Benthic community structure on offshore northern shrimp (*Pandalus borealis*) grounds north of Iceland

Ingibjörg G. Jónsdóttir[1*], Chris Yesson[2], Kirsty M. Kemp[2] & Steinunn H. Ólafsdóttir[1]

[1] Marine and Freshwater Research Institute, Fornubúðir 5, 220 Hafnarfjörður, Iceland

[2] Institute of Zoology, Zoological Society of London, Regent's Park, London, NW1 4RY, UK

* Corresponding author: tel: + 354 575 2000; email: ingibjorg.g.jonsdottir@hafogvatn.is

Running head: Benthic community structure on northern shrimp grounds

Abstract

The main fisheries of northern shrimp in Icelandic waters are located west and north of Iceland. These locations are studied in an annual survey to estimate stock size and distribution of northern shrimp. In July 2015, an additional survey was conducted to study the benthic community structure and function to describe the habitat where the northern shrimp fisheries take place. Underwater images were taken from 26 stations, grab samples were collected at 11 stations and in addition, by-catch was collected from the annual Icelandic shrimp survey in August 2015. The sampling sites, despite being distributed throughout a relatively large area north of Iceland, were rather uniform in relation to sediment type and fauna composition. The stations were similar in grain size and dominated by soft sediment of sand and silt/mud and soft sediment fauna. The infauna was mainly burrowing infauna with affinity to soft sediment and surface deposit feeding. The epifauna were free living crawlers with affinity for predation feeding habit. No relationship with environment was observed for either the epifauna or the infauna. Species diversity and community composition did not vary with depth, likely because of the narrow depth range of the sites. This study provides the first data on benthic in- and epifauna in northern shrimp fishery locations north of Iceland, which can later be used to estimate possible changes and/or the effect of shrimp fishing within this area.

Introduction

Marine ecosystems are diverse; species diversity varies among ecological communities and the structure of the communities may change over a range of temporal and spatial scales (Witman et al. 2004; Woolley et al. 2016). Changes in marine benthic communities may be fisheries-induced (Hiddink et al. 2006; Reiss et al. 2009) but may also be caused by other factors, like sea water temperature (Yesson et al. 2015). Knowing the variability of benthic communities is necessary to effectively manage ecosystems for sustainable use and conservation.

The benthic community is influenced by numerous factors; it changes over geographical gradients, both latitudinally and longitudinally (Hillebrand 2004; Witman et al. 2004), and it is strongly associated with sediment composition (Sswat et al. 2015), sediment grain size (Brown et al. 2002) and depth (Sswat et al. 2015; Zhulay et al. 2019). The presence of harder substrate in the form of gravel/pebble or cobble/boulder is associated with a higher incidence of sessile, settling fauna such as corals and hydroids. However, sandy and muddy bottoms are generally dominated by infaunal organisms and the motile fraction of the macrofaunal community, such as starfish, holothurians, and fish (Watling & Norse, 1998).

The first studies on benthic invertebrates in Icelandic waters were conducted by the Danish Ingolf Expedition in 1895 and 1896 (Wandel 1899) in deeper waters off Iceland. A century later, the most extensive research effort to study the benthic invertebrates was conducted by the project Benthic Invertebrates of Icelandic waters (BIOICE), which was carried out between 1991 and 2004 (Guðmundsson et al. 2014). More recently, the IceAGE project (Icelandic marine Animals: Genetics and Ecology, by Senckenberg am Meer) has collected samples within the deep Icelandic waters with emphasis on population genetics and ecological modelling (Meißner et al. 2014, 2018). Benthic habitat mapping has been conducted by the Marine and Freshwater Research Institute (MFRI) in Iceland with underwater cameras, with emphasis on vulnerable habitats, mainly in the deep waters around Iceland (Ólafsdóttir et al. 2020).

Northern shrimp (*Pandalus borealis*) is found offshore in the waters north and northeast of Iceland between depths of 100 and 700 m. They generally stay close to the seabed during daytime but rise up in the water column during the night in search for food (Shumway et al., 1985). The offshore northern shrimp fishery was initiated in 1974 and northern shrimp was a commercially important species in Icelandic waters in the 1980s and 1990s, peaking in 1994-1997 when the annual catch reached 62,000 t (MFRI, 2021). In the following years, shrimp biomass and catch decreased, and the biomass reached historically low values in 2004 when the annual catch was only 600 t. In 2018, the inshore and offshore northern shrimp fisheries entered the Marine Stewardship Council certification program (DNV-GL 2017), bringing new scrutiny of the seabed habitats of northern Iceland and the impact of trawling activities upon them. However, little information exists on benthic habitats in the offshore shrimp fishing areas. The purpose of this present study is to describe the benthic habitats of offshore shrimp fishing grounds north of Iceland. The specific objectives were to identify benthic species from grabs, images and by-catch and record the substrate type.

Materials and methods

The study area was the main fishing area for offshore shrimp, north of Iceland (Fig. 1). Sample sites were selected from areas where most of the shrimp catches have been taken throughout time thereby representing the main habitats encountered by shrimp fishery (Fig. 1).

Grab samples and images were collected on a cruise with the RV Magnus Heinason between July 4th – 7th in 2015. A Shipek bottom grab was used to collect samples of the bottom at a total of 11 stations (Fig. 1; Table 1). Three grab replicates were taken at each station, each grab sample covering 0.04 m^2 area of bottom. A sub-sample was taken for grain size analysis from one grab sample at each station. Coordinates and depth were recorded when the first and third grab was at the bottom. For each sample, care was taken to record volume, colour, texture, and presence of H_2S odour. Samples were washed through a 0.5 mm mesh sieve on board. All organisms were placed in plastic containers and fixed in a solution of 4% formalin in seawater, buffered with borax. In the lab, the samples were rinsed using a 0.25 mm sieve to remove formalin and then placed in 70% ethanol solution. All individuals were identified to the lowest taxonomic level possible. Abundance of individuals of each species was estimated as number of individuals per m^2 and was calculated as the mean number from the three replicates taken at each station.

Images were taken at a total of 26 stations. The primary equipment was a benthic camera system. The unit consisted of a stills camera (Model DSC-10000 Digital, Ocean Imaging Systems, USA) in a 2000 m-rated underwater housing, a flash unit (200 W-S Remote Head Strobe Model 3831, Ocean Imaging Systems, USA), and a remote trigger. These were fixed to a frame that was lowered to the seafloor on a winch wire. Images were taken according to the protocol described in Yesson et al. (2015), in brief: 10 stills per station, taken at 1 min drift intervals, each image area = 0.3 m^2. All macrofauna visible on the images were identified to the lowest level possible and counted. As some images were unsuitable for analysis (sediment disturbance), counts were normalised to a standard 10 images (normalised count = 10 x count / number of images).

By-catch epifauna were collected using shrimp bottom trawl during the annual Icelandic shrimp survey (ISS) on RV Bjarni Sæmundsson in August 2015 (Jónsdóttir et al. 2017). Epifauna were collected from the same 11 stations that grab samples were taken in July 2015 (each tow covering approximately 0.063 km^2). Benthic fauna was sorted on-board, taken aside and photographed. All individuals were later identified from the images to species level if possible and counted.

Grain size analysis was performed at the Research station in Sandgerði, Iceland, according to the following protocol:

1) Wet weight recorded. 2) About 100 g (wet weight) was set in water and allowed to stand, with occasional stirring, for a few hours. 3) When the sample was well mixed with the water, it was

filtered through a 1 mm mesh and a 0.063 mm mesh and rinsed until run-off water was no longer cloudy. 4) Buckets containing run-off water (sediment < 0.063 mm) were allowed to stand until the sediment settled to the bottom. Then, water was drained off and sediment was put into a beaker, dried at 50°C and weighed. 5) Sediment > 0.063 mm was dried at 50°C. Then, the dried sample was put into an agitator over a series of sieves (4, 2, 1, 0.5, 0.25, 0.125, 0.063, < 0.063 mm and bottom). Samples were agitated for 5-10 minutes. 6) Sediment caught in each sieve was weighed and recorded. The sediment was classified into five classes (granulate > 2 mm; coarse 0.5-2 mm; medium 0.25-0.5 mm; fine 0.063-0.25 mm; silt/mud < 0.063 mm) based on their size following Ellingsen et al. (2007).

Temperature and depth data were collected using a data storage tag (DST) centi-ex produced by Star Oddi. The DST was attached to the camera unit and recorded temperature and depth every 30 seconds.

Effort data were collected from the Vessel Monitoring System (VMS) for the study area at a 0.125°grid resolution. The VMS data included both shrimp- and bottom trawlers operating in the area. Both gears are bottom touching, utilized within the research area and could have impact on the habitat, but bottom trawlers only crossed a few of the sampling sites. To get indication of the fishing pressure on the sampling locations the cumulative effort was calculated as the number of tow-minutes per grid unit for the years 2010 - 2015. The values were collected for the four grid units closest to the sampling site and average values were used for further analysis.

Diversity at each station was analysed using the Shannon's diversity index. It takes into account information on both species richness and the distribution of individuals among species. It was calculated according to the following equation: $H' = - \Sigma P_i \log P_i$ where P_i is the proportional number of species *i* in the sample.

Multivariate linear regressions were performed to test the response of diversity to depth, percentage mud, temperature, and fishing effort. Three metrics of diversity were tested, Shannon's diversity, total abundance and total taxa, each was analysed in seperate model for both the epifaunal and infaunal data (a total of 6 models). Fishing effort was square root transformed to normalise the distribution (validated by a Shapiro-Wilk test of normality).

Communities were analysed at family level for grab data (89% of samples could be identified at this level), while image data were analysed at class level (97% of samples could be identified at this level). Using more detailed taxonomic resolution resulted in a >40% drop in the number of samples being identified at that level in both datasets.

A multidimensional scaling analysis (MDS) was performed on two datasets (grab samples and images) using the metaMDS function in the R package vegan, using Bray Curtis similarities and 'autotransform' of abundance values (square root + wisconsin transformation). Vectors representing the environmental factors, depth, percentage mud, temperature, and fishing effort, were fitted to the ordination using the *envfit* function, to look for significant relationships between composition and environment. The envfit analysis examines the relationship between environmental gradients and ordination space and assesses significance of the fit via a permutation test (1000 permutations used). Environmental factors were only included in the dataset from the images as sample size of the other dataset (grab samples) was too small.

Diversity and community patterns were calculated with the R package vegan (Oksanen et al. 2020). All statistical analyses were conducted using R (R Core Team 2021).

Two trait databases were used to record selected behavioural and environmental traits for the grab samples and the by-catch epifauna; The Arctic Traits Database (Degen & Faulwetter, 2019) specifically focused on benthic invertebrates from the Arctic regions and the Polytraits database (PolytraitsTeam, 2020), which was used for biological traits (mobility of adults and feeding type) of polychaetes (bristle worms, Polychaeta: Annelida) (Appendix 3).

Three behaviour traits and two environmental traits were selected i.e., living habit (LH), mobility of adult/adult movement (MV), feeding type/feeding habit (FH), substrate affinity (SA) and environmental position (EP) (Appendices 2 and 3). In the case of polychaeta, if both databases included information on the species/taxa, they were both registered, separated with "/". These traits were chosen firstly because they were recorded for most of the species found, but several of the traits were only recorded for a few of the species. They were also selected as they give insight into the functionality of the animals, their position and how they move on the seafloor, how they feed and what substrate is preferred. This is all important when evaluating the structure of the community.

Not all species are selective to single trait modalities/trait categories. To indicate to what an extent taxon exhibits each trait category/modalities, fuzzy coding is applied. It ranges from 0 to 3 where 0 means no affinity for a trait category while 3 means that the taxon has total and exclusive affinity for certain trait categories. Similarly, 2 means high affinity and 1 means low affinity for a trait. Fuzzy coding for the identified taxa were downloaded in matrix format from the Arctic Trait Database website (Degen & Faulwetter, 2019).

Results

Soft sediment of sand and silt/mud was the dominant sediment type of the study area (Table 1). No smell of H_2S was detected and the entire volume of the Shipek grab came up with sediment except on station 20 where the sediment was coarser.

The cumulative fishing effort at the sampling locations ranged from 0 to 148 (number of tow-minutes per unit) with the average pressure being 49 (Appendix 1; Fig. 1). High fishing effort was observed at demarcated areas closer to shore, but lower fishing effort was observed at the northernmost areas.

A total of 83 taxa were identified from the grab samples, with 28 - 41 taxa/species seen at each station (Appendix 4). The annelids Paraonidae*, Aricidea suecica, Scoloplos armiger, Scoletoma fragilis* and *Galathowenia oculate* along with Bivalvia were found at all stations. Uniques (taxa restricted to one station) totalled 24 (29% of all taxa) and duplicates (species restricted to two stations) totalled 10 (12% of all taxa).

A total of 53 taxa belonging to ten Phyla were identified from the images (Appendix 5). The number of taxa per station ranged from 1 to 13 taxa. The most abundant taxa were *Nothria conchylega* (Polychaeta, Fig. 3C), Ophiuroidea, and Arthropoda. Eleven sponges were found at eight stations. The sea pen *Virgularia* sp(p). was found at four stations and the cauliflower coral *Gersemia* sp. was found at two stations, both are listed as Vulnerable Marine Ecosystem (VME) indicator species (ICES, 2020).

The number of individuals caught as by-catch epifauna in the ISS was in general low and each species was usually only observed at one station (Appendix 6). The most common species was the mud star *Ctenodiscus crispatus* (Asteroidea) found at 5 stations. The cauliflower coral *Duva florida* and five porifera taxa, Axinellidae, *Cladorhiza* sp., *Polymastia thielei*, *Mycale* sp., and *Phakellia* spp. are listed as VME indicator species (ICES, 2019). These species were only observed at a single station each, except for *Phakellia* spp. They were all found in low abundance.

The MDS plot summarises community similarities between stations (Fig. 2). For the infauna differences detected by axis 1 separated mainly between stations at shallower and greater depth while fishing effort was broadly aligned with axis 2. However, no significant relationship of community composition and environment was detected. For the epifauna (image data) there was no significant composition response to environment, although fishing effort showed the strongest response (p = 0.085), again aligned with axis 2 of the ordination, with higher effort stations tightly clustering, although that is partly driven by the presence of shrimp in the images (notice in Fig. 2 the fishing effort arrow points directly at Malacostraca, which is dominated by observations of the target of the main fishery, *Pandalus borealis*).

In general, no significant response of diversity metrics to either depth, temperature, percentage mud or fishing effort was detected (Table 2).

A total of 79 taxa of the 83 taxa identified (95%) were included in the fuzzy code analysis (Table 3). It showed that the living habit of most of the infauna taxa (62%) was burrowing (LH4 type). Free living and tube dwelling taxa were also abundant (46 and 43%). Most of the taxa (79%) were burrowers (MV2) but the other types of adult movements were similarly used (27 to 40%). About 74% were surface deposit feeders (FH1). Most of the taxa (97%) showed soft substrate affinity (SA1) and about 82% of the taxa are infauna (EP1).

Thirty two of the 53 taxa (60%) identified from the images were included in the fuzzy code analysis for the epifauna (Table 3). It showed that living habit of most of the taxa (73%) was free living (LH1 type) followed by burrowing (53%). Their adult movements were rather evenly assigned to all the four types (MV1-4) with crawling (MV3) a bit higher than the others (69%). The taxa were mostly predators (FH5) (76%) followed by filter/substrate feeders (FH3) (59%) and showed similar affinity to both soft and hard substrate (91% and 86.4%) and predominantly considered to be epifauna (EP2) (96%).

Nineteen of the 25 taxa (76%) in the by-catch epifauna were included in the fuzzy code analysis (Table 3). It showed that the living habitat of the by-catch was either free living (LH1) or burrowing (LH4) (69 and 62%). Most movements were crawling (MV3) or sessile (MV1) (63 and 50%). The feeding habit was predator (FH5) (65%) or filter/suspension feeders (FH3) (59%). There was both preference for hard (SA2) and soft substrate (SA1) (88 and 81%) and they were mainly epifauna (EP2) (88%).

Discussion

The sampling sites in the present study, despite being distributed throughout a relatively large area north of Iceland, were rather uniform. They were similar in grain size and dominated by soft sediment of sand and silt/mud and soft sediment fauna. Species diversity and community composition did not vary with depth, likely because of the narrow depth range of the sampling sites. We found no significant response of composition or diversity to environmental conditions and likely reflects the small sampling size and limited environmental range of the study. This study provides the first data on benthic in- and epifauna in northern shrimp fishery locations north of Iceland, which can later be used to estimate possible changes and/or the effect of shrimp fishing within this area.

Northern shrimp grounds in the offshore areas north of Iceland are similar to northern shrimp grounds observed in other North Atlantic regions (Haynes & Wigley 1969; Horsted & Smidt 1956). The infauna was dominated by burrowing, surface deposit feeders, mostly polychaetes and due to the high degree of biological and ecological adaptation they show little change in gradient with latitude or depth (Dauvin et al. 1994). Most common species/groups observed in the images were epibenthic, free living, crawling and predators. Brittle stars, found in high quantities, are known to dominate communities on Arctic shelves and can locally reach high abundances (Piepenburg & Schmid, 1996). Shrimp species (Caridea, Decapoda) were found at almost half of the stations, which was to be expected as we targeted common shrimp grounds. The by-catch epifauna was a mixture of free living and burrowing taxa, crawlers with mixed feeding habits (predators, filter/suspension feeders and surface deposit feeders). The low abundance of species sampled in ISS may indicate that epifauna abundance was low in this area or that the shrimp trawl was not removing much epifauna in the area. As the number of epifauna individuals were higher from the images it is likely that the latter is more accurate. Further registration of by-catch would be useful to estimate the impact or the catch efficiency of the shrimp fishing gear.

Despite the uniform sediment type observed here, this does not mean that shrimp may not be found living in other habitat types. In fact, shrimp have been observed inhabiting various seabed types or biogenic substrate in images taken around Iceland; examples are the polychaete structure of *Filograna implexa* and the cold-water coral reefs of *Desmophyllum pertusum* (Marine and Freshwater Research Institute unpublished data). Furthermore, the offshore area north of Iceland is not so uniform as seen at these 26 stations. It has a unique geology due to its geographical location across the Mid Atlantic Ridge, providing a diverse range of niches for benthic organisms (Omarsdottir et al. 2013). However, our samples were taken at common shrimp fishing grounds and there are various locations where shrimp fishing cannot take place, such as the Kolbeinsey Ridge, that rises from the seafloor in the middle of the study area (Fig. 1). Kolbeinsey Ridge is a part of the Mid-Atlantic Ridge and is partly active. Furthermore, it includes an active seafloor hydrothermal system that is located between some major shrimp grounds (Dekov et al. 2008). The fauna on the ridge differs considerably from the soft bottom fauna found at the shrimp fishing area (Fig. 3E). Shrimp fishing is therefore currently conducted at what are considered to be more resilient locations north of Iceland.

The results of this present study show community structure in a single year and can only represent the targeted locations. They cannot be interpreted for shrimp habitats in other areas, even adjacent areas nor can they be used for interpretation of change in habitats due to the impact of fishing activity in the area as no prior information on benthic communities in this area exists. Even though these results are merely baseline information on species diversity in the offshore shrimp area north of Iceland, it may be of use in later comparisons. Further monitoring in the area is needed to provide information on community and estimate the effect of environmental changes and/or fishing activity on the offshore shrimp grounds.

Acknowledgements

We would like to thank: the captain and crew of the research vessel Magnus Heinason; Chris Turner for assisting with the fieldwork; Ragnhildur Ólafsdóttir for analysis of the grab samples; Einar Hjörleifsson for producing the VMS data; Jennifer Choyce for her initial work on annotations. This project was supported by Eurofleets (project name “Benthic habitats in Iceland shrimp trawl grounds (BenthHabIceland)” Grant agreement n° 312762). Chris Yesson and Kirsty Kemp are funded by Research England. We thank four reviewers whose input greatly improved the manuscript.

Disclosure statement No potential conflict of interest was reported by the authors

Availability of data and material The dataset generated that support the findings of this study is available as supplement to the paper

References

Brown CJ, Cooper KM, Meadows WJ, Limpenny DS, Rees HL. 2002. Small-scale mapping of sea-bed assemblages in the Eastern English Channel using sidescan sonar and remote sampling techniques. Estuarine, Coastal and Shelf Science 54:263–278.

Dauvin JC, Kendall M, Paterson G, Gentil F, Jirkov I, Sheader M, de Lange M. 1994. An initial assessment of polychaete diversity in the north-eastern Atlantic Ocean. Biodiversity Letters 2:171–181. doi: 10.2307/2999658

Degen R, Faulwetter S. 2019. The Arctic Traits Database - A repository of Arctic benthic invertebrate traits. Earth System Science Data 11:301–322. doi: 10.5194/essd-11-301-2019

Dekov V, Scholten J, Garbe-Schönberg CD, Botz R, Cuadros J, Schmidt M, Stoffers P. 2008. Hydrothermal sediment alteration at a seafloor vent field: Grimsey Graben, Tjörnes Fracture Zone, north of Iceland. Journal of Geophysical Research: Solid Earth 113. doi: 10.1029/2007JB005526

DNV-GL. 2017. Initial assessment of the ISF Iceland northern shrimp fishery (inshore and offshore). DNV-GL Business Assurance, Høvik, Norway.

Ellingsen K, Hewitt J, Thrush S. 2007. Rare species, habitat diversity and functional redundancy in marine benthos. Journal of Sea Research 58:291-301. doi: 10.1016/j.seares.2007.10.001

Guðmundsson G, Ottósson JG, Helgason G V. 2014. Botndýr á Íslandsmiðum (BIOICE). Náttúrufræðistofnun Íslands NÍ-14004. [In Icelandic]

Haynes EB, Wigley RL. 1969. Biology of the northern shrimp, *Pandalus borealis*, in the Gulf of Maine. Transactions of the American Fisheries Society 98:60–76.

Hiddink JG, Jennings S, Kaiser MJ, Queirós AM, Duplisea DE, Piet GJ. 2006. Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. Canadian Journal of Fisheries and Aquatic Sciences 63:721–736. doi: 10.1139/f05-266

Hillebrand H. 2004. Strength, slope and variability of marine latitudinal gradients. Marine Ecology Progress Series 273:251–267. doi: 10.3354/meps273251

Horsted SA, Smidt E. 1956. The deep sea prawn (*Pandalus borealis* Kr.) in Greenland waters. Meddelelser fra Danmarks fiskeri- og havundersøgelser Bind I.

ICES. 2019. ICES/NAFO Joint working group on deep-water ecology (WGDEC). ICES Scientific Reports 1:1–119. doi: 10.17895/ices.pub.5567

ICES. 2020. ICES/NAFO Joint working group on deep-water ecology (WGDEC). ICES Scientific Reports 2:1–188. doi: 10.17895/ices.pub.7503

Jónsdóttir IG, Bragason GS, Brynjólfsson SH, Guðlaugsdóttir AK, Skúladóttir U. 2017. Yfirlit yfir rækjurannsóknir við Ísland, 1988-2015. Northern shrimp research in Icelandic waters, 1988-2015. Marine and Freshwater Research in Iceland HV2017-007:1-92. [In Icelandic]

Meißner K, Brenke N, Svavarsson J. 2014. Benthic habitats around Iceland investigated during the IceAGE expeditions. Polish Polar Research 35:177–202.

Meißner K, Brix S, Halanych KM, Jazdzewska AM. 2018. Preface-biodiversity of Icelandic waters. Marine Biodiversity 48:715–718. doi: 10.1007/s12526-018-0884-7

MFRI. 2021. Northern shrimp *Pandalus borealis.* MFRI Assessment Reports, Marine and Freshwater Research Institute, Hafnarfjörður, Iceland.

Oksanen J et al. 2020. vegan: Community Ecology Package. R package version 2.5-7 [online] Available from: https://cran.r-project.org/package=vegan

Ólafsdóttir SH, Burgos JM, Ragnarsson SA, Karlsson H. 2020. Kóralsvæði við Ísland. Rannsóknir 2009-2012. Lýsing - útbreiðsla - verndun. Marine and Freshwater Research in Iceland HV2020-31:1–84. [In Icelandic]

Omarsdottir S, Einarsdottir E, Ögmundsdottir HM, Freysdottir J, Olafsdottir ES, Molinski TF, Svavarsson J. 2013. Biodiversity of benthic invertebrates and bioprospecting in Icelandic waters. Phytochemical Reviews 12:527–529.

Piepenburg D, Schmid MK. 1996. Brittle star fauna (Echinodermata: Ophiuroidea) of the arctic northwestern Barents sea: composition, abundance, biomass and spatial distribution. Polar Biology 16:383–392.

PolytraitsTeam. 2020. Polytraits: A data base on biological traits of polychaetes. LifewatchGreece, Hellenic Centre for Marine Research.

R Core Team. 2021. R: a language and environment for statistical computing. R foundation for statistical computing, Vienna. www.R-project.org/

Reiss H, Greenstreet SPR, Sieben K, Ehrich S, Piet GJ, Quirijns F, Robinson L, Wolff WJ, Kröncke I. 2009. Effects of fishing disturbance on benthic communities and secondary production within an intensively fished area. Marine Ecology Progress Series 394:201–213. doi: 10.3354/meps08243

Shumway SE, Perkins HC, Schick DF, Stickney AP. 1985. Synopsis of biological data on the pink shrimp, *Pandalus borealis* (Krøyer, 1838). FAO Fisheries Synopsis No. 144. 92 pp.

Sswat M, Gulliksen B, Menn I, Sweetman AK, Piepenburg D. 2015. Distribution and composition of the epibenthic megafauna north of Svalbard (Arctic). Polar Biology 38:861–877.

Wandel CF. 1899. Report of the voyage. The Danish Ingolf Expedidtion 1:1–21.

Watling L, Norse EA. 1998. Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. Conservation Biology 12:1180–1197.

Witman JD, Etter RJ, Smith F. 2004. The relationship between regional and local species diversity in marine benthic communities: A global perspective. Proceedings of the National Academy of Sciences 101:15664–15669. doi: 10.1073/pnas.0404300101

Woolley SNC, Tittensor DP, Dunstan PK, Guillera-Arroita G, Lahoz-Monfort JJ, Wintle BA, Worm B, O'Hara TD. 2016. Deep-sea diversity patterns are shaped by energy availability. Nature 533:393–396. doi: https://doi.org/10.1038/nature17937

Yesson C, Simon P, Chemshirova I, Gorham T, Turner CJ, Hammeken Arboe N, Blicher ME, Kemp KM. 2015. Community composition of epibenthic megafauna on the West Greenland Shelf. Polar Biology 38:2085–2096. doi: 10.1007/s00300-015-1768-y

Zhulay I, Iken K, Renaud PE, Bluhm BA. 2019. Epifaunal communities across marine landscapes of the deep Chukchi Borderland (Pacific Arctic). Deep Sea Research Part I: Oceanographic Research Papers 151:103065. doi: 10.1016/j.dsr.2019.06.011

Figure legends

Fig. 1. Sampling locations with camera (black dots) and with a bottom grab and shrimp trawl (stars). Numbers indicate the station number. The contour shows the distribution of the main northern shrimp fishing grounds in 2010-2015 and the effort (cumulative tow minutes per unit over these 6 years). The brown area shows the Kolbeinsey Ridge, which is a part of the active mid ocean ridge (from Emodnet).

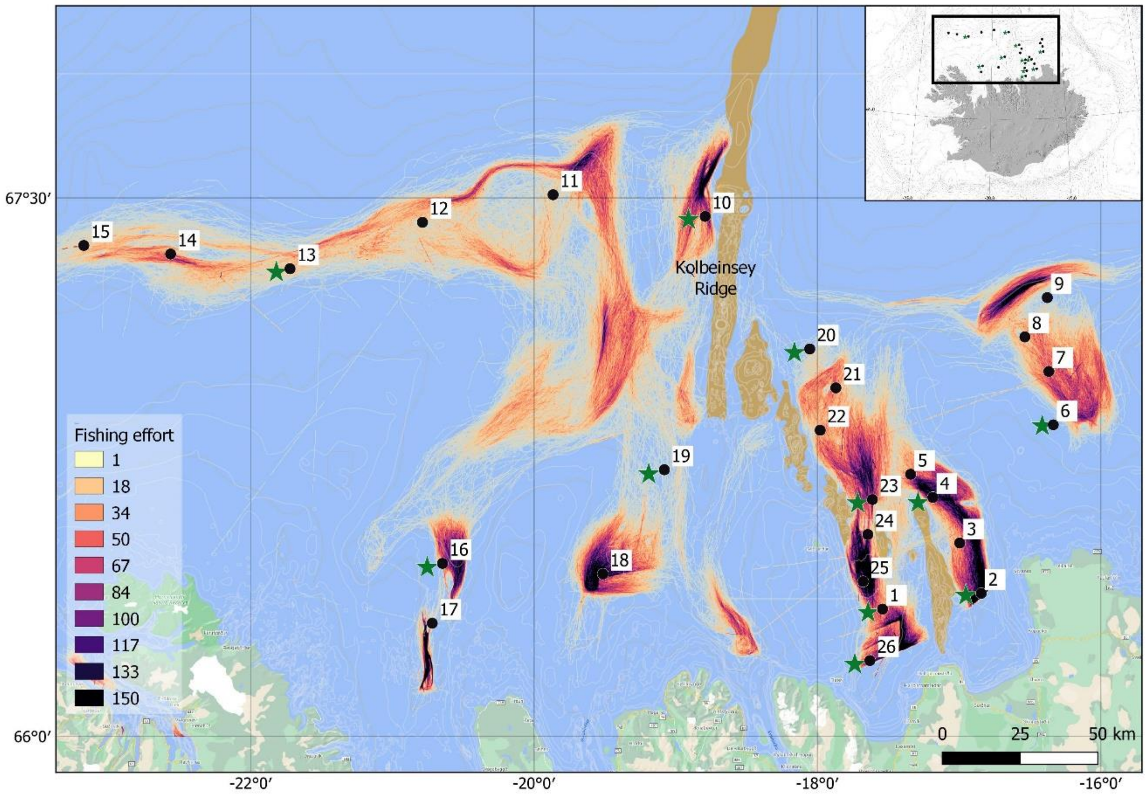


Fig. 2. Plots of the multidimensional scaling analysis (MDS) based on A) the grab samples and B) the image data. Points represent stations, with nearby stations having similar compositions. Taxa are positioned relative to the ordination and show the location in ordination space where these are most abundant. Grab data analysed at the family level. Central colours represent fishing effort (darker = greater effort), while the outer ring denotes depth and is darker for deeper stations. Image data is analysed at the class level. The larger dataset allows for environmental analysis, and there is no significant relationship between fishing effort and composition (red line). The blue lines are depth contours (relative to the stations positions in ordination space).

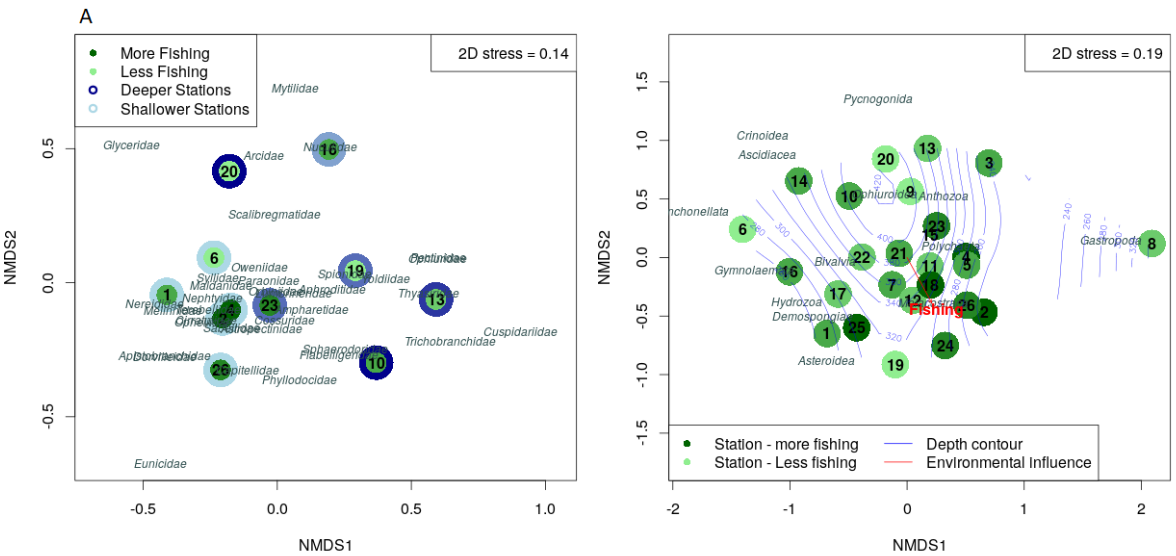
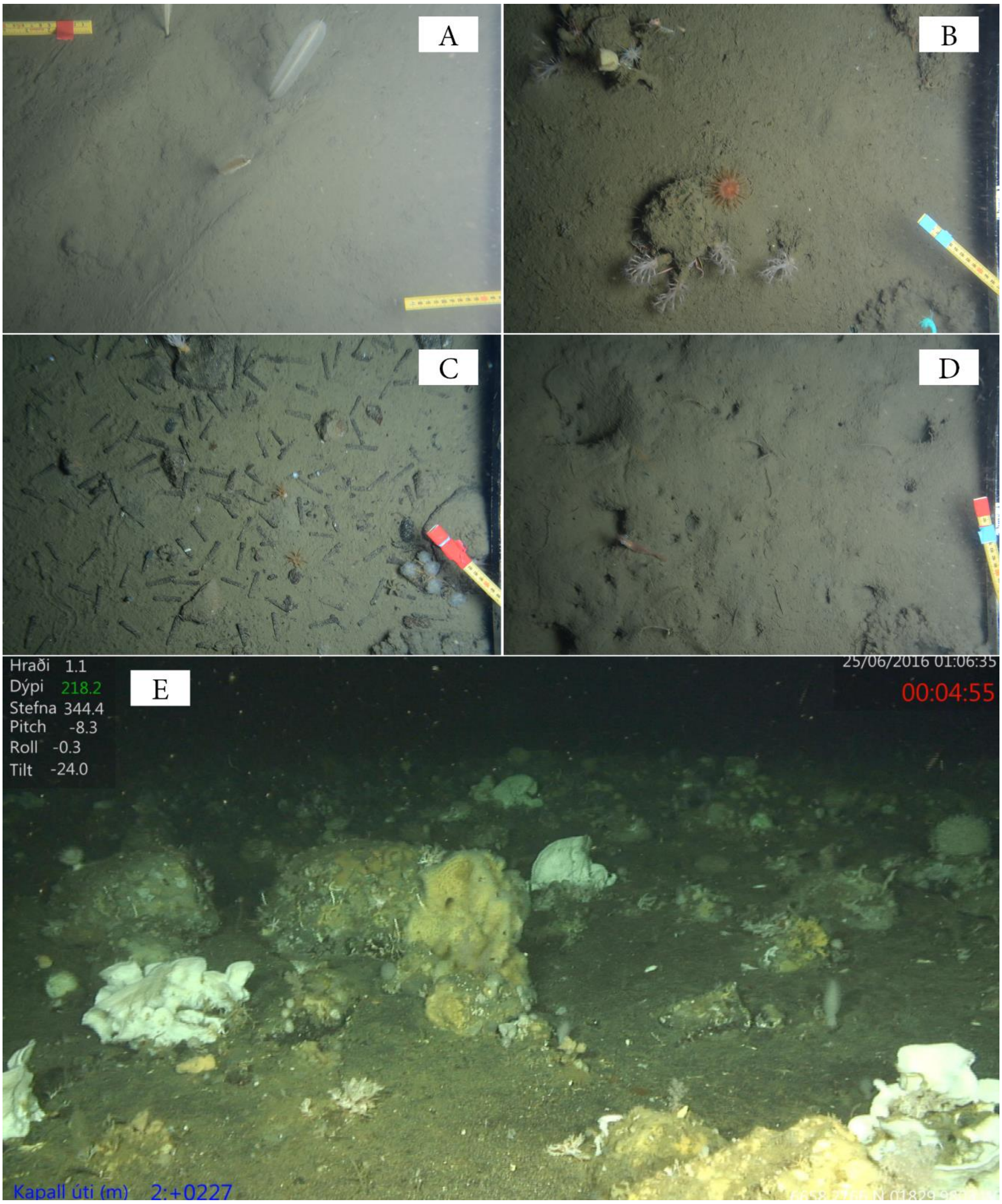


Fig. 3. Underwater photographs from the study area (A-D) and from Kolbeinsey Ridge (E). A) Virgulariidae sea pens on soft bottom station 4. B) Sediment covered cobbles with associated fauna (station 9). C) High density of *Nothria conchylega* (station 20). D) *Pandalus borealis* on soft sediment (station 26). E) Sponge community from the Kolbeinsey Ridge area.



Tables

Table 1. Sediment grain size, where sand is indicated as coarse, medium and fine. Fine is a combination of fine (0.125-0.25) and very fine (0.063-0.125).

Station	Sediment grain size mm				
	Granulate	Coarse	Medium	Fine	Silt/mud
	>2	0.5-2	0.25-0.5	0.063-0.25	<0.063
1	0.3	0.3	1.5	29.4	68.5
2	0.0	0.0	0.04	1.5	98.5
4	0.0	0.0	0.06	2.4	97.5
6	0.0	0.0	0.2	29.8	70.0
10	0.0	0.0	0.8	44.2	55.0
13	3.3	0.4	4.1	30.8	61.4
16	0.0	6.8	25	16.7	51.5
19	0.0	0.4	1.4	11.6	86.6
20	5.1	13.1	16.4	13.5	51.9
23	0.0	0.0	0.5	24.9	74.6
26	0.0	0.1	1.8	10.4	87.8

Table 2. Results of linear models testing the response of diversity to depth, fishing effort, temperature and percentage mud. Est. = estimate of parameter. Est. = parameter estimate. Err. = Standard error of parameter. t is the t value estimate. p(t) is the p-value associated with the relevant explanatory variable.

Dataset	Response	F stat.	R^2	p (model)	Depth				Fishing effort				Temperature				Percentage mud			
					est	err	t	p(t)	est	err	t	p(t)	est	err	t	p(t)	est	err	t	p(t)
Epifauna	Abundance	1.92	0.10	0.16	0.00	0.01	0.14	0.89	-0.09	0.08	-1.16	0.26	-0.18	0.32	-0.56	0.59				
	Taxon No.	2.70	0.18	0.07	0.02	0.01	1.86	0.08	-0.24	0.11	-2.10	0.05	0.68	0.48	1.42	0.17				
	Shannon H	1.13	0.02	0.36	0.00	0.00	1.32	0.20	-0.05	0.03	-1.37	0.19	0.23	0.14	1.69	0.11				
Infauna	Abundance	0.46	-0.28	0.77	0.00	0.01	0.03	0.98	-0.04	0.12	-0.35	0.74	0.26	0.62	0.42	0.69	-0.01	0.03	-0.20	0.85
	Taxon No.	1.35	0.12	0.35	0.02	0.05	0.51	0.63	0.37	0.38	0.98	0.37	2.07	1.99	1.04	0.34	0.08	0.11	0.76	0.48
	Abundance	1.59	0.19	0.29	0.00	0.01	0.28	0.79	0.06	0.06	1.09	0.32	-0.03	0.29	-0.11	0.92	0.01	0.02	0.39	0.71

Table 3. Fuzzy coding of the fauna from grab samples (infauna), images (epifauna) and by-catch (epifauna).

	LH1	LH2	LH3	LH4	LH5	LH6	MV1	MV2	MV3	MV4	FH1	FH2	FH3	FH4	FH5	FH6	SA1	SA2	SA3	SA4	EP1	EP2	EP3
Fauna from grab samples																							
Counts	36	11	34	49	12	7	21	60	31	26	57	25	33	23	31	10	69	31	29	2	61	39	7
%	46	14	43	62	15	9	28	79	41	34	74	33	43	30	40	13	97	44	41	3	82	53	10
Fauna from images																							
Counts	22	7	6	16	7	10	13	13	18	12	14	4	17	14	22	7	20	19	13		12	24	5
%	73	23	20	53	23	33	50	50	69	46	48	14	59	48	76	24	91	86	59	0	48	96	20
By-catch fauna from ISS																							
Counts	9	3	4	8	5	4	8	7	10	4	9	3	10	8	11	5	13	14	7	1	7	14	1
%	69	23	31	62	39	31	50	44	63	25	53	18	59	47	65	29	81	88	44	6	44	88	6

Appendices

Appendix 1. Station list with coordinates (decimal degrees), depth bottom temperature and effort value (cumulative tow minutes per 0.01 nm unit square).

Station	Latitude	Longitude	Depth (m)	Bottom temperature (°C)	Effort
1	66.36274	-17.5403	239	4.4	44
2	66.40728	-16.8439	223	4.0	154
3	66.5493	-16.9953	239	3.9	35
4	66.67696	-17.1848	257	3.9	106
5	66.74154	-17.3416	251	3.9	49
6	66.87921	-16.3349	241	4.1	0
7	67.02666	-16.3661	352	1.3	38
8	67.12159	-16.5356	362	0.8	19
9	67.22931	-16.3773	400	0.5	3
10	67.45001	-18.7923	442	1.1	54
11	67.50877	-19.8661	398	0.8	24
12	67.43404	-20.7879	357	0.9	12
13	67.30797	-21.723	353	1.8	14
14	67.34795	-22.566	345	1.2	46
15	67.37126	-23.1787	424	1.2	13
16	66.49178	-20.6464	302	3.9	33
17	66.32272	-20.7189	277	4.8	8
18	66.46194	-19.5141	275	4.7	145
19	66.75417	-19.0805	306	1.4	4
20	67.08849	-18.0542	402	0.4	1
21	66.98131	-17.8701	425	1.4	36
22	66.86394	-17.9806	344	1.9	21
23	66.671	-17.6118	347	2.7	73
24	66.57296	-17.6444	340	2.5	84
25	66.44079	-17.6777	330	3.8	142
26	66.21676	-17.6296	212	4.6	78

Appendix 2. List of traits selected for this study adapted from Arctic Trait Database (Degen & Faulwetter, 2019).

Living habit:		
Free living	(LH1)	Able to move freely within and/or on the sediments
Crevice dwelling	(LH2)	Adults are cryptic
Tube dwelling	(LH3)	Tube may be lined with sand, mucus or CaCO3
Burrowing	(LH4)	Species inhabiting permanent or temporary burrows
Epi/endi zoic/phytic	(LH5)	Living on or in other organisms
Attached	(LH6)	Adherent to a substratum
Adult movement:		
Sessile/none	(MV1)	No movement as adult
Burrower	(MV2)	Movement in the sediment
Crawler	(MV3)	An organism that moves along the substratum via movements of its legs, appendages (e.g. parapodia and chaetae) or muscles
Swimmer (facultative)	(MV4)	Movement above the sediment
Feeding habit:		
Surface deposit feeding	(FH1)	Active removal of detrital material from the surface
Subsurface deposit feeding	(FH2)	Removal of detrital material from within the sediment matrix
Filter/suspension feeder	(FH3)	Sponge, coral, hydrozoa, bivalves
Opportunist/scavenger	(FH4)	An organism that can use different types of food sources/an organism that feeds on dead organic material
Predator	(FH5)	An organism that feeds by preying on other organisms
Parasite/commensal/symbiotic	(FH6)	An organism that lives in or on the host, from which it obtains food and other requirements; or an organism containing symbionts
Substratum affinity:		
Soft	(SA1)	Soft substrata, sand or mud
Hard	(SA2)	Hard substrata, rock, gravel
Biological	(SA3)	Epizoic or epiphytic life style
None	(SA4)	Species is hyper/supra benthic and has no affinity for a certain substrate
Environmental position:		
Infauna	(EP1)	Lives in the sediment
Epibenthic	(EP2)	Lives on the surface of the seabed
Hyper-benthic	(EP3)	Living in the water column, but feeds on the bottom; bentho-pelagic

Appendix 3. List of traits specifically for polychaetes based on Polytrait database (PolytraitsTeam, 2020). Numbers for modulates are added.

Feeding type:	**No**	
Predator	1	An organism that feeds by preying on other organisms, killing them for food
Suspension feeder	2	Any organism which feeds on particulate organic matter, including plankton, suspended in the water column
Non-selective deposit feeder (detrivore)	3	An organism that feeds on mud or sand and may show a little discrimination in the size or type of particles eaten
Selective deposit feeder (detrivore)	4	Some deposit feeders do not ingest sediment haphazardly but use their palps or buccal organs to sort organic material from the sediment prior to ingestion
Deposit feeder (selective or non-selective) (detrivore)	5	"Umbrella term". Any organism which feeds on fragmented particulate organic matter from the substratum
Omnivore	6	Organisms which feed on a mixed diet including plant and animal material
Scavenger	7	Any organism that actively feeds on dead animals
Herbivore	8	An animal that feeds on plants or algae, or parts of them
Mobility of adult:		
Crawler	1	An organism that moves along on the substratum via movements of its legs, appendages (e.g. parapodia and chaetae) or muscles
Burrower	2	An organism that lives or moves in a burrow in soft sediments
Swimmer	3	An organism that moves through the water column via movements of its fins, legs or appendages, via undulatory movements of the body or via jet propulsion
Non-motile / semi-motile (sedentary)	4	Permanently attached to a substratum (non-motile) or capable of movement across (or through) it (semi-motile)

Appendix 4. List and abundance of specimens (per m^2) in the grab samples.

		Station										
		1	2	4	6	10	13	16	19	20	23	26
Nematoda		25				50	33.3	25	25	41.7		8.3
Nemertea		8.3	58.3	25	83.3	25	8.3	33.3	50	8.3	41.7	41.7
Porifera								25				
Cnidaria												
	Actinaria										8.3	
	Hydrozoa									8.3		8.3
Annelida												
Oligochaeta								16.7				
Polychaeta			25							16.7	8.3	
Scolexcida	Capitellidae	50	25	16.7	33.3	100					33.3	33.3
	Cossura longocirrata	16.7	16.7	16.7	25		41.7		8.3			8.3
	Maldanidae	50		100	225	16.7	8.3	41.7		16.7	41.7	66.7
	Maldane sarsi	1225	100	625	508.3	33.3	8.3	91.7	50		83.3	58.3
	Praxillella											33.3
	Praxillella gracilis											16.7
	Praxillella praetermissa	33.3	16.7									
	Opheliidae	8.3						8.3				75
	Paraonidae	225	133.3	141.7	8.3	50	58.3	58.3	41.7	66.7	83.3	83.3
	Aricideasuecica	33.3	25	33.3	33.3	8.3	33.3	8.3	16.7	16.7	16.7	16.7
	Scalibregmatidae		8.3		16.7			25	8.3		8.3	
	Scalibregma inflatum		25	16.7	8.3	8.3				25		
	Scoloplos armiger	108.3	8.3	116.7	58.3	116.7	41.7	25	41.7	83.3	166.7	83.3
Eunicida	Dorvilleidae		25									
	Eunicidae											16.7
	Lumbrineridae			58.3								
	Scoletoma fragilis	241.7	125	83.3	75	225	166.7	66.7	108.3	108.3	291.7	208.3
	Nothria conchylega									41.7		
Sabellida	*Galathowenia oculata*	5666.7	16.7	16.7	2041.7	216.7	1575	391.7	16.7	66.7	441.7	41.7
	Owenia fusiformis	2700				8.3		16.7			16.7	
	Oweniidae				583.3							
	Sabellidae	41.7	141.7	116.7	66.7		58.3	25			108.3	316.7
Phyllodocida									8.3			
	Aphroditidae	8.3			8.3		16.7					
	Ceratocephale loveni											25
	Eteone longa	8.3	8.3			25						
	Glyceralapidum									8.3		
	Glyceridae	8.3										
	Phyllodocidae										8.3	
	Nephtyidae		50	16.7	41.7					8.3	16.7	16.7
	Nephtys										8.3	
	Nereididae	12.5	83.3	66.7	58.3					16.7	16.7	
	Pholoe minuta	8.3								25		
	Syllidae			8.3	16.7							
	Exogone (Exogone) veruga	708.3		200	41.7							
	Syllis cornuta	8.3										
	Sphaerodoridae	16.7	25	8.3		8.3	33.3					
Spionida	Spionidae		25	33.3	8.3	33.3	100	491.7	291.7		66.7	8.3
	Apistobranchus tullbergi		8.3									
	Polydora	16.7	50	16.7	8.3							
	Prionospio						2308.3	416.7	550	458.3	825	666.7
	Prionospio steenstrupi	158.3	533.3	333.3		933.3						
Terebellida		25	50	8.3							8.3	25

	Ampharetidae			33.3	8.3		16.7					
	Bradabyssavillosa				16.7	8.3						
	Cirratulidae	8.3	8.3	75	66.7						8.3	
	Chaetozone								8.3			8.3
	Chaetozone setosa	25	8.3								25	8.3
	Flabelligeridae					8.3						
	Laphania boecki				8.3							
	Melinna cristata	8.3		25	25					8.3	8.3	41.7
	Melinna islandice										8.3	
	Pista									8.3		
	Terebellidae	75	50	33.3	8.3	33.3				8.3		
	Terebellides stroemii						83.3					16.7
Sipuncula				8.3	33.3	16.7	25		25	183.3		
Arthropoda												
	Amphipoda	25		16.7	16.7	25	25	16.7	8.3	25	25	8.3
	Copepoda	16.7	8.3	8.3	8.3	16.7			25	8.3	16.7	
	Cumacea	50	8.3	8.3	25			8.3		8.3	16.7	33.3
	Isopoda				16.7					16.7		
	Ostracoda				8.3		8.3	8.3		16.7		16.7
	Pycnogonida									8.3		
	Tanaidacea					8.3	8.3		8.3	16.7		
Mollusca												
	Aplacophora		25		8.3	16.7			8.3			
	Astarte						25					
	Bathyarca	8.3			16.7			8.3	8.3	8.3		
	Bivalvia	225	208.3	50	133.3	300	333.3	100	158.3	83.3	16.7	33.3
	Caudofoveata									25		
	Cuspidaria					8.3	33.3		8.3			
	Dacrydium				8.3			8.3				
	Ennucula							8.3			8.3	
	Pecten		16.7	33.3	8.3	216.7	316.7	58.3	16.7	41.7	16.7	16.7
	Portlandia			8.3								
	Scaphopoda		75					8.3				
	Thyasira	8.3		8.3	8.3							
	Thyasira flexuosa					216.7	525	8.3	183.3	16.7	8.3	
	Bryozoa	8.3	100		100					50		41.7
Echinodermata												
	Astropecten irregularis										8.3	
	Ophiura sarsi	8.3				8.3	33.3	8.3				
	Ophiuroidea					8.3	50		8.3	8.3		8.3

Appendix 5. Species richness and abundance from image analysis.

		Station																									
	Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**
Nemertea																											
	Nemertea unid.														1						1	1					
Cnidaria																											
	Ptychogastria polaris																						1				
	Octocorallia															0					3						
	Actiniaria									2				1		1											
	Ceratocaulon wandeli									5											6						
	Ceriantharia											4	0														
	Corymorpha sp.	1					1																				
	Gersemia sp.										1											1					
	Halcampa cf. *arctica*							3			1		1	1		6	1				5	2	1	1			
	Virgularia sp(p).			1	5	2													1								
Porifera																											
	Porifera unid.						2			1																	
	Demospongiae														1												
	Hymedesmia sp.									1																	
	Semisuberites cribrosa																1	1									
	Stylocordyla borealis									1																	
	Suberites sp.	1						1																		1	
Annelida																											
	Polychaeta	1	48	1	1	2		1				1					1						1	6		1	52
	Errantia						1			1																	
	Nothria conchylega									405											425						
	Sabellida									4					1			2						4			
Arthropoda																											
	Pycnogonida																				3						

	Crustacea									1		1														
	Peracarida		3		1		4					1			2			1			1	1		1	1	
	Amphipoda			5			3		1		1	1			1		1									
	Eusirus holmi										1															
	Asellota													1									1		1	
	Caridea	1		1	6		2			1	1	2			1		1		1						3	
	Pandalus sp.																	2			1					4
	Pandalus borealis	1																			4					
Mollusca																										
	Bivalvia									3																
	Buccinidae							1			1												1			
	Gastropoda											1									1					
	Pectinida sp.																								1	
Echinodermata																										
	Crinoidea													2												
	Hymenaster sp.																		1							
	Pontaster sp.															1										
	Ophiuroidea					2	1		57	21	2	6	26	105	20	9	6	1	2	253	17	9	4			
	Ophioscolecida																				2	1				
	Ophioscolecidae								2																	
	Ophiuridae												5	31	8		4					1				
	Ophiacantha sp.															3	4									
	Ophiura sp.					2	3		2	24		3	22	90	23		1		4	3		9	3		1	1
	Ophiura robusta													2												
	Stegophiura sp.												1													
Bryozoa																										
	Bryozoa-branching								1													5				
	Caberea ellisii															1	1									
	Reteporella sp.					4																				
Brachiopoda																										

	Brachiopoda unid.						2	2				4	3						2	11		2	4		1		
	Terebratula sp.						1																				
Tunicata																											
	Aplousobranchia						2								4												
	Kukenthalia borealis																				5						
	Didemnidae						2																				
	Colonial tunicate						2			2																	
	Grand Total	**5**	**51**	**2**	**12**	**11**	**21**	**20**	**1**	**484**	**52**	**15**	**19**	**56**	**238**	**62**	**17**	**21**	**7**	**19**	**704**	**32**	**33**	**20**	**2**	**9**	**57**
	Taxa number	**5**	**2**	**2**	**4**	**4**	**11**	**9**	**1**	**14**	**7**	**8**	**10**	**6**	**10**	**9**	**7**	**9**	**5**	**5**	**9**	**10**	**10**	**7**	**2**	**7**	**3**

Appendix 6. Taxa identification and counts from the images by-catch epifauna. VME indicator species are marked with x. C=Class, F=Family, G=Genus, O=Order, S=Species.

		Station											
Taxa	**VME ind.**	**6**	**4**	**2**	**1**	**23**	**23**	**20**	**19**	**16**	**10**	**13**	**Total**
2015													
Amphipoda [O]				1									1
Aplousobranchia [O]						1							1
Axinellidae [F]	x	1											1
Bathyarca [G]											1		1
Bathyarca glacialis [S]						6			28				34
Brada inhabilis [S]												1	1
Buccinidae [F]											1		1
Cladorhiza [G]	x									2			2
Colus islandicus [S]										1			1
Craniella cranium [S]												1	1
Ctenodiscus crispatus [S]		1	1		1	6				3			12
Duva florida [S]											1		1
Echinoidea [C]		1											1
Hormathiidae [F]											1		1
Mycale sp.[G]	x											1	1
Ophiura sarsii [S]					1		1		1				3
Ophiurida [O]									1				1
Ophiuridae [F]												1	1
Phakellia sp.[G]	x									2			2
Polychaeta [C]						1							1
Polymastia thielei [S]												1	1
Polynoidae [F]												1	1
Porifera [P]				4	4		1	1					10
Pycnogonida [C]											1	2	3
Sabellida [O]												1	1
Grand Total		**3**	**1**	**5**	**6**	**14**	**2**	**1**	**30**	**8**	**5**	**9**	**84**
Number of taxa		3	1	2	3	4	2	1	3	4	5	8	25