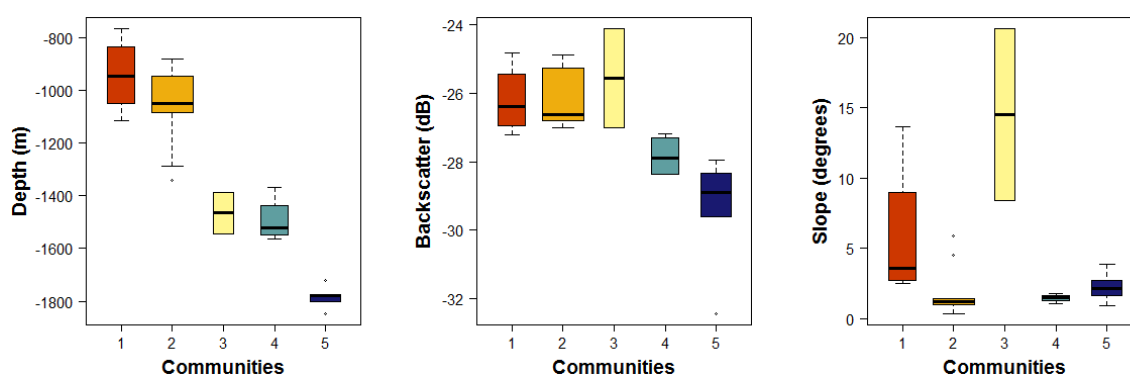
Figure 2.5 Box plots showing distributions (median, interquartile range, and outliers) of selected environmental variables (depth, backscatter, and slope) for communities 1-5.

Community identification is also affected by the type of gear used. Agassiz trawl data are not optimal for habitat mapping since they are considered at best semi-quantitative (van Rein et al., 2009). It was therefore necessary to heavily transform taxa abundances before conducting multivariate analysis. Furthermore, the Agassiz trawl is not intended for use on hard sediments. While soft sediments dominate the study site, photographs taken during the sampling cruise reveal the presence of apparently extensive rocky areas with a distinct associated fauna. This indicates that some of the communities in the study site have not been captured by the present study. The Agassiz trawl and similar gears are increasingly being replaced by less destructive, more representative sampling techniques, with the vast majority of benthic studies now using video and photograph data. However, Agassiz trawl data are not without advantages. Often, Agassiz trawl samples contain more taxa than video and photographs taken in the same or similar locations (P. Buhl-Mortensen, Dolan, & Buhl-Mortensen, 2009; Piepenburg & Schmid, 1996). This may be because some taxa are too small to be visible in videos and photographs or are hidden (e.g., behind sponges, corals, or stones). Moreover, it is often possible to identify taxa in Agassiz trawl samples to lower taxonomic levels because physical samples are collected. Taxa identified in the present study that may not have been sampled or identified to such low taxonomic levels if only video and photograph data had been used include 20 polychaete families, 24 crustacean families, 5 crustacean species, and 15 mollusc species. Many modern habitat mapping studies use

underwater cameras as their main sampling gear and subsample using gears such as the Agassiz trawl (e.g., L. Buhl-Mortensen, Buhl-Mortensen, Dolan, & Holte, 2015), thus gaining the advantages conferred by both types of gear. Future research in the northern Dreki area should consider combining sampling methods in this manner.

Table 1.2 Average between-community dissimilarity (%) calculated using SIMPER. The numbers in bold represent the five communities identified.

	1	**2**	**3**	**4**
2	40.9			
3	45.0	52.8		
4	53.4	46.3	52.5	
5	61.9	61.0	51.0	49.8

2.4.2 Community characteristics

Within-community similarity was moderate (mean: 63.9%) and generally comparable with or slightly higher than that reported in other bottom-up analyses (e.g., Hewitt et al., 2004; Shumchenia & King, 2010; J. Smith et al., 2015). Between-community dissimilarity (mean 51.5%) was perhaps a little lower than average when compared to other studies (e.g., Hewitt et al., 2004; LaFrance et al., 2014; J. Smith et al., 2015), suggesting that the identified communities are not very distinct. Indeed, the typical taxa for each community as determined by SIMPER (Table 2.1) overlap considerably, with many taxa being typical of multiple communities. This is particularly the case for communities 2 and 4, which both have *Nymphon* sp., Oweniidae, and *Ophiocten gracilis* among their top five typical taxa. Lack of distinctness may be due to methodological issues, or may simply be because the communities in the Dreki area are less distinct than those found at other study sites. Research suggests that benthic community distribution in offshore areas is often characterised by faunal gradients rather than sharp discontinuities due to the lack of strong environmental changes (Brown et al., 2011). The presence of generalist taxa occurring across a wide range of environmental conditions may also reduce between-community dissimilarity (Brown, Sameoto, & Smith, 2012). Apparent generalists among the typical taxa identified in the present study include *Bythocaris gracilis*, Oweniidae, Aphroditidae, and Calliopidae, the latter being one of the top five typical taxa for a ridge, slope, and basin community. Note, however, that several of these taxa may represent more than one species, and identification to higher taxonomic levels may reveal that different species are present in different communities. Better taxonomic identification could therefore potentially produce a more well-defined set of communities.

Comparison of the communities identified in this study with those identified in other studies is hindered by the use of Agassiz trawl data, since most other studies use video and photograph data. One of the problems arising from this is that many of the typical taxa in this study are relatively small polychaetes or crustaceans that are not easily visible or identifiable in videos and photographs. There have been no quantitative studies of megafauna communities in deep (> 500 m) Icelandic waters. However, Meißner et al. (2014) provide qualitative descriptions of widely-spaced video and photograph samples, four of which are located in deep waters (631-2160 m) on the continental margin north of Iceland.

The communities described bear little resemblance to those identified in this study, which is partially because Meißner et al. (2014) include taxa such as Euphausiacea, Chaetognatha, and Cephalopoda, which were removed from this study (see Section 2.2.2). However, one sample at 1243 m depth in the Denmark Strait shares three typical taxa in common with community 2 (Pantopoda [taxonomic order to which *Nymphon* sp. belongs], Porifera, and *Ophiopleura borealis*), suggesting that the ridge communities in the northern Dreki area may share some similarities with Icelandic continental slope communities at similar depths. Outside of Icelandic waters, the closest study is located on the main Jan Mayen Ridge, around 100 km north of the northern Dreki area study site (P. Buhl-Mortensen, 2012). Samples consisted of 24 video transects at 388-1574 m depth. Similar to the northern Dreki area study site, sediments were described as relatively uniform, with soft sediments dominant and large areas of consolidated sediment only observed at one station. Four groups of stations (mean depths: 670 m, 749 m, 915 m, 1447 m) were identified using multivariate analysis. The typical taxa identified share Ophiuroidea, *Pontaster*, Alcyonacea, *Bathybiaster*, and *Bythocaris* in common with the typical taxa identified for ridge and slope communities in the northern Dreki area study site; however, resemblance is generally very low. It is not possible to estimate to what extent this is due to real differences between study sites or differences arising from the different methodologies employed. The communities identified in the northern Dreki area study site share some general similarities with communities defined at study sites in other deep-water Arctic locations, such as offshore Greenland and Norway. For example, communities at depths > 1500 m are very often characterised by the holothuroid *Elpidia* (e.g., Elvenes et al., 2014; Mayer & Piepenburg, 1996), as is the case for community 5 in the present study.

Table 2.3   Results of envfit analysis showing the strength of the correlation between environmental variables and the NMDS axes.

	r2	Pr(>r)
depth	0.91	0.001
backscatter	0.56	0.001
slope	0.38	0.009
TPI	0.17	0.163
eastness	0.06	0.505
northness	0.05	0.579

2.4.3 Prediction

Random forest was an effective approach for generating a full-coverage community map from transect-coverage biological samples. The classification (OOB) error rate of the random forest model was moderate (25%), and indicates that the predicted community map should be used with some caution. Error may have been caused by the fact that the number of samples was small relative to the size of the study site, since the predictive accuracy of random forest is known to be significantly affected by sampling density (Bučas et al., 2013). The fact that classification error was lowest for communities 2 and 5 (0%), moderate for communities 1 and 4 (50%), and highest for community 3 (100%) is likely in part due to imbalanced sample sizes: Communities 2 and 5 have the highest numbers of samples with nine and five samples, respectively, whereas communities 1 and 4 have four samples apiece,

and community 3 has only two samples. Such imbalances are known to lead to the misclassification of minority classes (Van Hulse, Khoshgoftaar, & Napolitano, 2007). Future research should aim to collect a larger number of samples or concentrate on a smaller study site, and should also consider resampling data prior to prediction in order to reduce class imbalances. Sample size would ideally be large enough for samples to be split into training and testing datasets prior to analysis in order to allow for more robust accuracy assessment. It is further worth noting that the predicted community map only provides a snapshot of community composition and distribution in a particular year and season. The composition of Arctic deep-sea benthic megafauna communities is not static, with recent studies indicating that composition can vary significantly over time scales of years (Bergmann, Soltwedel, & Klages, 2011; Meyer, Bergmann, & Soltwedel, 2013). It is expected, however, that each identified community maintains a species composition that is different to other identified communities (Degraer et al., 2008).
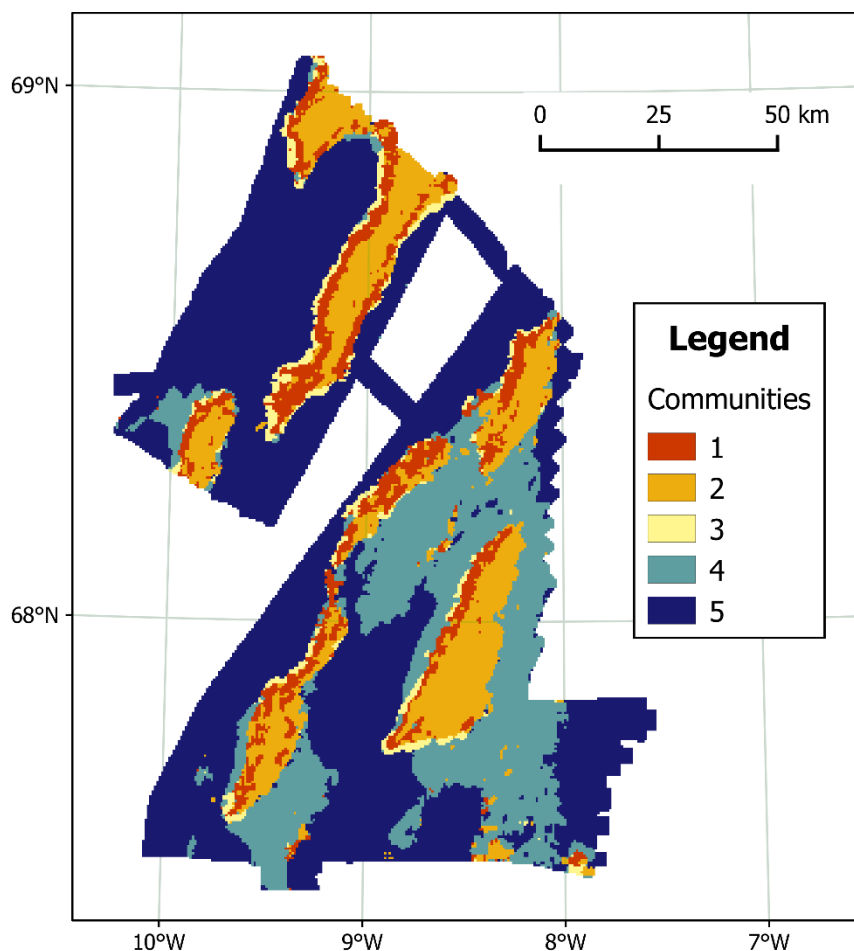
Figure 2.6 Predicted distribution of communities 1-5 in the northern Dreki area study site. Communities are mapped at 500 m resolution. A 3x3 pixel moving window calculating modal values was used to reduce local variations in community prediction.

2.4.4 Environmental variables

It is clear that predicted community distribution is strongly linked to broad-scale topography, with communities 1 and 2 mostly confined to the ridges, community 3 mainly on steep slopes, and communities 4 and 5 almost exclusively present in the basins. Of the suite of six environmental variables (depth, backscatter, slope, eastness, northness, TPI) included in the present study, the results of both the envfit and the random forest analyses indicate that depth, backscatter, and slope have the most explanatory power with regards to community composition and distribution. Depth was the single most important driver identified by both analyses, and has been recognised as such in other bottom-up community mapping studies from the Arctic and elsewhere (e.g., Dolan et al., 2009; Holmes et al., 2008). The depth ranges of the five identified communities show some overlap (Figure 2.5); however, it is clear that community composition generally undergoes a non-repeating change with increasing depth (Howell, 2010). Depth zonation is a trend very commonly observed in the Arctic and world oceans, although its cause is much debated (Bluhm et al., 2011; Piepenburg, 2006). Depth itself does not affect community composition; it is a proxy for other variables that affect biological processes, and, by extension, species distribution (ICES, 2014). Depth zonation has been attributed to many different variables that were not measured in this study, including water pressure, temperature, currents, and food availability (Soltwedel et al., 2009). Similarly, backscatter and slope can be considered proxies for unmeasured environmental variables such as current exposure and sediment characteristics. The present study relies entirely on proxy variables derived from acoustic survey data due to the lack of other full-coverage datasets at appropriate resolutions. The incorporation of parameters that potentially directly affect species distribution (e.g., sediment characteristics) in the analysis would allow better identification of the drivers of community composition and would likely improve the model (Elvenes et al., 2014). Recent research indicates that if the study site is relatively large (> 1000 km^2) or the depth range relatively broad (> 100 m), as is the case in the present study, significant variations in oceanographic properties (e.g., currents, temperature) are likely to occur, and model accuracy may be low if these variables are not incorporated (L. Buhl-Mortensen, Buhl-Mortensen, Dolan, & Gonzalez-Mirelis, 2015; ICES, 2014). The development of high-resolution spatial models of oceanographic variables should therefore be a priority for future studies in the northern Dreki area.

2.4.5 Implications: Vulnerability to hydrocarbon exploitation

The predicted community map allows preliminary assessment of the potential effects of hydrocarbon operations on the northern Dreki area. The main phases of hydrocarbon operations are prospecting, exploration, development, production, transport, and demolition, and each phase has associated impacts and risks (Kark et al., 2015). With respect to benthic communities, the primary concerns identified in the literature include the discharge of drilling waste (drilling fluids and drill cuttings) and the risk of accidental oil spillage (Ellis, Fraser, & Russell, 2012; Ramirez-Llodra et al., 2011). The physical and ecological consequences of specific impacts are difficult to predict since they depend upon a wide range of complex and interacting factors such as the nature of the impact itself (e.g., type and discharge volume of drilling fluid/spilled oil), the nature of mitigation activities (e.g., type and quantity of chemical dispersants used after an oil spill), the abiotic characteristics of the area in question (e.g., current speed, substrate type, depth), the biotic characteristics (e.g., life history of species, sensitivity of species to contaminants, trophic relationships), the occurrence of other potentially synergistic impacts (e.g., ocean acidification), and the

contamination history (Blackburn et al., 2014; Ellis, Fraser, & Russell, 2012; Olsen et al., 2007; Ramirez-Llodra et al., 2011). However, the main physical consequences of the impacts associated with hydrocarbon operations commonly include elevated sediment concentrations of substances such as trace metals and hydrocarbons, smothering/oiling of the seafloor, and benthic anoxia (Blackburn et al., 2014; Ellis, Fraser, & Russell, 2012; Gates & Jones, 2012). Ecologically, this often translates to decreases in overall species diversity and abundance and increases in the abundances of more tolerant species (Blackburn et al., 2014; Ellis, Fraser, & Russell, 2012). Effects can be acute or chronic, as well as lethal or sublethal, and their extent can vary (Blackburn et al., 2014). For example, the maximum extent of observed effects of modern drilling fluids on the benthos was found to range from 100 to 1000 m in different drilling locations (Ellis, Fraser, & Russell, 2012), while the Deepwater Horizon oil spill affected a coral community located at a distance of 22 km from the wellhead (Fisher, Hsing, et al., 2014).

Degree of vulnerability to the potential impacts of hydrocarbon operations varies among communities and taxa. For instance, hard-bottom communities are generally more vulnerable than soft-bottom communities to the effects of drilling waste discharge (Ellis, Fraser, & Russell, 2012). Soft sediments predominate in the northern Dreki area, however, photographs reveal the presence of apparently extensive areas of consolidated sediments and stony bottoms in several ridge and ridge slope locations. These hard-bottom environments can be considered rare anomalies in the deep sea since rocky substrates are thought to occupy less than 4% of the deep sea floor (Glover & Smith, 2003). Unfortunately, drilling in the northern Dreki area will occur on the ridges, i.e., in proximity to or even within these rare hard-bottom habitats. Deep-sea communities may also be particularly vulnerable to various impacts. Typical deep-sea conditions (e.g., low temperatures, low organic carbon and nutrient concentrations, low current speeds) may lead to higher contaminant stability and increased likelihood of drill cutting accumulation, and typical deep-sea faunal characteristics (e.g., slow reproduction/metabolism rates) may lead to slower community recovery rates (Ellis, Fraser, & Russell, 2012; Montagna et al., 2013). Indeed, one year after the Deepwater Horizon oil spill at ~1500 m depth, contaminants persisted on the ocean floor of the impact zones, and macrofauna richness and diversity were 22.8% and 35.9% lower, respectively, than in surrounding non-impacted areas (Fisher, Montagna, & Sutton, 2016; Montagna et al., 2016). It is thought possible that full community recovery in the affected areas will take decades or even centuries (Montagna et al., 2013). However, the majority of studies on the effects of hydrocarbon operations investigate continental shelf environments, and research on waters deeper than 500 m is very limited (Ellis, Fraser, & Russell, 2012; Kark et al., 2015). Biogeographic region is a further factor that may affect vulnerability. In their laboratory comparison of the sediment oxygen demand of Arctic and temperate sediment cores exposed to crude oil and drill cuttings, Olsen et al. (2007) demonstrated that 'pristine' Arctic communities are likely more sensitive than temperate communities to hydrocarbon contamination. As a deep-sea environment located in the Arctic, the northern Dreki area may therefore be particularly vulnerable to the impacts of hydrocarbon operations.

Responses to the impacts of hydrocarbon operations are taxa specific and influenced by factors like feeding mode and ability to process contaminants (Blackburn et al., 2014). Studies have shown that the discharge of drilling waste leads to decreases in suspension feeder abundances and increases in deposit feeder abundances (Ellis, Fraser, & Russell, 2012). After oil spill events, Echinodermata, Amphipoda, and Gastropoda populations often dramatically decrease or disappear altogether (Blackburn et al., 2014), and high rates of coral

mortality have also been observed (Fisher, Demopoulos, et al., 2014). In contrast, populations of opportunistic species such as Polychaeta and Nematoda often flourish in response to the various impacts of hydrocarbon operations (Blackburn et al., 2014; Ellis, Fraser, & Russell, 2012). All five of the communities identified in the present study have taxa that are potentially vulnerable to the routine and accidental impacts associated with hydrocarbon operations among their top five typical taxa, indicating that all could be significantly altered if drilling goes ahead in the northern Dreki area. The communities that are most likely to be affected by the impacts of hydrocarbon operations are those on the ridges, i.e., communities 1 and 2, since this is where drilling will take place. The taxa most typical of community 1 are soft corals (Alcyonacea), and typical taxa also include Calliopiidae (Amphipoda), *Pontaster* (Echinodermata), Bryozoa, and Ascidiacea, all of which may be at high risk from hydrocarbon operations. Typical taxa at risk in community 2 include four echinoderms (*Pontaster*, *Ophiocten gracilis*, *Ophiopleura borealis*, and *Bathybiaster vexillifer*). Communities 1 and 2 are among the most biodiverse and rare (in terms of area) in the northern Dreki area study site, and, being ridge communities, are likely to represent rare communities within the Icelandic EEZ and surrounding waters since ridges cover a very small proportion of the deep ocean floor. Their conservation should thus be assigned high priority. It is therefore of considerable concern that many of the typical taxa of communities 1 and 2 are likely to be affected by hydrocarbon operations, and future environmental impact assessments undertaken in relation to hydrocarbon operations in the northern Dreki area should certainly take this into account.

2.5 Conclusion

This study used a bottom-up approach to investigate the composition and distribution of benthic megafauna communities at a topographically complex deep-water Arctic study site. Five benthic communities were identified using multivariate analysis, and random forest was used to model the relationship between communities and variables derived from acoustic survey data. The resulting map of predicted community distribution indicates that the routine and accidental impacts of hydrocarbon operations could significantly alter community composition in the northern Dreki area, since many of the typical taxa within the communities are potentially vulnerable to such impacts. However, this map is the first to be produced in Icelandic waters, and, as such, the methods used and the map itself should be regarded as preliminary. The reliability of the results is affected most notably by the low sample size and by the use of semi-quantitative Agassiz trawl data. Future refinement of methods should look to address these issues through the collection of more samples and the use of video and photograph data, and should also aim to include non-acoustic environmental variables such as oceanographic variables.

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