UiT The Arctic University of Norway

Faculty of Biosciences, Fisheries and Economics, Department of Arctic and Marine Biology

Distribution, reproductive ecology, and colouration of the Arctic skate *Amblyraja hyperborea* (Collett, 1879) in the North Atlantic Ocean

Rebeca López Climent

BIO-3950 Master's Thesis in Biology, June 2021

Faculty of Biosciences, Fisheries and Economics
Department of Arctic and Marine Biology

Distribution, reproductive ecology, and colouration of the Arctic skate *Amblyraja hyperborea* (Collett, 1879) in the North Atlantic Ocean

Rebeca López Climent

–

Master of Science in Biology – Marine Ecology and Resource Biology

June 2021

Supervisor:

Arve Lynghammar, UiT - The Arctic University of Norway

Table of Contents

List of Tables

List of Figures

1 Abstract

Amblyraja hyperborea is the cartilaginous fish with the widest distribution across the Arctic seas and shelves and yet, large parts of its biology remain unknown. In a changing climate where the ice cover in the polar regions is retreating and fisheries are expanding northward, studying poorly known species is more important than ever. To provide a more exhaustive understanding of this species, horizontal and vertical distributions and temporal trends in the North Atlantic Ocean were evaluated, length at first maturity (L_{50}) was estimated and potential nursery grounds were searched for. Additionally, the most common patterns of ventral colouration were described, and the variation of the colouration coverage was investigated. A transboundary approach was applied with data provided by four countries. *Amblyraja hyperborea* was found in every area surveyed, though not being evenly distributed and clustering along the shelf breaks, and the abundance observations of was found to decrease below 65ºN. The vertical distribution did not depend on sex nor size, and the majority of the observations were made from 200 to 1000 m depth. No conclusive temporal trends could be defined. The estimated L_{50} for females was of 70.5 cm total length (TL) and for males of 66.8 cm TL, and some indices of potential nursery grounds were found in Iceland and the Barents Sea. Lastly, distribution was found to play a role in the ventral colouration coverage, with lighter individuals being dominant in the eastern side of the study area, and darker individuals being most present in the western side. Overall, the transboundary approach was successful in the in-depth study of *A. hyperborea,* even with the limitations of the data. This study can serve as a baseline for future studies regarding other poorly known transboundary species.

2 Introduction

Amblyraja hyperborea (Collett, 1879), commonly known as Arctic skate, is a marine species of skate that belongs to the Rajidae family. It has been found at depth ranging from 92 to 2925 m (Mecklenburg *et al.*, 2016), being most commonly seen between 300 to 1500 m (Whitehead *et al.*, 1984), and in cold waters ranging from -1 to 4ºC (Dolgov *et al*., 2005; Mecklenburg *et al*., 2016). It is a benthic species (Coad & Reist, 2004), typically meso- to bathybenthic, associated to muddy substrate (Mecklenburg, 2018) and reaches at least 92 cm of total length (TL) and 5.2 kg (Wienerroither *et al.*, 2011). It is also known to be an oviparous species and the hatching size has been recorded to vary between 15 and 18 cm TL (Bigelow & Schroeder, 1953; Last *et al.*, 2016; Mecklenburg *et al.*, 2018).

This species has the widest distribution among cartilaginous fishes across the Arctic seas and shelves (Lynghammar *et al.*, 2013). From all the chondrichthyan species found in the Arctic Ocean and adjacent seas, only *A. hyperborea* is considered a true Arctic species (Andriashev & Chernova, 1994; Lynghammar *et al.*, 2012). It can be found in the Arctic ocean basins and along continental slopes from eastern Canada at Jones Sound, Smith Sound, and Baffin Bay to the Greenland, Norwegian, Barents, Kara, and Laptev Seas; as well, at the Chukchi and Beaufort Seas from the Chukchi Borderland to Banks Islands (Mecklenburg *et al.*, 2018). It has also been suggested to have a more cosmopolitan distribution, being found on both hemispheres in cold water regions, and the vernacular name of "Boreal skate" was coined (Last *et al.*, 2016). Despite this, *A. hyperborea*'s taxonomy is still unresolved, and remains to be thoroughly investigated (Mecklenburg *et al.*, 2018). In any case, it is clear that *A. hyperborea* has a wide distribution range. In addition to distribution, the only other studies carried out on *A. hyperborea* have been diet studies (Andriyashev, 1954; Bjelland *et al*., 2000; Dolgov, 2005; Jónsson *et al*., 2006; Ebert & Bizzarro, 2007; Byrkjedal *et al*., 2015) and movement behaviour studies (Peklova *et al*., 2014), leaving large gaps in their biology.

Historically, the polar regions have been relatively safe from large-scale human settlement and disturbance thanks to the harsh environment. But with a changing climate, these regions are getting warmer and providing a better environment for fisheries to rapidly expand as sea ice cover continues to retreat (Schrank, 2007). Given the large data deficiencies for many Arctic fish species, regional fisheries development is of concern; however, it also offers the opportunity to incite pro-active fisheries management before the expansion of the fisheries take place (e.g., Peklova *et al*., 2014). In order to be able to adopt such precautionary approaches, ecology data of little-known Arctic marine species, such as *A. hyperborea*, is of great importance. These data include information about spatial distribution (horizontal, vertical and temperature) in order to resolve habitat use, multi-species overlap distributions and the scale of species-fisheries interactions, together with temporal distribution as to elucidate how environmental parameters affect species dispersal, regional relative abundance and movement; and information about reproductive effort, size at maturity (L_{50}) and nursery grounds giving insight into the reproductive ecology and resilience of the species.

Given its wide distribution range, *A. hyperborea* falls into the category of transboundary species, these are species that occur within the Exclusive Economic Zone (EEZ) of two or more neighbouring countries (Baudron *et al*., 2020; Palacios-Abrantes *et al*., 2020). Species of this category are subjected to many different policy, legal and institutional structures, and management and governance regimes as countries' territories they inhabit, which makes them difficult to assess. In order to fill these gaps in knowledge about *A. hyperborea*'s spatiotemporal and ecological biology, transboundary assessments are required, meaning there is a need to combine surveys across international boundaries (Ramesh *et al*., 2019; Baudron *et al*., 2020). If survey data is properly combined, it may allow near-seamless comparisons of species distribution and abundance in space and time (Maureaud *et al*., 2020). However, this will not be without challenges. In the case of demersal commercial species, their habitats are only partially covered by surveys since they are designed to sample soft bottoms or mostly shallow continental shelves (Maureaud *et al*., 2020). Other challenges highlighted by Maureaud *et al*. (2020)'s study are the differences in formatting and languages used in the data collection process, and the lack of user expertise on the survey that can limit the ability of using the data appropriately, though this can be mitigated somewhat through open data principles. When studying demersal non-commercial species like *A. hyperborea*, more challenges arise. Historically, a scientific surveys' primary purpose was to provide fishery-independent data to assess commercially important species and their populations. Only in recent years has the purpose been extended to multidisciplinary ecosystem monitoring. Moreover, scientific surveys are expensive, which means that resources allocation is driven by priority. This usually translates to a lack of experts on non-commercial species and thus, in poorer quality data collection.

Amblyraja hyperborea's external morphology is one of this species characteristics that has previously been speculated about (Bigelow & Schroeder, 1953; Sulak *et al*., 2009; Ebert, 2014), but of which no studies have been carried out. The external morphology of *A. hyperborea* is characterized by a grey to brown dorsal side, often with light and dark spots, and a blotched ventral side. These blotches are dark grey to black in colour and over a white background, with their distribution and coverage largely variable among individuals. This colouration trait is not exclusive to *A. hyperborea*. Other studies have observed similar colourationpatterns in other species of the same genus [e.g., *A. jenseni* (Sulak *et al*., 2009; Orlov & Cotton, 2015, Last *et al*., 2016), *A. georgiana*, *A. doellojuradoi*, *A. taaf*, *A. radiata*, *A. reversa*, *A. frerichsi* (Last *et al*., 2016)]. Despite it being a common trait within the genus, *A. hyperborea* together with *A. jenseni* seem to present greater variability between individuals, ranging from all white to completely dark ventral surfaces. For *A. hyperborea*, the ventral colouration has been suggested to have changes with ontogeny, with smaller individuals being lighter –this is, with less blotches– and larger individuals being darker (Sulak *et al*., 2009; Ebert, 2014). This premise was also suggested for *A. jenseni*, (Bigelow & Schroeder, 1953; Sulak *et al*., 2009). Orlov & Cotton (2015) found no ontogenetic explanation for the variability among individuals. Instead, their results provided insight into the geographical variation in colouration of *A. jenseni*. In their study, Orlov & Cotton (2015) categorized the ventral coloration into “light” and “dark” morphotypes and found that “light” morphs appeared in the North-East and North-West Atlantic, and “dark” morphs appeared in the Mid-Atlantic ridge. Even though the number of individuals used for this study was significantly larger than in previous studies, it is worth keeping in mind it was still low (n = 22).

Usually, pelagic fishes present a countershading colouration to hide better from other organisms (Ruxton *et al*., 2004). This kind of camouflage extends to benthic and deep-water fish shifting dorsal colours from greys to colours like the grounds they inhabit (Carrier *et* al., 2012) and ventral sides remaining paler as there is no need to invest energy in them as it is facing or in contact with the ocean floor. But there are always exceptions to the norm and some species will present darker specks on light background on their ventral side, like we observe in some species of the Myliobatidae family (Marshall *et al*., 2009), which is used by researchers as a natural marking for individual identification. Additionally, it is known that colouration patterns in for communication, warning and sexual recognition too (Protas & Patel, 2008). An example of this is how the polychromatism in Midas cichlid *Cichlasome citrinellum* can affect the communication of aggressive and mating behaviour and how this polychromatism is directly caused by the clearness of the lake they live in (Barlow, 1983). Thus, different colouration patterns may in part depend on the environment and the communicative necessities of the species.

Within the present project the aim was to further our understanding of *A. hyperborea*'s biology, specifically aiming to (1) describe the distribution (horizontal and vertical) and temporal patterns over the North Atlantic range of the species, (2) estimate the length at maturity and search for potential nursery grounds, and (3) describe the variation and the most common patterns of the ventral colouration. An additional goal of this study was to explore the potential that large datasets can have to investigate the ecology of species of low commercial value.

3 Materials and Methods

3.1 Study area

The area of study covers part of the North Atlantic Ocean and part of the Arctic Ocean, from 73ºW to 86ºE, and from 60ºN to 83ºN (**Figure 1**). The bathymetry of this area is mainly characterized by rather shallow continental shelves that end on steep slopes where the ocean depth increases abruptly from less than 200 m to approximately 4000 m in the central area of the North Atlantic Ocean. The continental shelf of West Greenland is separated from that of Labrador and Baffin Island by a narrow strip of deep water the (Labrador Sea and Baffin Bay), and Iceland sits astride the Mid-Atlantic Ridge and is surrounded by a broad region of the shallow ocean. This shallow zone forms a broad ridge extending across the ocean from Greenland to the Faroe Islands (Fitton & Larsen, 2001). Off the northern coast of Norway and Russia, the shelf is relatively shallow and uniform, throughout the entirety of the Barents Sea has an average depth of 230 m (Ozhigin *et al*., 2011).

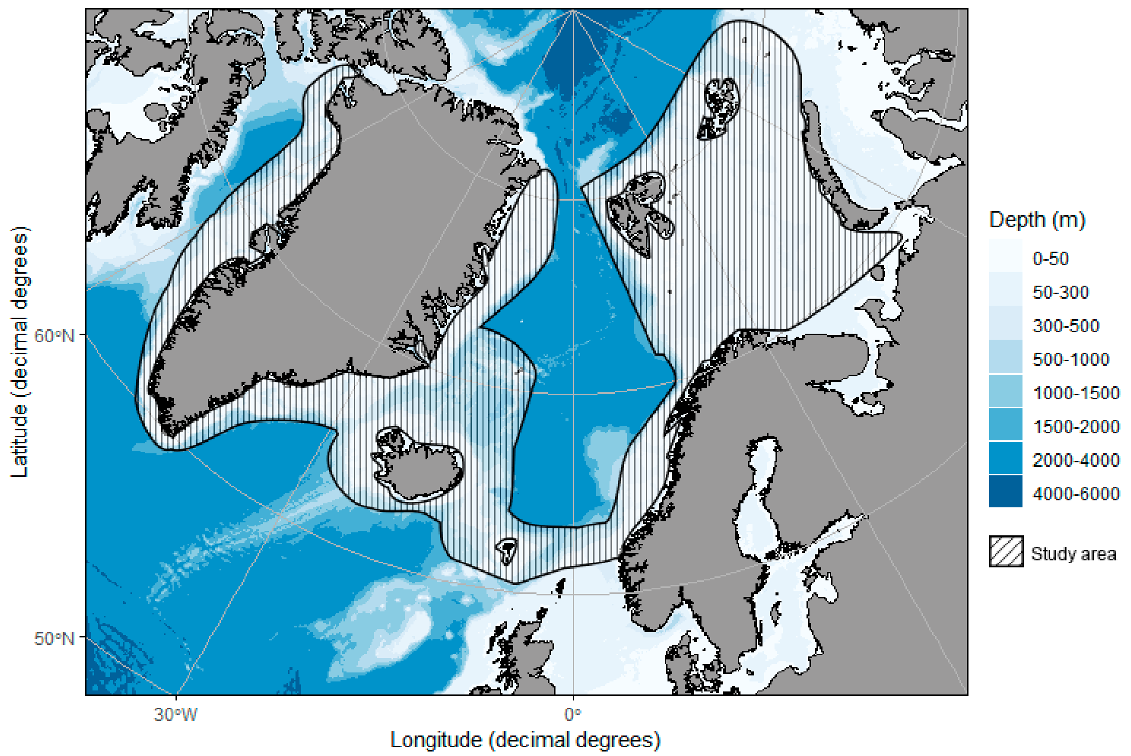


Figure 1. *Map of northeast Atlantic Ocean. Shading showing the study area of the present project.*

3.2 Data and analysis

Bottom trawl data from 13 scientific surveys and one commercial vessel using longline were provided by multiple research entities located in waters of several of the countries of the North Atlantic Ocean inhabited by *A. hyperborea* (**Table 1**). The data consisted of 3210 individuals over the span of 12 years (2009-2020), and each was recorded with date, geographical location, and depth of the capture, as well as total length (TL) of the individuals. As evident from **Table 1**, the time series were of unequal length for each of the surveys. Nearly 80% of the individuals were sexed, and maturity stage was available for 26% of the data, of which the 42% was from the Norwegian data (Institute of Marine Research and UiT – The Arctic University of Norway), and the 58% was from the Icelandic data. Individual weight was available for a portion of the data, but its use was dismissed because TL was available for all individuals, and it represented the individuals more accurately. Bottom temperature was only available from the Greenlandic and Faroese data. However, this variable was not used for any of the analyses. Only presence data was considered for this study.

Given the different origins of the data and the different aims the surveys, the information available was heterogeneous among them. In this regard, three separate subsets were created based on the strengths of each individual survey in order to meet the requirements for the (1) analysis of the species' distribution and temporal trends, (2) reproductive ecology, and (3) ventral colouration. These subsets are defined on the following subsections.

Table 1. *Summary of the surveys used for the assessment of* A. hyperborea *in the North Atlantic Ocean. Information about the providers, area covered and aim of each survey are provided, as well as mesh size used and number of observations (N).*

Provider	Survey	Area covered	Aim	Years	Mesh size	N	Contact person
Greenland Institute of Natural Resources, Greenland	Greenland Shrimp and Fish Survey	West and east Greenland shelf	*Pandalus* sp, *Gadus morhua*, *Sebastes* spp	2009-2019	20 mm	157	Julius Nielsen
	Greenland deep-water survey	West and east Greenland shelf and slope	*Reinhardtius hippoglossoides*	2009-2019	30 mm	1250	
Marine and Freshwater Research Institute, Iceland	IS-SMH	Shelf and shelf break around Iceland	*Reinhardtius hippoglossoides*, *Gadus morhua*, *Melanogrammus aeglefinus*, *Sebastes* spp	2009-2019	42 mm	983	Klara Jakobsdóttir
Faroe Marine Research Institute, Faroe Islands	Greenland halibut survey	Slope of Faroe Plateau	*Reinhardtius hippoglossoides*	2009-2019	135 mm	114	Hannipoula Olsen Lise Helen Ofstad
	Deep-water survey	Mainly the Banks southeast of Faroes	Ecosystem overview with focus on: *Gadus morhua*, *Melanogrammus aeglefinus*, *Pollachius virens*	2009-2019	40 mm	27	
	Faroe Plateau summer survey	Faroe Plateau		2009-2019	40 mm	1	

Table 1. *Summary of the surveys used for the assessment of* A. hyperborea *in the North Atlantic Ocean. Information about the providers, area covered and aim of each survey are provided, as well as mesh size used and number of observations (N). (Continuation)*

Provider	Survey		Area covered	Aim	Years	Mesh size	N	Contact person
Institute of Marine Research, Norway	Egga	Nor	Northern outer shelf and upper slope of Norway (68 – 80º N)	*Reinhardtius hippoglossoides*, *Sebastes* spp	2009, 2011, 2013, 2015, 2017, 2019	20 mm	381	Elvar H. Hallfredsson
		Sør	Southern outer shelf and upper slope of Norway (62 – 73.5º N)		2010, 2012, 2014, 2016, 2018	20 mm	54	
	Joint Norwegian/ Russian Ecosystem Survey	Norway	Barents Sea	Ecosystem based approach with focus on commercial species	2009-2019	20 mm	696	Herdis Langøy Mørk
		Russia			2009-2020	20 mm	89	Thomas de Lange Wenneck
	Environmental survey in Jan Mayen		Jan Mayen ocean ridge	Benthos and deep-sea fish	2011	20 mm	21	Petter Fossum
	MarBank		Northwest off Svalbard	Ecosystem overview	2011	20 mm	7	Kjersti Lie Gabrielsen
UiT-The Artic University of Norway	TUNU		North-east Greenland (70 – 78º N)	Euro-Arctic marine fish fauna at large	2010, 2011, 2013, 2017	20 mm	33	Arve Lynghammar
	–		South-west Uummannaq, Greenland*	*Reinhardtius hippoglossoides*	2014	–	30	Kim Præbel

*The individuals from the south-west Uummannaq do not come from a bottom trawl scientific survey, but from a commercial vessel from area of west Greenland with longline.

In order for the data to be comparable between surveys, standardization was required. Sex was coded with “f” for females, “m” for males, and “NA” when sex was not available as a standard. A guide to the standardization is presented in **Table 2**. All the data apart from of that provided by the UiT – The Arctic University of Norway (UiT) needed to be converted.

Table 2. *Sex variable conversion chart. GINR: Greenland Institute of Natural Resources, Greenland; MFRI: Marine and Freshwater Research Institute, Iceland; FMRI: Faroe Marine Research Institute, Faroe Islands; IMR: Institute of Marine Research, Norway.*

Standard	GINR	MFRI	FMRI	IMR
f	F	2	1	1
m	M	1	2	2
NA	U	NA	NA	NA

Generally, skates have little commercial value and, so, none of the surveys used in this study were designed to catch them. These scientific surveys are often aimed towards the assessment of commercial species stocks in a fishery-independent way, and fewer are designed to give a general overview of the state of the ecosystem surveyed. As shown in **Table 1**, of the 13 surveys used for this study, half of them targeted commercial species such as Greenland halibut *Reinhardtius hippoglossoides*, haddock *Melanogrammus aeglefinus*, Atlantic cod *Gadus morhua*, and redfish *Sebastes* spp. The other half aimed to assess the state of the ecosystem at large (e.g., Christiansen, 2012; Fossum *et al*., 2012), but the sampling effort of four of them still focused on commercial species (Anon., 2011). For this reason, on some occasions if the number of individuals caught in a haul was significantly high, only a selection of those individuals was measured. This happened both with the Icelandic and the Norwegian data. Thus, from now on, when referred to “observations” it must be understood as individuals recorded in the data, and not the real number of individuals caught. Lastly, shortcomings of the data were potential misidentifications. In the North Atlantic Ocean *A. hyperborea* can be easily confused with *A. radiata*, among others. Given that *A. radiata*’s maximum total length (TL_{max}) is smaller than that of *A. hyperborea*, it was not possible to correct for those possible misidentifications. However, all the individuals surpassing 92 cm of TL were removed from the data in order to limit the misidentifications with other species, considering *A. hyperborea* rarely surpasses this length (Wienerroither *et al*., 2011). Nonetheless, and at least for the surveys performed by the Institute of Marine Research, the misidentification problem has been improved in recent years. Freezing of certain species difficult to identify or not known to the area is routinely done for later identification on shore by taxonomists (Wienerroither *et al*., 2011).

3.2.1 Subset 1: North Atlantic distribution

This subset included the Greenlandic, Icelandic and Faroese data, together with the Egga and Joint Norwegian/Russian Ecosystem Survey from the Norwegian data for having a substantial time series length (2009-2019) (see **Table 1**). It consisted of 3089 observations containing information on capture (geographic position, date, and depth) and specimen (TL and sex). Afterwards, the data was categorized into five different areas. These areas were Greenland, Iceland, Faroe Islands, Norway, and Barents Sea (**Figure 2**). Greenland, Iceland, and Faroe Islands corresponded to the areas covered by their respective surveys, Norway enclosed the area covered by the Egga Nor and Egga Sør surveys, and the Barents Sea circumscribed the area covered by the Joint Norwegian/Russian Ecosystem Survey. Data preparation and statistical analysis took place in R software v4.0.0 (R Core Team, 2020), and it was based off distribution and temporal maps plotted using the R package "ggOceanMaps" version 0.4.3 (Vihtakari, 2021), and basic plots.

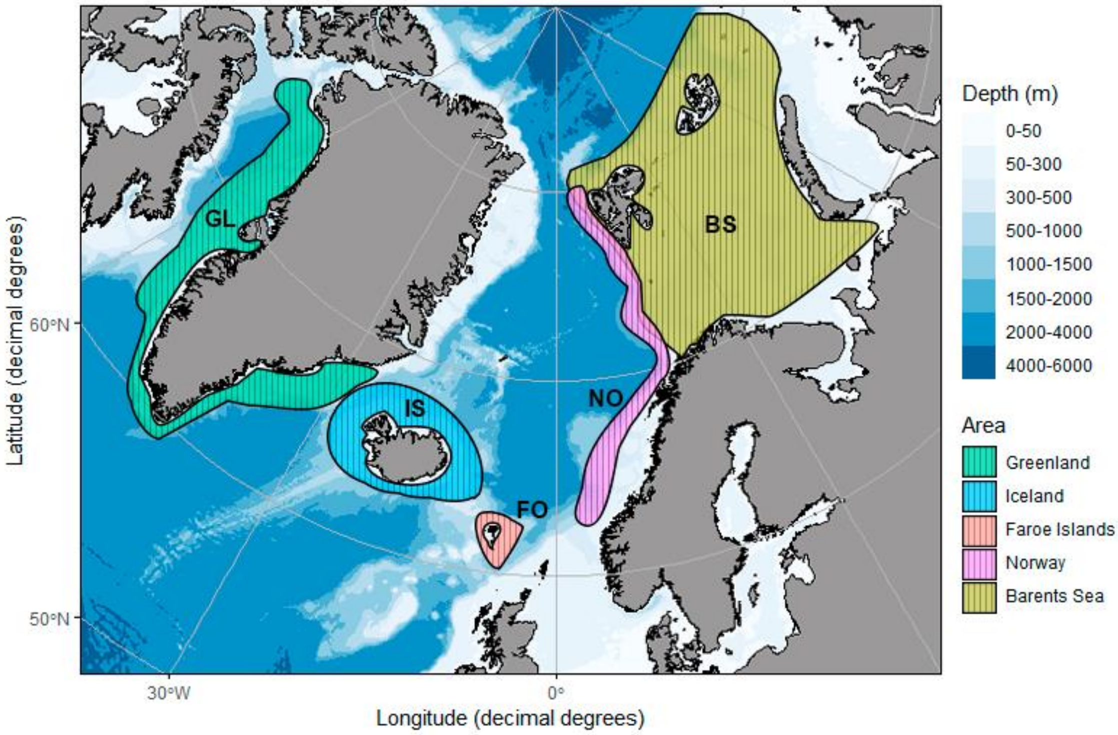


Figure 2. *Areas defined for the analysis of* A. hyperborea *distribution in the North Atlantic Ocean from 2009 to 2019. GL: Greenland, IS: Iceland, FO: Faroe Islands, NO: Norway, and BS: Barents Sea.*

3.2.2 Subset 2: Reproductive ecology

This subset included observations from the Icelandic and the Norwegian data of which maturity stage information was available and consisted of a total of 1011 observations. In order for the data to be comparable, maturity stages needed to be standardized. The standard adopted was the notation proposed in Valetta (2010), this being "1" and "2" for immature individuals, and "3a", "3b", "4a" and "4b" for mature individuals. The data provided by the Institute of Marine Research (IMR) and the Icelandic data required standardization. The former used a modified notation from Valetta (2010) for easier data collection on board the vessels, and the latter used a notation modified from Stehmann (2002). The equivalences between the respective notations and Valetta (2010) are presented in **Table 3** and **Table 4**, respectively.

Table 3. *Maturity stage conversion chart for oviparous cartilaginous fishes from the modified Valetta (2010) maturity stage notation used by the Institute of Marine Research (IMR) to Valetta (2010).*

FEMALE

IMR	Valetta (2010)
1	1
2	2
3	3a
4	3b
5	4a
6	4b

MALE

IMR	Valetta (2010)
1	1
2	2
3	3a
4	3b
5	4a

Table 4. *Maturity stage conversion chart for oviparous cartilaginous fishes from MFRI maturity stage notation to Valetta (2010). MFRI: Marine and Freshwater Research Institute, Iceland.*

FEMALE

MFRI	Short description of MFRI staging	Valetta (2010)
1	Immature	1
2	Small numerous oocytes	2
22	Large ovaries	3a
31	Large yolk eggs but no egg capsules yet visible	3a
32	Large yolk eggs passing into egg capsules. Egg capsules formed but soft	3b
6	Egg capsule hardened	3b
7	Extruded	4a

MALE

MFRI	Short description of MFRI staging	Valetta (2010)
1	Claspers shorter than posterior pelvic fin lobes	1
2	Claspers becoming extended longer than the posterior pelvic fin lobes, but skeleton still soft and flexible	2
22	Claspers' skeleton stiffer and extended. Sperm ducts meandering filled with sperm	3a
3	Claspers' glands swollen. Sperm flowing by pressure. Seminal vesicle well filled	3b
7	Spent	4a

3.2.2.1 Size at first maturity

Most of the observations of this subset came from Iceland (n=590) and the Barents Sea (n=349). Therefore, size at first maturity (L_{50}) was estimated for the complete subset, as well as for the Icelandic individuals and the individuals from the Barents Sea independently. For this, the R package "sizeMat" version 1.1.2 (Torrejón-Magallanes, 2016) was used. In the regression analysis, the TL is considered the explanatory variable and the stage of sexual maturity is considered the response variable, which must be binomial. For this reason, the maturity stages needed to be reclassified into two categories: immature and mature. These variables were fitted to a logistic function with the form:

$$y = 1/[1 + e^{-(A+B*X)}] \tag{1}$$

Where:

y is the probability of an individual of being mature at a determinate X total length.

A (intercept) and B (slope) are estimated parameters.

Then, the L_{50} is calculated as:

$$L_{50} = -A/B \tag{2}$$

In addition to the parameters described above, the maturity ogives were provided.

3.2.2.2 Potential nursery grounds

Regarding the search for potential nursery grounds of the species, it would have been optimal to have information about distribution of egg cases. Since this information was unavailable, a different approach was used. It was assumed that new-born individuals would have limited swimming abilities, and thus be a good proxy for nursery grounds. The distribution of hatchlings (females and males <20 cm TL) and mature females was used. Given that only a portion of the data (26%) contained information about maturity, the estimated L_{50} estimated was extrapolated to the data used in the distribution. Finally, both hatchlings and mature females were plotted on a map using the R package "ggOceanMaps" version 0.4.3 (Vihtakari, 2021).

3.2.3 Subset 3: Ventral colouration

This subset consisted of data provided by the UiT and the IMR with a total of 139 individuals caught from 2009 to 2020 (**Figure 3**). Capture (date, geographic position, and depth) and individual (TL and sex) information were included. The ventral colouration was characterised and colouration coverage (%) assessed, according to **Figure 4** and **Table 5**.

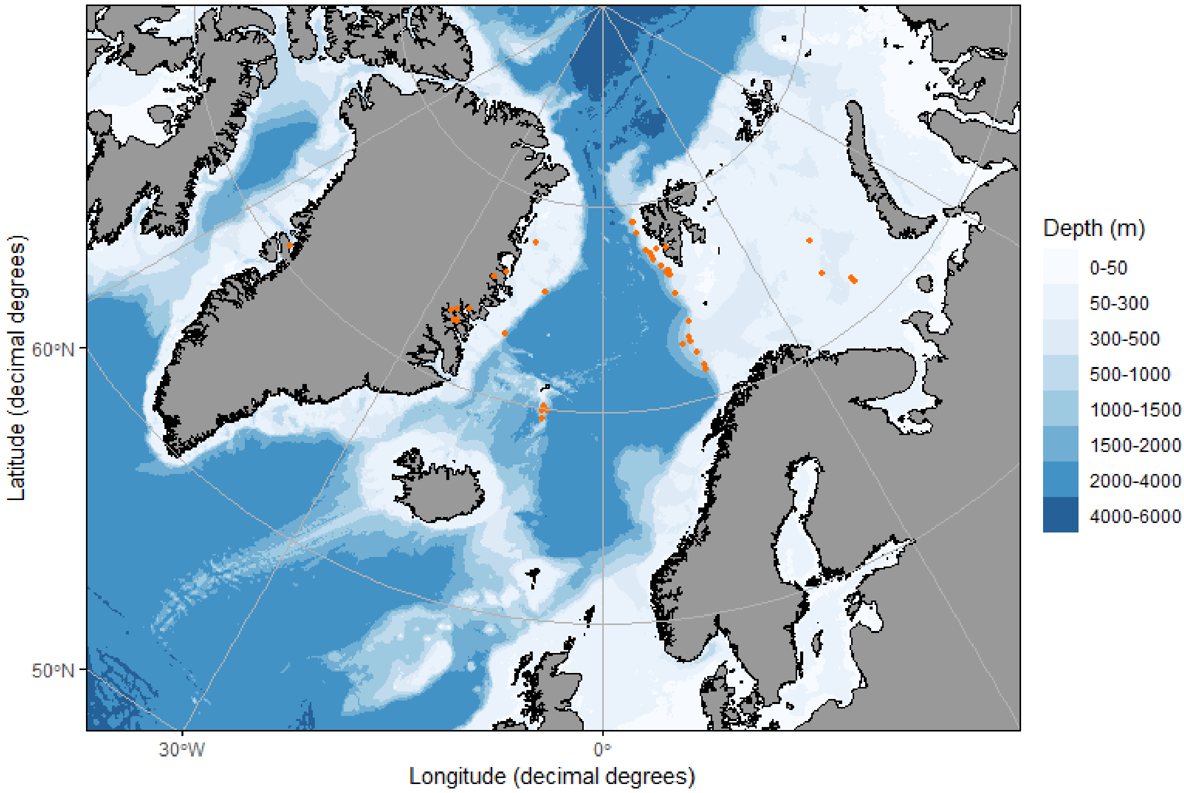


Figure 3*. Geographic distribution of the individuals used for the colouration analysis (n = 139).*

3.2.3.1 Most common patterns

Defining the most common patterns of colouration in an objective manner is very difficult when there is a lot of variation. For this, after a first preliminary analysis, a set of areas were defined (**Figure 4A**). First, 6(7) main areas were defined: snout, thorax, abdomen, wings, pelvic fins, tail, and in the case of male individuals, claspers. In turn, the largest of these main areas were subdivided in order to help provide a finer scale description of the patterns (**Figure 4B**; **Table 5**).

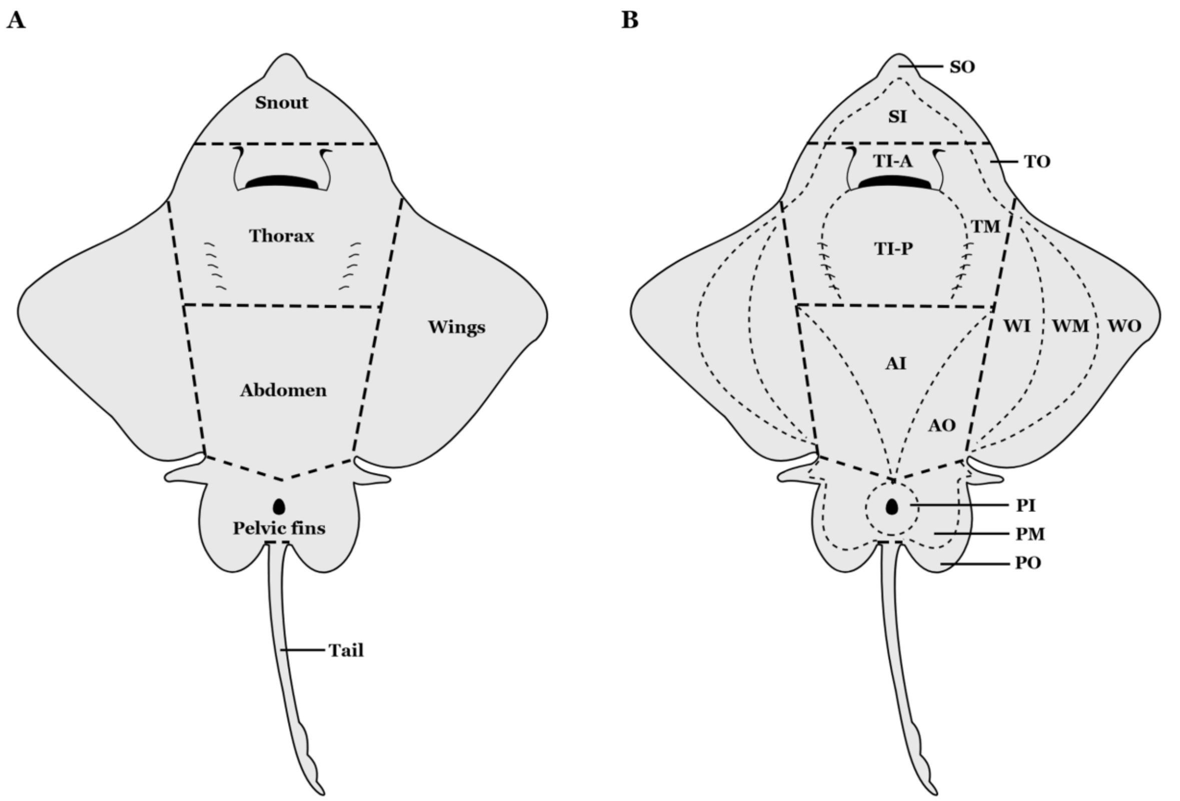


Figure 4. *Illustrations presenting the ventral side of* A. hyperborea *(female). The dashed lines delimit the areas chosen to describe the most common patterns of colouration. In case of a male individual, the claspers would be considered as a separate area. In A the main areas are portrayed, and in B the subdivisions of the largest areas. SO: outer snout, SI: inner snout, TO: outer thorax, TM: middle thorax, TI-A: inner thorax anterior to the mouth, TI-P: inner thorax posterior to the mouth, AO: outer abdomen, AI: inner abdomen, WO: outer wing, WM: middle wing, MI: inner wing, PO: outer pelvic fin, PM: middle pelvic fin, PI: inner pelvic fin. (Illustrations by Rebeca López Climent)*

Table 5. *Description of the areas designated for the description of the colouration patters observed on the ventral side of* A. hyperborea*. For a visual reference, refer to* ***Figure 4****.*

Main areas	Subdivisions	Description
Snout	**SO**	Outer snout: Border area of the snout.
	SI	Inner snout: Centre part of the snout.
Thorax	**TO**	Outer thorax: Border area on both sides of the thorax.
	TM	Middle thorax: Area comprised between the outer thorax and the imaginary line drawn from the gill slits to the outer corner of the mouth. Both sides of the thorax.
	TI-A	Inner thorax anterior to the mouth: Area anterior to the mouth and comprised between both nasal flaps and the imaginary line drawn from nostril to nostril.
	TI-P	Inner thorax posterior to the mouth: Area posterior to the mouth and comprised between both middle thorax areas.
Abdomen	**AO**	Outer abdomen: Triangle-shaped outer areas of the abdomen.
	AI	Inner abdomen: Triangle-shaped inner area of the abdomen.
Wings	**WO**	Outer wings: Border area of the wings.
	WM	Middle wings: Centre part of the wings.
	WI	Inner wings: Wings’ area that is closer to the body.
Pelvic fins	**PO**	Outer pelvic fins: Border area of the pelvic fins.
	PM	Middle pelvic fins: Centre area of the pelvic fins.
	PI	Inner pelvic fins: Inner area of the pelvic fins around the cloaca.
Tail	–	The entirety of the tail’s ventral area.
Claspers*	–	The entirety of the claspers’ ventral area.

*This character is only present in males.

Additionally, different tiers of coverage were applied: I for up to 1/3, II for up to 2/3 and III for up to 3/3 of coverage of said area, and X when the area had no presence of blotches. In addition to the areas, two more variables were added to describe the morphologic characteristics of the blotches. The variable *scattering* referred to how widely spaced or how close together the dots that form the blotches presented, and the variable *size* referred to how big or small the dots were. Then dots categorized into *scattered* or *dense*, and *large* (mole-like) or *small* (freckle-like) (**Figure I1**; **Figure I2**; **Figure I3** in Appendix I). When recording this data, the patterns were assumed to be symmetric and so, for paired areas like the wings, were only recorded once.

3.2.3.2 Colouration coverage

As to calculate the colouration coverage of the dark blotches present in the species ventral side, the pictures were loaded into Adobe Photoshop CC (2018). For each individual, the total area of the skate was selected and measured, as well as the area the blotches covered. These measurements were used to calculate the colouration coverage (CC):

$$CC = \frac{Blotches' area}{Total\ area} \times 100 \tag{3}$$

In order to test for correlation between CC and sex, size, depth, and geographic distribution, chi^2 tests –or Fisher's exact test where chi^2 was inappropriate– were performed. As to perform these tests, the continuous variables were transformed into categorical variables.

4 Results

4.1 North Atlantic distribution

4.1.1 Geographic and vertical distribution

Amblyraja hyperborea was found on all continental shelves covered by the surveys used in this analysis (**Figure 5**). Despite this, it was not evenly distributed throughout them, and for the most part, it appeared to cluster on the continental shelves' break. In terms of number of observations, Iceland was the area with the greatest amount with a total of 984 observations, followed by Greenland with 755 observations, Barents Sea with 694 observations, Norway with 516 observations and, lastly, the Faroe Islands with 140 observations (**Figure 6**). On a finer scale, off the west coast of Greenland there were two clusters on the break of the shelf, one north and one on the south-east part of the Baffin Bay, and one cluster closer to land off the coast of Ilulissat. The number of observations declined south of 65ºN. In Iceland they only appeared off the north and east coast on the break between the continental shelf and the Iceland Plateau. In the Faroe Islands they were observed off the east coast on the Faroe Shelf. Off the coast of Norway, they were observed from Storegga and northwards following the break of the shelf to west Svalbard. The number of observations in this area increased significantly above 70ºN. Lastly, the number of observations of *A. hyperborea* in the Barents Sea was more significant in the western area, at the Franz Viktoria Trough and the St. Anna Trough (**Figure 5**).

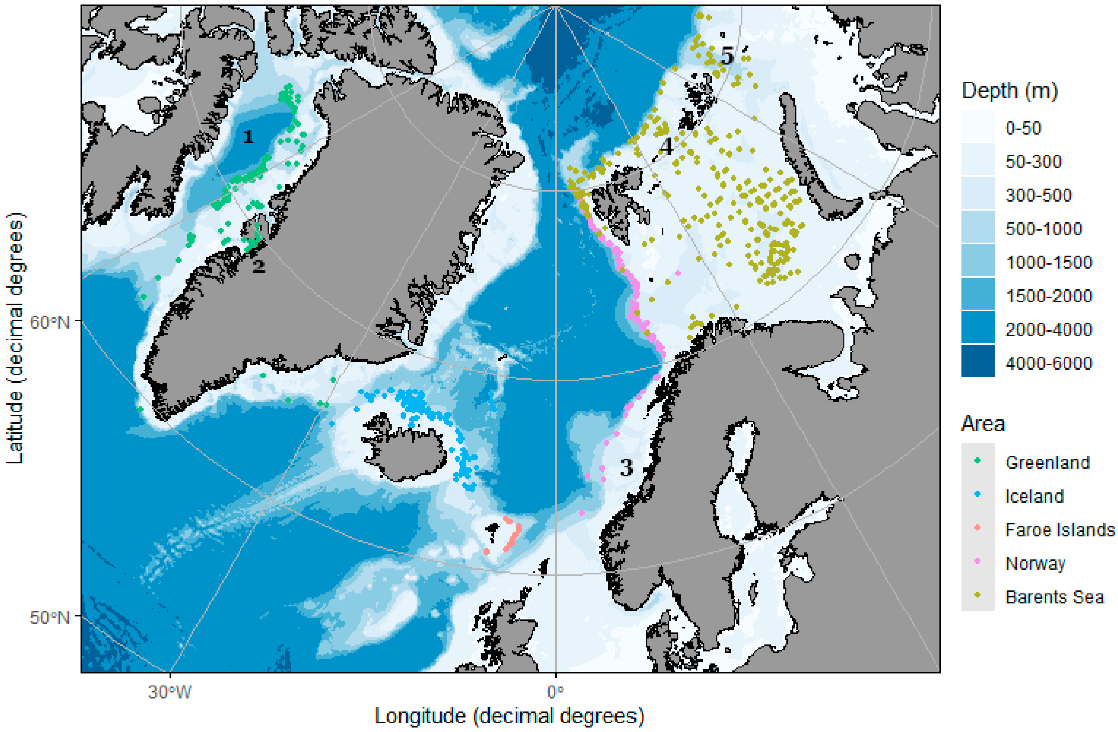


Figure 5. *Geographic distribution of* A. hyperborea *in the North Atlantic Ocean from 2009 to 2019. The observations are color-coded by region. 1:Baffin Bay; 2: Ilulissat; 3: Storegga; 4: Franz Viktoria Trough; 5: St. Anna Trough.*

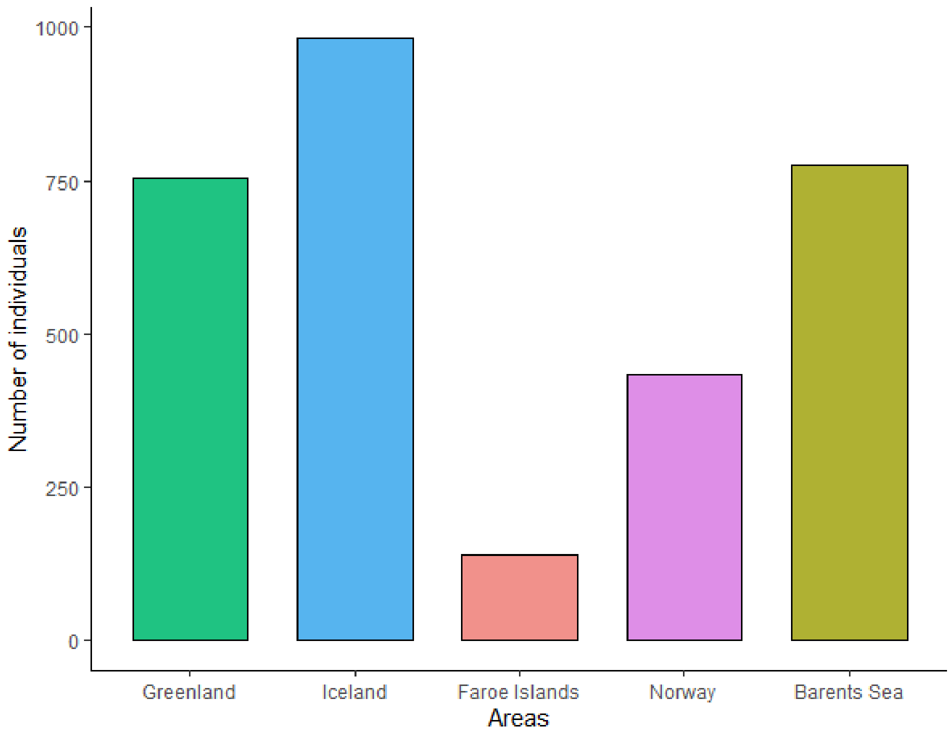


Figure 6. *Observations of* A. hyperborea *in the North Atlantic Ocean per region from 2009 to 2019.*

In terms of vertical distribution, in the present study *A. hyperborea* was caught in a reasonably wide range of depths from 49 to 1453 m (**Figure 7**). Despite this, most of the individuals were captured between 200 and 1000 m (81.2% of all individuals, n = 2509) and another fair amount were captured in the range of 1000-1400 m (17% of all individuals, n = 525).

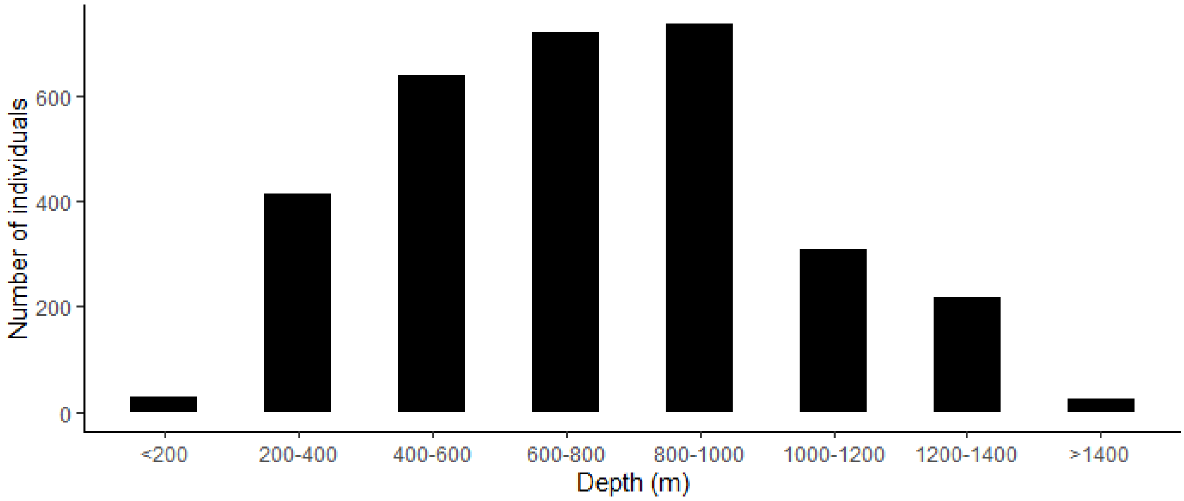


Figure 7. *Number of individual captures of* A. hyperborea *per depth range between 2009 and 2019 in the North Atlantic Ocean.*

However, no substantial differences were found in the vertical distribution with regard to size (**Figure 9**) or sex (**Figure 9**).

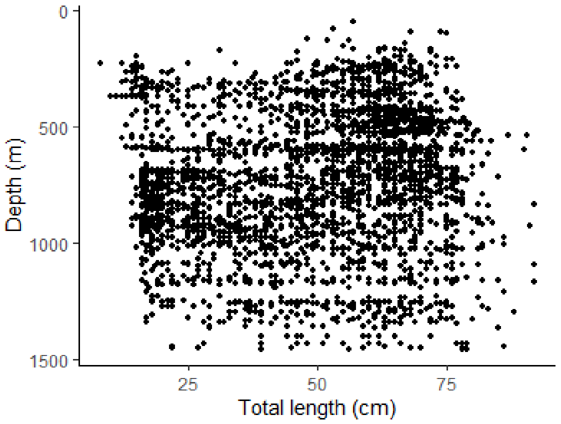


Figure 9*. Vertical distribution (depth, m) of* A. hyperborea *in the North Atlantic Ocean by size (total length, cm) from 2009 to 2019.*

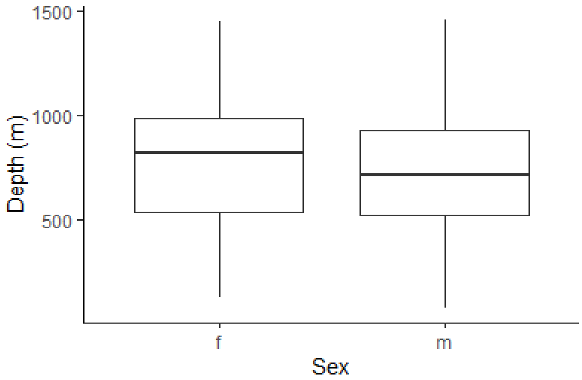


Figure 9. *Vertical distribution (depth, m) of* A. hyperborea *in the North Atlantic Ocean per sex from 2009 to 2019. f: females: m: males.*

4.1.2 Size and sex geographical distribution

The TL ranged from 8 to 92 cm with a mean of 47.54 cm. The most abundant size classes were 40-60 cm TL (30.5%) and 60-80 cm TL (31.37%), while the less abundant class was >80 cm TL (1.39%) (**Figure 10**).

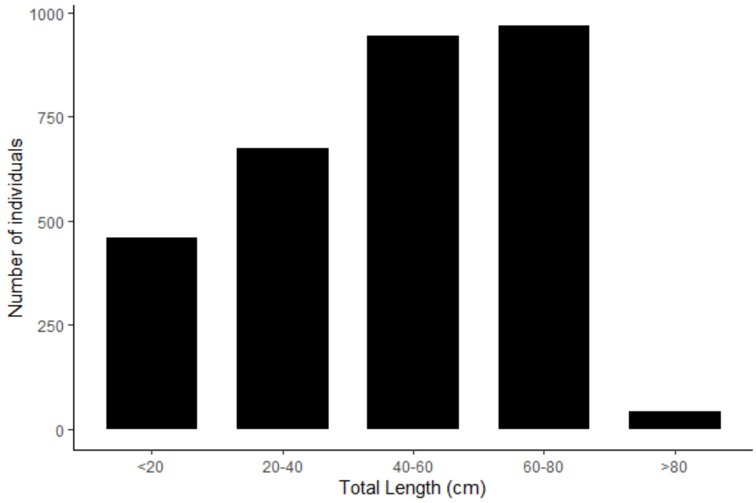


Figure 10. *Size distribution (total length) of* A. hyperborea *in the North Atlantic Ocean from 2009 to 2019.*

When assessed regionally, some differences arose (**Figure 11**). In Greenland all the size classes were present in a similar proportion except for the class >80 cm TL (1%). In Iceland the most abundant size class caught was 40-60 cm TL (35.6%). In the Faroe Islands it was 60-80 cm TL (85%) and the size classes <20 and 20-40 cm TL were missing. In Norway the size classes most often caught were 40-60 cm TL (30%) and 60-80 cm TL (53%). The size class 20-40 cm TL is very underrepresented for this area, which offers questions. For all areas, the least abundant size class was >80 cm TL which represented between 1 and 5% of the observations. Besides this, the smallest size (<20 cm TL) is the least represented among all areas.

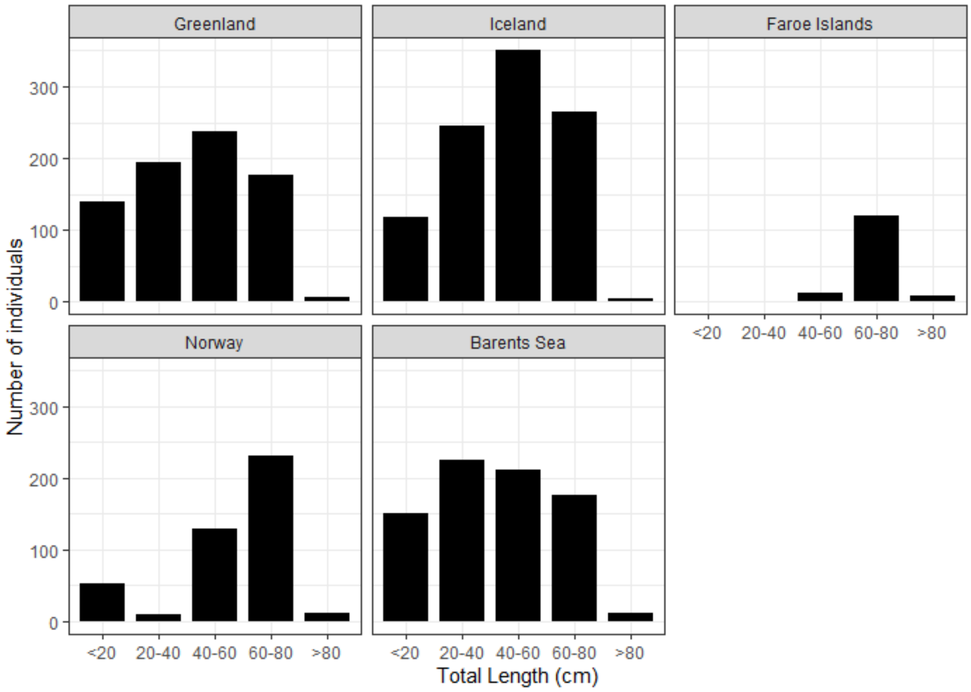


Figure 11. *Size distribution (total length) per region of* A. hyperborea *in the North Atlantic Ocean from 2009 to 2019.*

The sex ratio of females to males tended to 1:2 for the North Atlantic Ocean with a total of 826 females, 1537 males and 726 undetermined individuals. Regionally, the ratio stays higher for males than females, but differs between areas (**Figure 12**). In Greenland it tended to 1:2, in Iceland tended to 1:2.5, in the Faroe Islands only males were caught, in Norway it tended to 1:2.25, and in the Barents Sea it tended to 1:1. Regarding the undetermined data, it was significantly high in Greenland, Norway, and especially in the Faroe Island, which accounted for around a third of the observations while the other two thirds were male individuals. Iceland and the Barents Sea also had a large proportion of undetermined individuals but lower than in other areas.

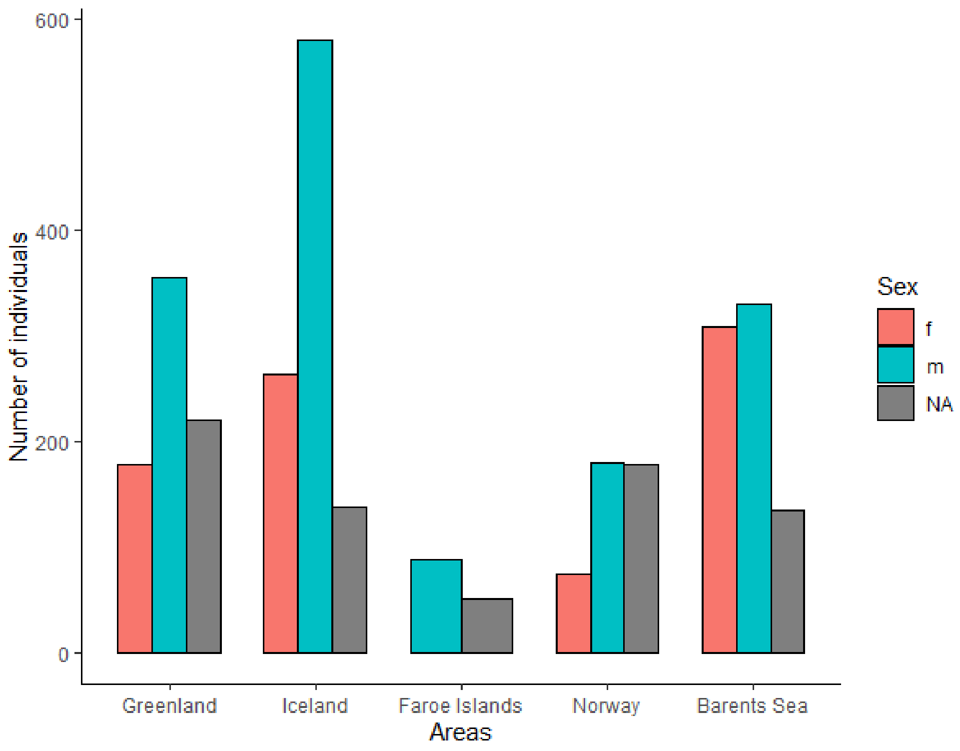


Figure 12. *Regional sex distribution of* A. hyperborea *in the North Atlantic Ocean from 2009 to 2019. Females are represented in pink, males in blue and non-sexed individuals in grey.*

4.1.3 Temporal trends

The total annual catches in the North Atlantic Ocean by the studied surveys stays rather stable through the years, except for 2009, 2010 and 2012 (**Figure 13**). These three years had double (2012) and triple (2009 and 2010) the number of recorded individuals.

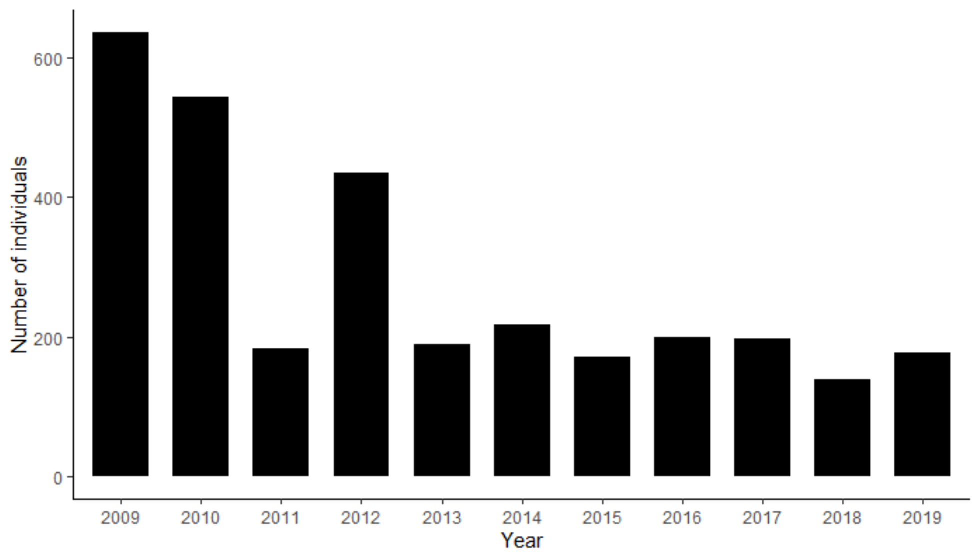


Figure 13. *Annual observations of* A. hyperborea *in the North Atlantic Ocean from 2009 to 2019.*

In order to evaluate further characteristics of these catches, the average TL per year was calculated (**Figure 14**). Despite the differences in number of individuals caught, the overall total length average stayed relatively consistent with a mean of 48.20 cm TL.

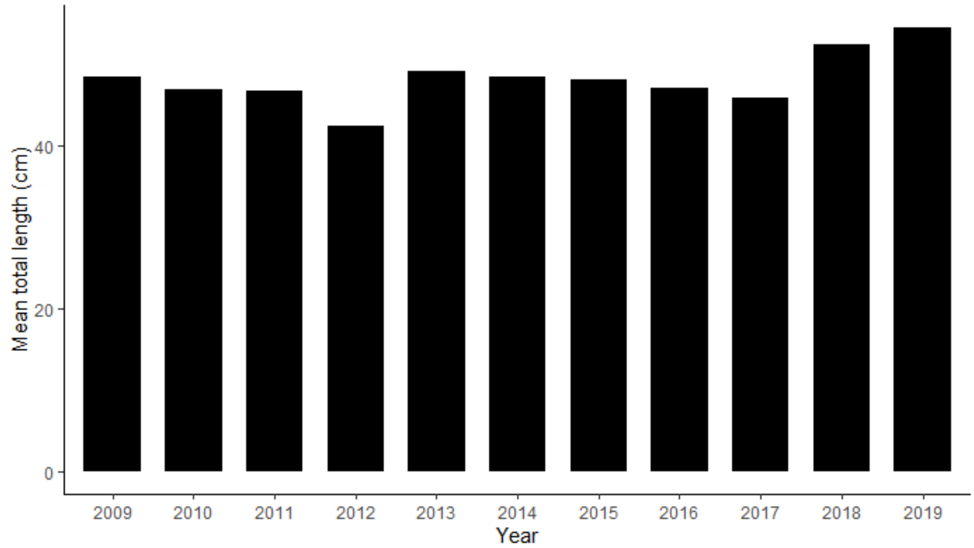
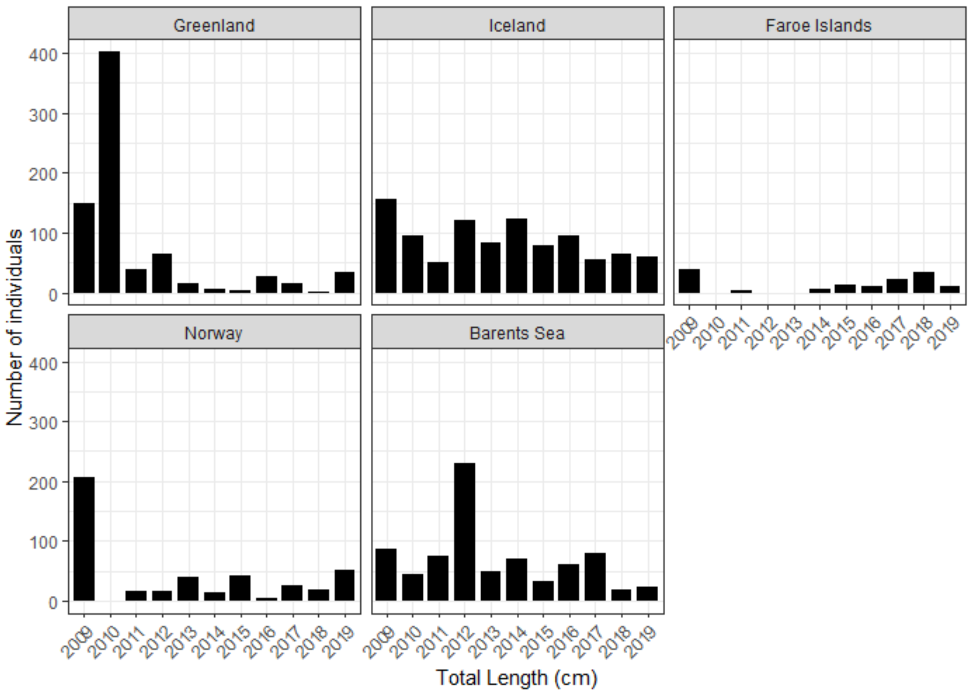


Figure 14. *Annual total length average (cm) of* A. hyperborea *in the North Atlantic Ocean from 2009 to 2019.*

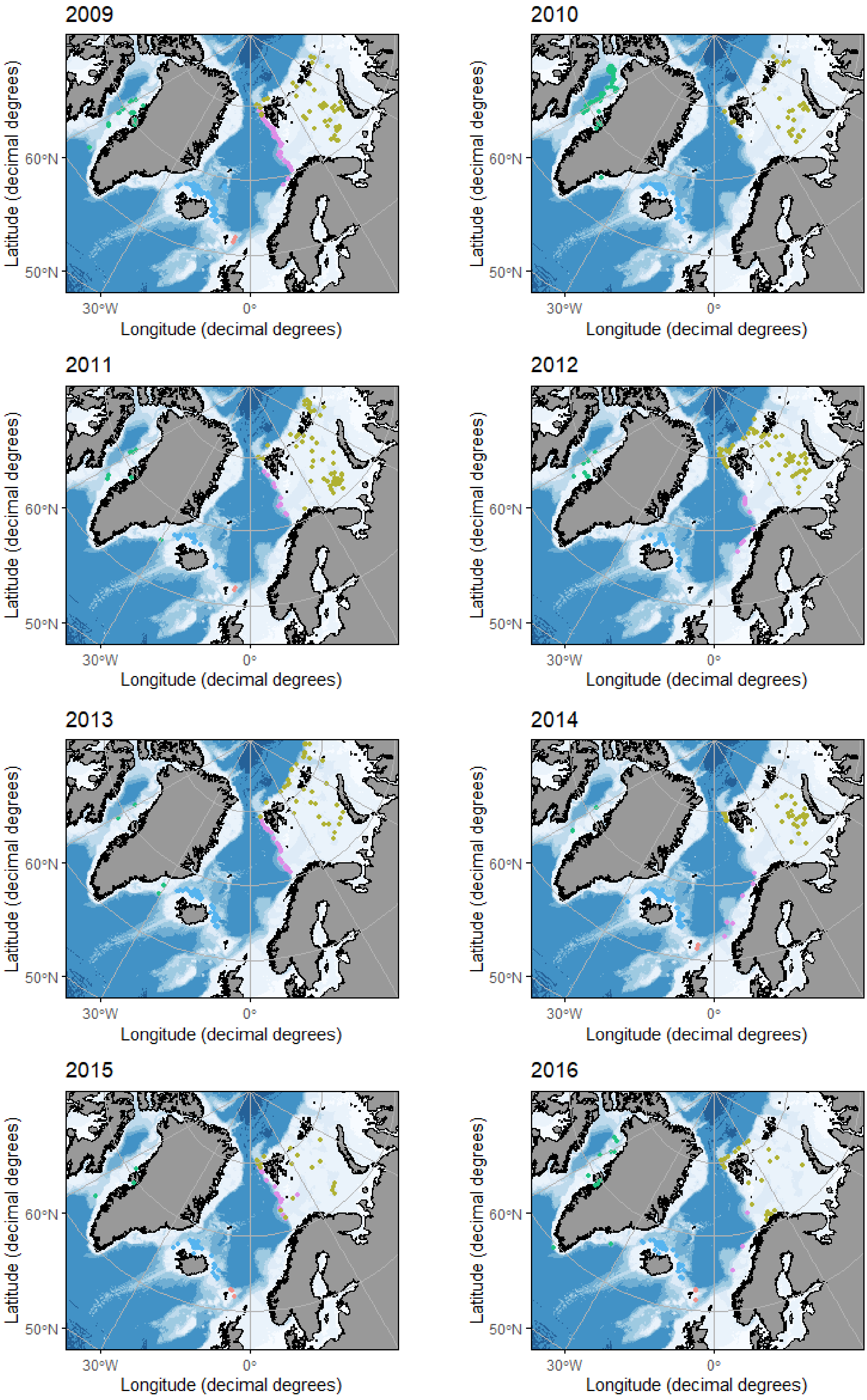
Regionally, the annual number of observations was highly variable, as shown in **Figure 15**.



.

Figure 15. *Annual observations per region of* A. hyperborea *in the North Atlantic Ocean from 2009 to 2019.*

In Greenland, for 2009 and 2010 there was a disproportionately high number of observations in comparison with the rest of the years, especially in 2010 with a total of approximately 400 observations. These high numbers correspond mainly to the clusters described before (see 4.1.1) on the north and south-east sides of the Baffin Bay (**Figure 16**). The contrary occurred in 2014, 2015 and 2018 when the count of observations was very low. In Iceland, the annual catches showed less variation than the in Greenland with a maximum of approximately 150 observations in 2009 and a minimum of around 50 observations in 2011. Generally, the observations were evenly distributed though the north and east of Iceland (**Figure 16**). In the Faroe Islands there was a peak of observations as in 2009 followed by 4 years with none or very few observations. After this, the observations increased steadily until reaching another peak in 2018 with a similar number of observations to the one from 2009. In Norway in 2009, over 200 observations were made whereas the mean for the other years was of around 25 observations. For this exceptional year, 68 individuals were captured near Bjørnøya of which only 7 individuals were measured and therefore were present in the data. This information was available in the data because recorders note how many individuals are caught and how many are measured and assessed. Thereafter, the number of observations had a frequent annual fluctuation. This corresponds with the alternating Egga surveys (North and South), showing a difference in abundances between the North and the South of this area (**Figure 16**). Lastly, in the Barents Sea there was also a fair amount of variation, with a peak in observations in 2012. The rest of the years presented a lot of fluctuations with 2018 and 2019 having particularly low counts in comparison. Even with the differences in counts, the individuals tended to cluster in the north and south-east of the Barents Sea (**Figure 16**). It is worth noting that in 2016 there was a cluster of individuals in Northern Norway off the coast of Finnmark that was not observed in any of the other years.


2009
2010
2011
2012
2013
2014
2015
2016
Latitude (decimal degrees)
60°N
50°N
30°W
0°
Longitude (decimal degrees)

(Continuation)

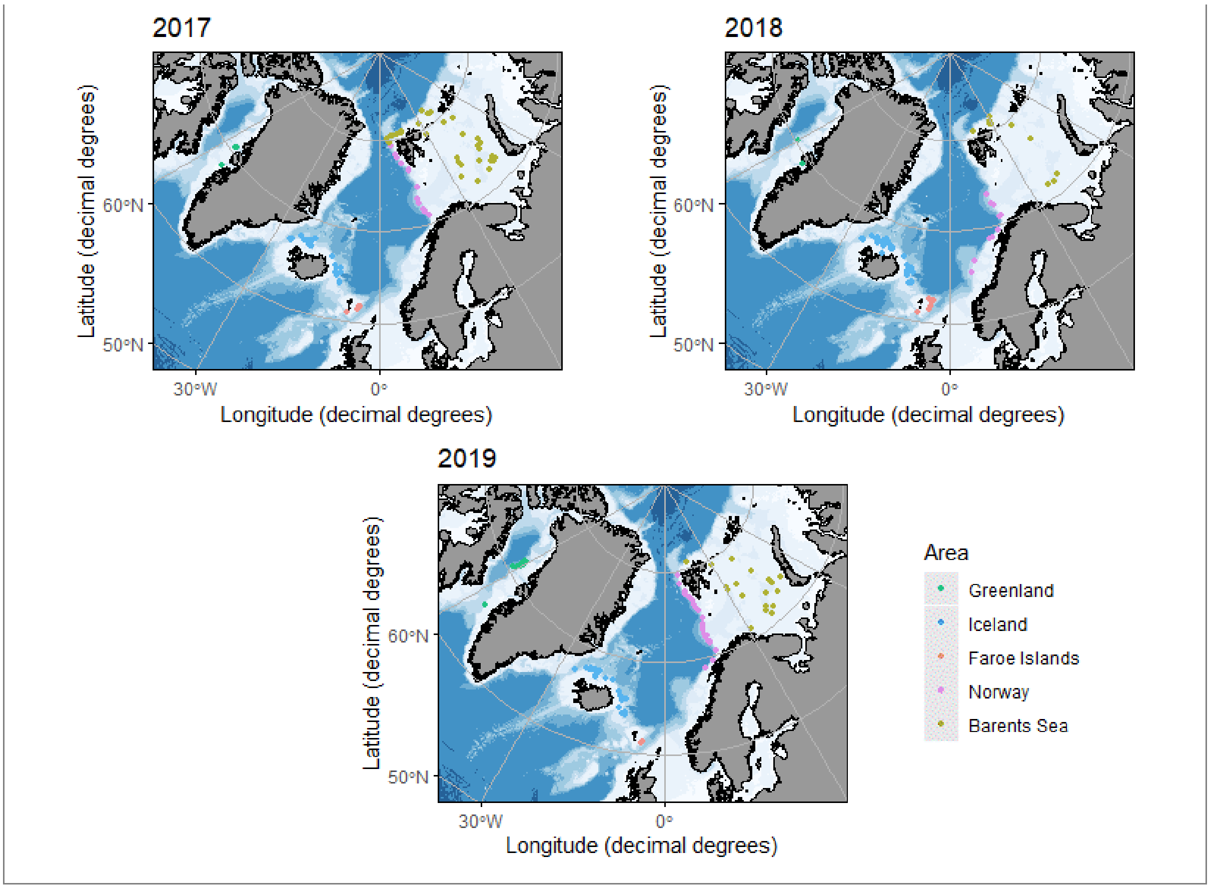


Figure 16. *Annual distribution of* A. hyperborea *in the North Atlantic Ocean from 2009 to 2019.*

The annual average length of the observations also presented some variation among areas, as well as within each area (**Figure 17**). From all the areas, Greenland is the one whose total length average varied considerably from year to year with a minimum of around 20 cm in 2017 to a maximum of over 55 cm in 2019. In Iceland, the total length average per year ranged from around 40 cm to 50 cm TL, with most of the years exceeding 45 cm TL. The Faroe Islands area was the one with the largest total length average above all areas with a minimum of 65 cm and a maximum of over 70 cm. In Norway the range was from around 50 cm to almost 65 cm TL, fluctuating annually. In the Barents Sea, the pattern of variation roughly followed the one described for Norway, but the total length average range was between over 40 cm and over 50 cm.

Figure 17. *Annual total length average (cm) per region of* A. hyperborea *in the North Atlantic Ocean from 2009 to 2019.*

4.2 Reproductive ecology

4.2.1 Size at first maturity

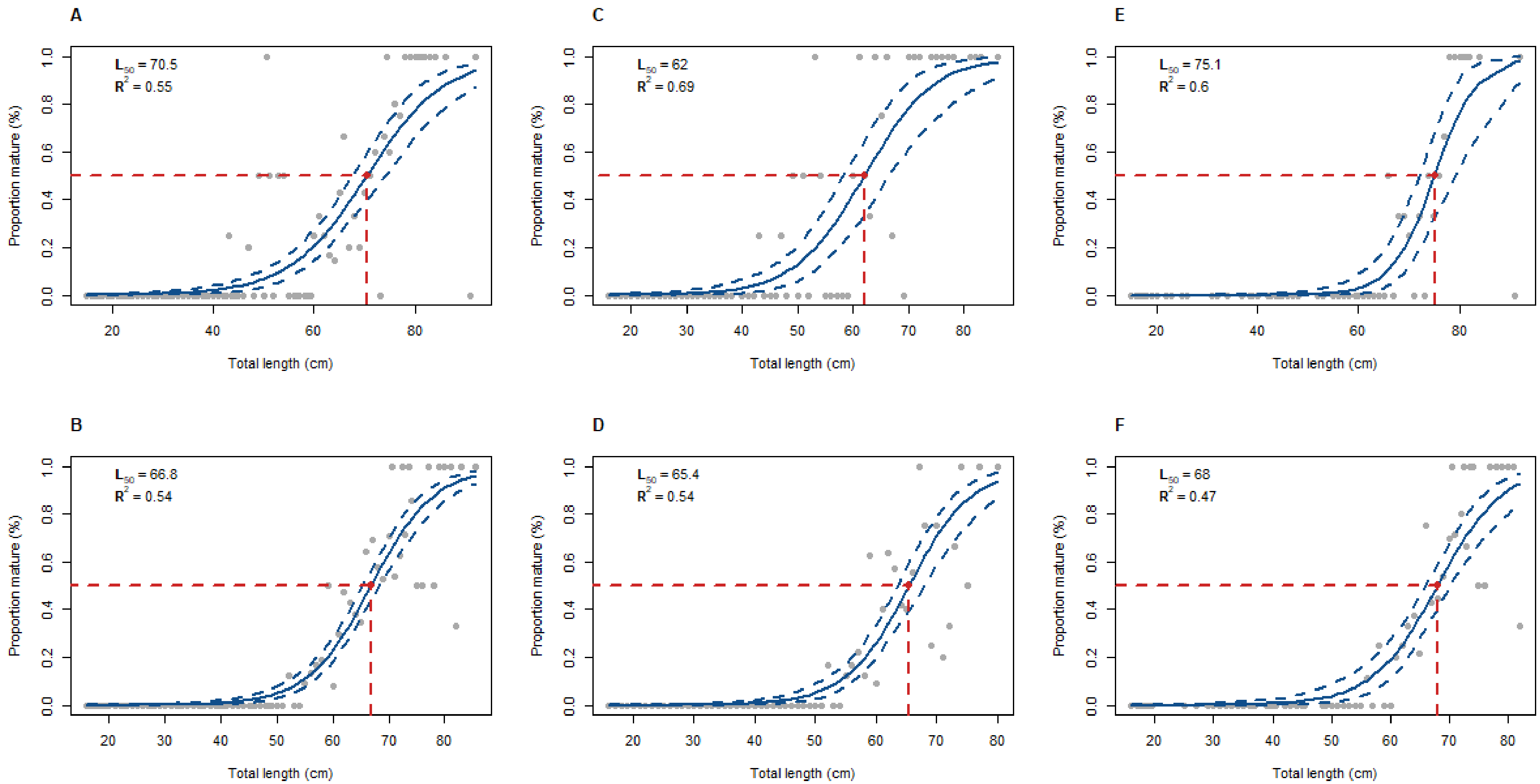
Firstly, the Bayesian logistic regression was applied to the full dataset (n=1011). This revealed that females (n=346) of *A. hyperborea* mature at a median L_{50} of 70.5 [67.6 – 74.3] cm, while males (n=665) mature at a median L_{50} of 66.8 [65.3 – 68.3] cm (**Table 6**; **Figure 18A & B**).

Table 6. *Parameters from the Bayesian logistic regression and estimation of L_{50} for female and male individuals of* A. hyperborea*.* A*: intercept;* B*: slope;* R^2*: coefficient of determination; and* CI*: confidence interval. For explanation on estimation of the parameters, refer to equations **(1)** and **(2)**.*

	FEMALES	**MALES**
	Bootstrap (median)	**Bootstrap (median)**
A	-9.05	-11.74
B	0.13	0.18
L_{50}	70.5	66.8
R^2	0.55	0.54
CI	67.6 – 74.3	65.3 – 68.3

Following, it was applied to the specimens caught in Iceland. In this case, the L_{50} estimated for females (n=193) was of 62 [58.2 – 66.3] cm, and for males (n=397) the L_{50} was of 65.4 [63.6 – 68] cm (**Table I1**; **Figure 18C & D**), which were lower than those estimated with the full dataset. Lastly, the Bayesian logistic regression was again applied to the individuals from the Barents Sea. For these individuals, the mean L_{50} for females (n=121) was of 75.1 [72.1 – 79.2] cm, and for males (n=228), it was of 68 [66 – 70.1] cm (**Table I2**; **Figure 18E & F**). These means were above of those estimated from the totality of the data.

Figure 18. *Logistic curves of relative frequency of mature individuals as a function of size. The L_{50} is then estimated by evaluating the logistic curve at 50%. Panels A and B correspond to the maturity ogives for females and males, respectively, calculated from the entirety of the reproductive ecology data. Panels C and D correspond to the maturity ogives for females and males, respectively, for the Icelandic individuals. Panels E and F correspond to the maturity ogives for females and males, respectively, for the Barents Sea individuals.*



4.2.2 Potential nursery grounds

With the aim of searching for possible nursery grounds, both hatchlings (female and male individuals of 20 cm of TL and under) and mature females were plotted together. As shown in **Figure 19**, these two groups of individuals overlapped north and south-east of the Baffin Bay in Greenland. In Iceland they overlapped off the north and east coasts. In Norway they appear together off the coast of the Troms and Finnmark municipality, near Bjørnøya and west and north off Svalbard. Lastly, in the Barents Sea they overlapped off the coast of south-west Novaya Zemlya.

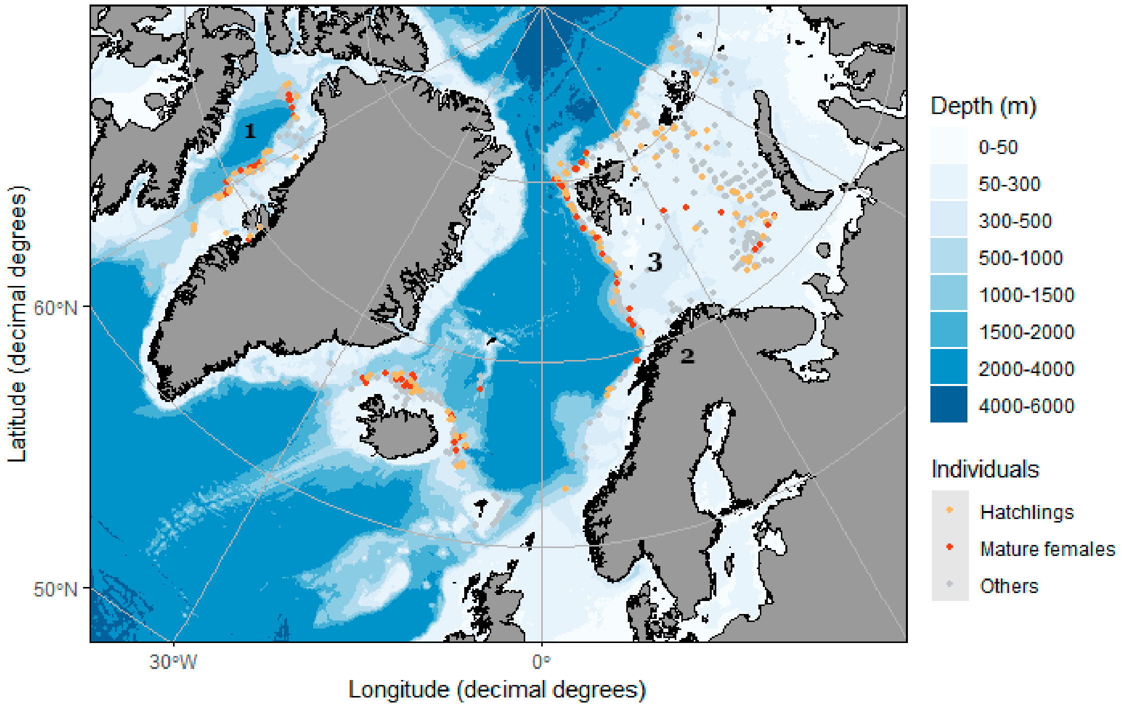


Figure 19. *Distribution map of hatchlings (female and male individuals <20 cm TL) and mature females. Hatchlings apear in orange and mature females in red. The rest of the data is represented in light grey to provide context.1: Baffin Bay; Troms and Finnmark municipality; 3: Bjørnøya.*

4.3 Ventral colouration

4.3.1 Most common patterns

The results of the ventral colouration analysis are presented in **Table 7**. In regard to the morphologic characteristics of the blotches, on most of the individuals they were dense (66.19%), and the size of the dots that formed these blotches was generally large (68.35%) (for visual reference refer to **Figure I1**; **Figure I2**; **Figure I3**). In most occasions the outer side of the snout remained unpigmented (53.96%) or lightly pigmented (33.09%), while the inner area remained white for the most part (72.66%). The outer and middle thorax were rarely pigmented (58.99% and 52.52% respectively), and when pigmented, they were heavily covered (20.86% and 26.09% respectively). The area anterior to the mouth was usually white (66.19%). On the other hand, the area posterior to the mouth had more variability, but for the most part it was not pigmented (37.41%) or lightly pigmented (30.22%). The inner abdomen had no pigmentation or very little, but the outer abdomen was very often pigmented with intermediate (24.46%) or heavy coverage (46.04%). The outer and inner wings were mostly lightly (28.78% and 22.30% respectively) or heavily pigmented (43.88% and 38.13% respectively), while the middle wings were white for the most part (53.24%). The pelvic fins followed approximately the same colouration pattern as the wings, but the inner pelvic fins were usually heavily pigmented (49.64%) or had an intermediate coverage (17.99%). The tail was heavily pigmented in the majority of the individuals examined (83.45%). In males (n=81), claspers were very often pigmented, and the proportion of light, intermediate, and heavy coverage was relatively equal throughout the individuals (25.61%, 29.27% and 31.71% respectively).

Table 7. *Summary of the variations in colouration patterns on the ventral surface of* A. hyperborea *(n = 139). For visual reference refer to* ***Figure 4****,* ***Figure I1****,* ***Figure I2*** *and* ***Figure I3****. SO: outer snout, SI: inner snout, TO: outer thorax, TM: middle thorax, TI-A: inner thorax anterior the mouth, TI-P: inner thorax posterior the mouth, AO: outer abdomen, AI: inner abdomen, WO: outer wing, WM: middle wing, MI: inner wing, PO: outer pelvic fin, PM: middle pelvic fin, PI: inner pelvic fin.*

		Categories (%)			
Descriptive characters		*Scattered*	*Dense*	*Both*	*None*
Scattering		7.91	66.19	20.86	5.04
		Small	*Large*	*Both*	*None*
Size		9.35	68.35	17.27	5.04
Areas		*I*	*II*	*III*	*X*
Snout	SO	33.09	5.04	7.91	53.96
	SI	16.55	6.47	4.32	72.66
Thorax	TO	17.27	2.88	20.86	58.99
	TM	9.35	12.23	25.90	52.52
	TI-A	15.11	13.67	5.04	66.19
	TI-P	30.22	14.39	17.99	37.41
Abdomen	AO	22.30	24.46	46.04	7.19
	AI	27.34	20.14	8.63	43.88
Wings	WO	28.78	17.27	43.88	10.07
	WM	19.42	7.19	20.14	53.24
	WI	22.30	15.83	38.13	23.74
Pelvic fins	PO	21.58	6.47	35.25	36.69
	PM	10.79	7.91	18.71	62.59
	PI	14.39	17.99	49.64	17.99
Tail		2.16	5.76	83.45	8.63
Claspers*		25.61	29.27	31.71	13.41

**Claspers are only present on males (n=81).*
I: 0-33%; II: 33-66%; III: 66-100% of coverage.

4.3.2 Colouration coverage

The only statistically significant link found was between CC (colouration coverage, see **¡Error! No se encuentra el origen de la referencia.**) and the geographic distribution with a *p-value* of $1.169e^{-07}$ (**Table 8**). In particular, lighter individuals predominate in the eastern side of the North Atlantic Ocean, while darker individuals do so in the western side of the North Atlantic (**Figure 20**).

Table 8. *Results of testing the correlation (Chi^2 test) between the colouration coverage and the relevant variables: sex, total length (TL) and geographic and vertical distribution.*

Variables tested	χ^2	**df**	***p-value***
Sex	8.632	4	0.07099
Total length*	–	–	0.09245
Geographic distribution	37.91	4	1.169e-07
Depth*	–	–	0.2179

**The correlation between these variables and the colouration coverage were assessed using the Fisher's exact test instead, since there were groups with a smaller number of observations than what it is expected by the Chi^2 test.*

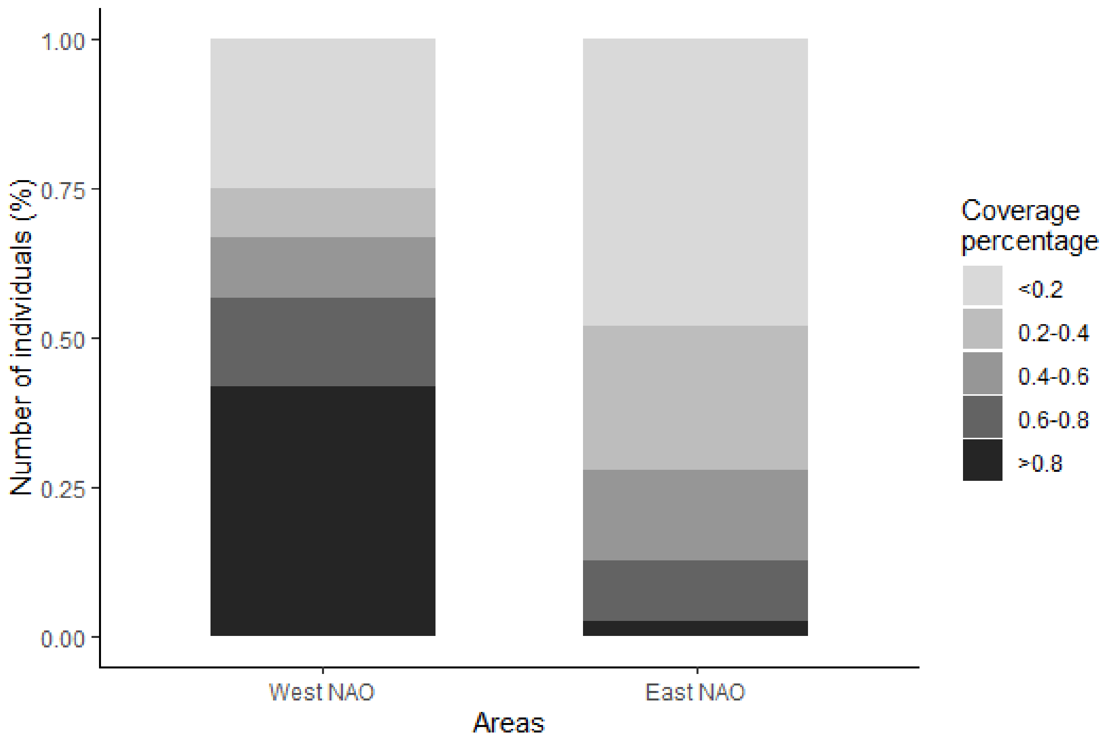


Figure 20. *Presence of the different percentages of coverage depending on area (western and eastern North Atlantic Ocean). The grey gradient follows the overall colouration coverage by the individuals, the darker the larger the higher the coverage percentage.*

5 Discussion

5.1 North Atlantic distribution

5.1.1 Geographic and vertical distribution

In the present study it was confirmed that *A. hyperborea* can be found in the Baffin bay, as well as in the Greenland, the Norwegian, and the Barents Seas (Mecklenburg *et al.*, 2018). It was also found that the abundance of catches decreased with latitude in Greenland, as well as in Iceland below about 65º N. As well, the catches registered in southern Norway (62 – 73.5ºN) were very low compared to those from northern Norway. Both cases can potentially be due to a higher bottom water temperature, since at those latitudes the temperatures stay higher than 4 ºC even with depth (Blindheim & Osterhus, 2005; Locarnini *et al*., 2018). In regard to the Barents Sea, it appeared that this species preferred the colder northern and eastern parts of the sea, i.e. north and east off the Polar front instead of the warmer western Barents Sea (e.g., Christiansen *et al*., 2015). In the western Barents Sea, they were found in deeper waters due colder water along the shelf break (Blindheim & Osterhus, 2005). From the five areas designated in this study, the Faroe Islands area was the one which presented lower abundances. This is consistent with a smaller area surveyed, together with the mesh size used in their surveys, which was considerably larger than those used by the surveys covering other areas [see **Table 1**]. This is supported by the fact that most of the individuals caught in the Faroe Islands were of larger sizes, mostly between 60 and 80 cm TL.

In the present study no differences in the vertical distribution of sex or size were found. Despite this, the minimum depth at which *A. hyperborea* was caught was shallower (49 m) than the minimum recorded in the literature (92 m) (Mecklenburg *et al.*, 2016). However, there is a possibility of this being a misidentification or a punching error while recording the data. The preferred depth range was of 200 – 1000 m, somewhat shallower and narrower than previously thought (300 – 1500 m) (Whitehead *et al.*, 1984), however, wider than Dolgov *et al*. (2005) observed for the Barents Sea (650 – 800 m).

5.1.2 Size and sex geographical distribution

According to the North Atlantic distribution data, the smallest size recorded was 8 cm TL, smaller than previously recorded size for hatchlings of 15 to 18 cm TL (Bigelow & Schroeder, 1953; Last *et al.*, 2016; Mecklenburg *et al.*, 2018). However, this could be due to an error while recording the data. The most abundant size classes found in the North Atlantic Ocean were 40-60 cm and 60-80 cm TL, and the least abundant was >80 cm TL. Even though it is expected for the smallest and the biggest sizes to be less represented, the abundance of the largest size class is very low compared to the smallest size class. In this regard, it is possible that *A. hyperborea* rarely reaches sizes larger than 80 cm TL. Regionally, there was somewhat of a normal distribution of the size classes for three of the five areas. However, that did not apply for the Faroe Islands and Norway, where the number of individuals in each size class was highly variable, and not normally distributed. In the Faroe Islands it is most likely that the large mesh size of the trawl used in their surveys had an influenced these results. The available information about the surveys used in the present study does not explain the low observations of the size class 20-40 cm TL in Norway; however, it remains a noteworthy observation.

The sex ratio between females and males estimated in the present study tended to 1:2 in the North Atlantic Ocean at large. However, regionally it varied between 1:1 in the Barents Sea, consistent with that found by Dolgov *et al*. (2005), and 1:2.5 in Iceland. Still, the number of undetermined individuals sampled was noticeably high and thus, make it difficult to reach a conclusion regarding sex ratios.

5.1.3 Temporal trends

Regarding temporal trends, the observations in the whole North Atlantic Ocean were very high at the start of the time series analysed, and somewhat stabilized in recent years (**Figure 13**). The main contributors to the high individual count for 2009 and 2010 were Greenland, Iceland, and Norway, and for 2012 the Barents Sea was the main contributor. Since the number of observations for these years is considerably disproportionate and does not fit to the average observed the other years, it is reasonable to think that part of them could be misidentifications. The most probable cause for these may be a lack of trained staff on board of said surveys. This is not intended to be a criticism to the coordinators of the surveys here used, but a remark to the importance of having trained personnel on board in order to be able to assess these species appropriately (Williams *et al*., 2008). Regionally, the catches were highly variable between and within some of the areas (**Figure 15**). However, other areas like Norway, had some consistency throughout the years. This phenomenon could potentially be due to the lack of trained staff, but also to a difference in the survey efforts. Another example of a potential misidentification could be a group of individuals recorded in 2016 off the coast of Northern Norway, since no individuals were observed in that area prior or after said year.

5.2 Reproductive ecology

5.2.1 Size at first maturity

The present study is the first attempt to estimate size at first maturity for *A. hyperborea*. Last et al. (2016) provided an estimate of 80–90 cm TL, but it was not stated how this estimate was calculated. In the present study female individuals matured at a larger size than male individuals with an L_{50} of 70.5 cm for females over an L_{50} of 66.8 cm for males. Size at first maturity being larger in females than in males is also found in other species of the genus, such as in *A. jenseni* (Kulka *et al*., 2020) and *A. radiata* (McKulli *et al*., 2012; Lynghammar *et al*., 2016, and references therein). The L_{50} estimate of the Icelandic individuals turned out to be smaller than that of the individuals from the Barents Sea for both sexes. The intraspecific differences in L_{50} for females and males between populations is not uncommon among skates. *Amblyraja radiata* was also found to have regional differences in size at maturity in the West North Atlantic Ocean, having larger L_{50} in the northernmost of its distribution, and smaller L_{50} off Grand Bank and St. Pierre Bank (Templeman, 1987).

Furthermore, the Icelandic individuals showed a larger size at first maturity for males than for females, contrary to what is common among elasmobranchs (Camhi, 1998). However, the same was found for *Psammobatis extenta*, *P. rudis* and *P. normani* (Braccini & Chiaramonte, 2002; Mabragaña & Cousseau, 2004), as well as for *Leucoraja erinacea*, *A. radiata* and *Malacoraja senta* off the eastern coast of Canada (McPhie & Campana, 2009). These differences in size at first maturity between the individuals from Iceland and the Barents Sea might suggest they could be two different populations. Even though Peklova *et al*. (2014) described *A. hyperborea* as a highly active species, the horizontal distance travelled by an individual was of around 30 km which, in addition to the topography between both areas, it seems unlikely that both groups are connected by migration, thus supporting this hypothesis.

This heterogeneity in size at sexual maturity among different skates species or populations of the same species suggests that selection pressure for larger size at maturity for females is not as strong in skates as among viviparous elasmobranchs (Klimley, 1987; Ebert, 2005). Oviparity seems to release skates from the constraint of holding many embryos simultaneously, which allows them to have higher fecundities than most viviparous elasmobranchs (Lucifora & García, 2004).

5.2.2 Potential nursery grounds

The biologic and oceanographic criteria for nursery ground selection are yet to be discovered. In recent studies, nursery sites have been documented to appear close to canyon heads and outer shelf areas (Hoff, 2010). Additionally, high productivity and moderate currents have been described as indicating features for potential skates' nursery grounds (Love *et al*., 2008). This seems to agree with Love et al. (2008) study, where the overlap between hatchlings and mature females appear to be located near canyon heads in western Greenland and associated to outer shelf areas and shelf slopes in Iceland and the western Barents Sea. Some overlap was also found in the south-eastern part of the Barents Sea off the coast of the smallest islands of Novaya Zemlya. The overlap at the shelf break in the Barents Sea roughly coincide with the locations where egg cases were found from 2010 to 2017 (Forsberg, 2018), alongside with the overlaps near Novaya Zemlya. However, Forsberg (2018) found some egg cases off the south east coast of Svalbard and in the central Barents Sea, while the present study found no overlap here. However, in Iceland, hatchlings and mature females clustered together on the north-west and on the east side of the island. These estimates coincide with data from the Icelandic Marine and Freshwater Research Institute, where egg cases and small individuals (<20 cm TL) were found in the IS-SMH survey in 2018 (pers. comm. Klara Jakobsdóttir). Nonetheless, it should be kept in mind that the results of this study are based upon the assumption that hatchlings have limited movement. Some studies have shown that for some skate species, newly hatched individuals leave quickly leave their nursery ground (Hoff, 2007; Hoff, 2010), even though this has not been investigated for *A. hyperborea*.

In addition to the results presented in this study, in 2009 in the Egga Nor survey captured 68 individuals in one haul off the coast of Bjørnøya, of which only seven were measured, assessed and recorded in the data here used. Simultaneously, around 200 km north a high number of egg cases were caught (Forsberg, 2018). Despite not being able to draw any significant conclusions, these observations remain noteworthy.

5.3 Ventral colouration

5.3.1 Most common patterns

Despite the high variability of the ventral surface colouration of *A. hyperborea*, it was possible to define the most common patterns. The nature of the blotches is mainly dense and formed by large dots. When larger and smaller dots appear together, they would also have a mix of dense and scattered pattern. These blotches appear most often framing the wings and pelvic fins on the outer and inner part, leaving the centre white. The abdomen is usually pigmented from the outer sides inwards leaving an inverted white triangle towards the centre of the animal. Tail and claspers (in males) are most often pigmented with some exceptions coinciding with low CC (colouration coverage, see **¡Error! No se encuentra el origen de la referencia.**). However, the snout and thorax usually remain white. These same patterns were also observed by Orlov and Cotton (2015) on *A. jenseni*.

5.3.2 Colouration coverage

Every CC was observed among all size classes, thus not supporting the previously assumed ontogenetic causes for the variability (Sulak *et al*., 2009; Ebert, 2014). However, it is worth noting that there was some variation in the blotches' color. While some were dark, others appeared more fainted to the point of not being clearly visible to the naked eye. This particular phenomenon was also observed by Orlov and Cotton (2015) on *A. jenseni* specimens. This lighter colour of the pigmentation was observed a number of times, usually in very small individuals, except for one larger specimen of 39 cm TL. This might explain why this characteristic was thought to vary with age (Bigelow & Schroeder, 1953; Sulak *et al*., 2009). Additionally, the whole range of CC was present in both sexes and at every depth range assessed in this study. On the contrary, the results of this analysis provided insight into the geographical variation in colouration of this species, lighter morphotypes being predominant in the eastern side of the North Atlantic Ocean and intermediate and darker morphotypes being more common on the western side. An influence of the geographic distribution on the ventral colouration patterns was also observed in *A. jenseni* (Orlov & Cotton, 2015).

Colouration can be regulated by environmental factors such as temperature (Barlow, 1983). In some polymorph species, one of the morphs performs better in colder environments than the others, such as the bridled Common Guillemot *Uria aalge* versus the non-bridled morph (Reiertsen *et al*., 2012). An enormous array of insects and vertebrates have dark coloration as a result of melanin expression, and temperature often plays a key role in this expression (e.g., True *et al*., 1999). In Siamese and Burmese cats, temperature-sensitive alleles result in a facemask and dark pigmentation on extremities (Lyons *et al*., 2005). Temperature-sensitive alleles are also present in fruit flies and mice affecting melanic expression (Kwon *et al*., 1989; O'Grady & DeSalle, 2000). Recently, melanistic populations of eastern mosquitofish *Gambusia holbrooki* have been found to have lower heat resistance than silver populations (Panayotova & Horth, 2018). While the blotches on the ventral surface of *A. hyperborea* do appear on the extremities of the animal, there is no indication that these blotches are temperature regulated, as in the Siamese cats. Despite the fact that melanin may not be a direct result of temperature-sensitive alleles, the darker morphotypes in presumably colder waters seem to indicate that overall colouration may play an important role in cold resistance. In other words, coloration patterns may not be regulated by temperature, but the overall coverage could perhaps be selected for.

Alternatively, the differences in ventral colouration could have a communicative function (Protas & Patel, 2008). For this to be viable, *A. hyperborea* should be able to swim into the water column in order for other individuals to see the colouration patterns. It was thought that given the flattened body form of skates, they had a decreased locomotor ability and thus, a sedentary lifestyle (Schaefer & Summers, 2005). A more recent study determined *A. hyperborea* displays high activity levels which were categorized into large continuous vertical movements and repeated small upward and downward movements; however, these could be related with opportunistic foraging and/or with the movement over heterogeneous bottom topography, and that the occupied depths are not strongly related to diel cycles (Peklova *et al*., 2014). However, light conditions play a key role in colouration recognition, and given the depths at which *A. hyperborea* inhabits, it is objective to assume the light conditions to be poor for the most part and so. Moreover, in the present study no links to sex, size class or vertical distribution were found, and so the communicative functions may not be the most plausible explanation.

6 Conclusion and future perspectives

The present project was set to provide a more exhaustive description of *A. hyperborea*'s biology, from its spatiotemporal distribution and reproductive ecology, to the description of a notable trait of its morphology. A more detailed description of the species distribution in the North Atlantic Ocean was provided, length at first maturity was estimated for the first time and potential nursery grounds were identified. Additionally, the most common patterns of the ventral colouration were described and an insight of the geographical distribution of these patterns was provided. Applying a transboundary approach and combining data from different surveys turned out to be a sound choice for the exhaustive study of *A. hyperborea*, even with the limitation the data presented. However, it highlighted the importance of implementing standard procedures, such as freezing the individuals for on-land identification by expert taxonomists (Wienerroither *et al*., 2011). As well, this study can serve as a baseline for future studies regarding other poorly known transboundary species.

Being morphologically adapted to a benthic lifestyle, skates usually coexist with demersal fish commonly targeted by commercial fisheries such as Atlantic cod, haddock, Greenland halibut and shrimp (Peklova *et al*., 2014). In addition, the total biomass of commercial species consumed by skates has been found to be high (Dolgov *et al*., 2005), showing the potential overlap in habitat use and the danger of bycatch in commercial cruises. *Amblyraja hyperborea* is a common bycatch species in Inuit and commercial Arctic fisheries (DFO, 2008; Dolgov *et al*., 2005a; Young, 2010; Peklova *et al*., 2014), still it is considered a species of 'Least Concern' in the IUCN Red List based on limited spatial overlap within the current fishing activities and the species' distribution at depths beyond most fishing gear (Kulka *et al.*, 2020). In contrast, as shown in this study *A. hyperborea* seemed to prefer depths at which commercial fisheries are still present. Taking into account the large size at maturity and the potential smaller TL_{max}, they are possibly more vulnerable to fisheries activities than previously thought. As well, *A. hyperborea* catches were somewhat unpredictable or declining. However, more research is needed, and it would be advisable to extend the area surveyed to the lower slopes in order to determine if catches in deeper waters decline due to habitat preference or due to poor research at those depths.

Additionally, given the fact that the colouration pattern stays the same throughout an individual's life, it might be possible apply a photo-ID approach to further studies on this species. This has already been done with some species of the Myliobatidae family (Marshall *et al*., 2009), in conservation, migration and population dynamic studies (e.g., Couturier *et al*., 2011; Couturier *et al*., 2014; Carpentier *et al*., 2019), and the same or similar studies can potentially be carried out for *A. hyperborea*.

7 Acknowledgements

I feel so fortunate and grateful to have had the opportunity to work in such an interesting project and to be able continue learning about the amazing world of elasmobranchs.

First and foremost, I am incredibly grateful to my supervisor Arve Lynghammar for trusting me with this exciting project. Thanks for the invaluable advice, support, and patience during this project, and for guiding me all along the way. Your expertise, and passion has truly shaped me into the researcher I am today, and for that I will forever be thankful.

To Julius Nielsen (Greenland Institute of Natural Resources), Klara Jakobsdóttir (Marine and Freshwater Research Institute, Iceland), Hannipoula Olsen and Lisa Helen Ofstad (Faroe Marine Research Institute), and Claudia Junge (Institute of Marine Research, Norway). Thank you all not only for providing me with the data used in this project, but for the unvaluable advise and in-depth knowledge of the data. Without you, this project would not have been possible.

To the fellow members of the RGG. Being part of this amazing group has been one of the best experiences I have had in academia. Thanks to all of you for the wholesome advice and environment you provided.

Last but not least, to my family, partner, and friends who gave me the emotional support needed to fulfil this titanic endeavour. For always encouraging me to do better, for trusting unconditionally in my capabilities and for being the ray of sunshine behind the clouds that kept me going.

Works cited

Adobe Photoshop CC. (2018). Berkeley, CA: Peachpit Press.

Andersson, L., & Georges, M. (2004). Domestic-animal genomics: deciphering the genetics of complex traits. *Nature Reviews Genetics, 5*(3), 202-212.

Andriashev, A. P., & Chernova, N. V. (1994). Annotated list of fishlike vertebrates and fish of the Arctic seas and adjacent waters. *Voprosy Ikhtyologii, 34*(4), 435 - 456 [In Russian; English translation 1995, Journal of Ichthyology 1935: 1981 - 1123].

Andriyashev, A. P. (1964). *Fishes of the Northern Seas of the U.S.S.R.* Jerusalem: Israel Program for Scientific Translations.

Anon. (2011). Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea August-October 2011. *IMR/PINRO Joint Report Series*(3/2011), 118.

Barlow, G. W. (1983). The benefits of being gold: behavioral consequences of polychromatism in the midas cichlid,Cichlasoma citrinellum. *Environmental Biology of Fishes, 8*(3), 235-247. doi:10.1007/BF00001089

Baudron, A. R., Brunel, T., Blanchet, M.-A., Hidalgo, M., Chust, G., Brown, E. J., . . . Fernandes, P. G. (2020). Changing fish distributions challenge the effective management of European fisheries. *Ecography, 43*(4), 494-505. doi:https://doi.org/10.1111/ecog.04864

Bigelow, H. B., & Schroeder, W. C. (1953). *Sawfishes, guitarfishes, skates and rays, Chimaeroids* (Vol. Part two). New Haven.

Bjelland, O., Bergstad, A. O., Skjæraasen, J. E., & Meland, K. (2000). Trophic ecology of deep-water fishes associated with the continental slope of the eastern Norwegian Sea. *Sarsia, 85*, 101–117.

Blindheim, J., & Osterhus, S. (2005). The Nordic Seas, main oceanographic features. *Geophysical Monograph-American Geophysical Union, 158*, 11.

Braccini, J., & Chiaramonte, G. (2002). Reproductive biology of Psammobatis extenta. *Journal of Fish Biology, 61*(1), 272-288.

Byrkjedal, I., Christiansen, J., Karamushko, O., Langhelle, G., & Lynghammar, A. (2015). Arctic skate Amblyraja hyperborea preys on remarkably large glacial eelpouts Lycodes frigidus. *Journal of Fish Biology, 86*(1), 360-364.

Camhi, M. (1998). Chapter 2: The Biology of Chondrichthyan Fishes. In *Sharks and their relatives: ecology and conservation*: IUCN.

Carpentier, A. S., Berthe, C., Ender, I., Jaine, F. R. A., Mourier, J., Stevens, G., . . . Clua, E. (2019). Preliminary insights into the population characteristics and distribution of reef (Mobula alfredi) and oceanic (M. birostris) manta rays in French Polynesia. *Coral Reefs, 38*(6), 1197-1210. doi:10.1007/s00338-019-01854-0

Carrier, J. C., Musick, J. A., & Heithaus, M. R. (2012). *Biology of sharks and their relatives*: CRC press.

Christiansen, J. (2012). The TUNU-Programme: Euro-Arctic Marine Fishes—Diversity and Adaptation. *Adaptation and Evolution in Marine Environments, 1*, 35-50. doi:10.1007/978-3-642-27352-0_3

Christiansen, J. S., Sparboe, M., Sæther, B. S., & Siikavuopio, S. I. (2015). Thermal behaviour and the prospect spread of an invasive benthic top predator onto the Euro-Arctic shelves. *Diversity and Distributions, 21*(9), 1004-1013.

Coad, B. W., & Reist, J. D. (2004). *Annotated list of the Arctic marine fishes of Canada*: Fisheries and Oceans Canada Winnipeg, Canada.

Couturier, L. I. E., Dudgeon, C. L., Pollock, K. H., Jaine, F. R. A., Bennett, M. B., Townsend, K. A., . . . Richardson, A. J. (2014). Population dynamics of the reef manta ray Manta alfredi in eastern Australia. *Coral Reefs, 33*(2), 329-342. doi:10.1007/s00338-014-1126-5

Couturier, L. I. E., Jaine, F. R. A., Townsend, K. A., Weeks, S. J., Richardson, A. J., & Bennett, M. B. (2011). Distribution, site affinity and regional movements of the manta ray, <i>Manta alfredi</i> (Krefft, 1868), along the east coast of Australia. *Marine and Freshwater Research, 62*(6), 628-637. doi:https://doi.org/10.1071/MF10148

DFO. (2008). Cumberland Sound Greenland halibut (turbot) inshore fishery. *DFO Canada Canadian Science Advisory Secretariat Science Advisory Report 2008/040*.

Dolgov, A. (2005). Feeding and consumption by the Barents Sea skates. *Journal of Northwest Atlantic Fishery Science 35,* 495–503.

Dolgov, A., Drevetnyak, K., & Gusev, E. (2005). The Status of Skate Stocks in the Barents Sea. *Journal of Northwest Atlantic Fishery Science, 35*, 249-260. doi:10.2960/J.v35.m522

Ebert, D. (2005). Reproductive biology of skates, Bathyraja (Ishiyama), along the eastern Bering Sea continental slope. *Journal of Fish Biology, 66*(3), 618-649.

Ebert, D. (2014). *Deep-sea Cartilaginous Fishes of the Indian Ocean. Volume 2. Batoids and Chimaeras. FAO Species Catalogue for Fishery Purposes. No. 8, Vol. 2. Rome. FAO. 129 p*.

Ebert, D., & Bizzarro, J. (2007). Standardized diet compositions and trophic levels of skates (Chondrichthyes: Rajiformes: Rajoidei). *Environmental Biology of Fishes, 80*, 221-237. doi:10.1007/s10641-007-9227-4

Fellows-Jensen, G. (2001). *Denmark and Scotland: The Cultural and Environmental Resources of Small Nations* (Vol. 82): Kgl. Danske Videnskabernes Selskab.

Fitton, G., & Larsen, L. M. (2001). The geological history of the North Atlantic Ocean. In G. Fellows-Jensen (Ed.), *Denmark and Scotland: the cultural and environmental resources of small nations. Det KongeligeDanske Videnskabernes Selskab, Historisk-filosofiskeMeddelelser* (Vol. 82, pp. 9-27). København: C.A. Reitzel.

Forsberg, H. (2018). *Indication of nursery grounds and morphological description of egg capsules of skates (Rajidae and Arhynchobatidae) in the Barents Sea* (Bachelor's Thesis in Biology). UiT-The Arctic University of Norway, Tromsø.

Fossum, P., Mork, K. A., Tverberg, V., Boitsov, S., Heldal, H. E., Bagøien, E., . . . Fauchald, P. (2012). *Beskrivelse av miljø og levende marine ressurser i havområdene ved Jan Mayen* (16-2012). Retrieved from

Gregor, D. J., Loeng, H., & Barrie, L. (1998). Chapter 3. The influence of Physical and Chemical Processes on Contaminant Transport. In AMAP (Ed.), *AMAP Assessment Report: Arctic Pollution Issues*. Oslo, Norway: Arctic Monitoring and Assessment Programme (AMAP).

Hoff, G. R. (2007). *Reproductive biology of the Alaska skate, Bathyraja Parmifera, with regard to nursery sites, embryo development, and predation.* University of Washington,

Hoff, G. R. (2010). Identification of skate nursery habitat in the eastern Bering Sea. *Marine Ecology Progress Series, 403*, 243-254.

Jonsson, G., Palsson, J., & Hlidberg, J. B. (2006). *Íslenskir fiskar*. Reykjavík: Vaka-Helgafell.

Kapoor, B. G., & Khanna, B. (2004). *Ichthyology handbook*: Springer Science & Business Media.

Klimley, A. P. (1987). The determinants of sexual segregation in the scalloped hammerhead shark, Sphyrna lewini. *Environmental Biology of Fishes, 18*(1), 27-40.

Kulka, D., Cotton, C., Anderson, B., Herman, K., Pacoureau, N., & Dulvy, N. (2020). *Amblyraja jenseni. The IUCN Red List of Threatened Species 2020*.

Kwon, B. S., Halaban, R., & Chintamaneni, C. (1989). Molecular basis of mouse Himalayan mutation. *Biochemical and Biophysical Research Communications, 161*(1), 252-260. doi:https://doi.org/10.1016/0006-291X(89)91588-X

Kyne, P. M., Carlson, J. K., Ebert, D. A., Fordham, S. V., Bizzarro, J. J., Graham, R. T., . . . Dulvy, N. K. (Eds.). (2012). *The Conservation Status of North American, Central American, and Caribbean Chondrichthyans*. Vancouver, Canada: IUCN Species Survival Commission Shark Specialist Group.

Last, P., Naylor, G., Séret, B., White, W., de Carvalho, M., & Stehmann, M. (2016). *Rays of the World*: CSIRO publishing.

Last, P., White, W., Pogonoski, J., & Gledhill, D. (2008). Descriptions of new Australian skates (Batoidea: Rajoidei).

Locarnini, M., Mishonov, A., Baranova, O., Boyer, T., Zweng, M., Garcia, H., . . . Smolyar, I. (2018). World ocean atlas 2018, volume 1: Temperature.

Love, M. S., Schroeder, D. M., Snook, L., York, A., & Cochrane, G. (2008). All their eggs in one basket: a rocky reef nursery for the longnose skate (Raja rhina Jordan & Gilbert, 1880) in the southern California Bight. *Fishery Bulletin, 106*(4), 471-475.

Lucifora, L., & García, V. (2004). Gastropod predation on egg cases of skates (Chondrichthyes, Rajidae) in the southwestern Atlantic: quantification and life history implications. *Marine Biology, 145*(5), 917-922.

Lynghammar, A., Christiansen, J., Mecklenburg, C., Karamushko, O., Møller, P., & Gallucci, V. (2013). Species richness and distribution of chondrichthyan fishes in the Arctic Ocean and adjacent seas. *Biodiversity, 14*(1), 57-66.

Lynghammar, A., Præbel, K., Bhat, S., Fevolden, S., & Christiansen, J. (2016). Wide spread physical mixing of starry ray from differentiated populations and life histories in the North Atlantic. *Marine Ecology Progress Series, 562*. doi:10.3354/meps11958

Lyons, L. A., Imes, D., Rah, H., & Grahn, R. A. (2005). Tyrosinase mutations associated with Siamese and Burmese patterns in the domestic cat (Felis catus). *Animal genetics, 36*(2), 119-126.

Mabragaña, E., & Cousseau, M. (2004). Reproductive biology of two sympatric skates in the south-west Atlantic: Psammobatis rudis and Psammobatis normani. *Journal of Fish Biology, 65*(2), 559-573.

Marshall, A. D., Compagno, L. J., & Bennett, M. B. (2009). Redescription of the genus Manta with resurrection of Manta alfredi (Krefft, 1868)(Chondrichthyes; Myliobatoidei; Mobulidae). *Zootaxa, 2301*(1), 1-28.

McCully, S. R., Scott, F., & Ellis, J. R. (2012). Lengths at maturity and conversion factors for skates (Rajidae) around the British Isles, with an analysis of data in the literature. *ICES Journal of Marine Science, 69*(10), 1812-1822. doi:10.1093/icesjms/fss150

McKinnon, J., & Pierotti, M. (2010). Colour polymorphism and correlated characters: Genetic mechanisms and evolution. *Molecular Ecology*. doi:10.1111/j.1365-294X.2010.04846.x

McPhie, R. P., & Campana, S. E. (2009). Reproductive characteristics and population decline of four species of skate (Rajidae) off the eastern coast of Canada. *Journal of Fish Biology, 75*(1), 223-246. doi:https://doi.org/10.1111/j.1095-8649.2009.02282.x

Mecklenburg, C. W., Lynghammar, A., Johannesen, E., Byrkjedal, I., Christiansen, J. S., Dolgov, A. V., . . . Steinkte, D. (2018). Marine fishes of the Arctic region.

Mecklenburg, C. W., Mecklenburg, A. T., Sheiko, B. A., & Steinke, D. (2016). *Pacific Arctic marine fishes*: CAFF International Secretariat.

O'Grady, P. M., & DeSalle, R. (2000). Insect evolution: How the fruit fly changed (some of) its spots. *Current Biology, 10*(2), R75-R77.

Orlov, A., & Cotton, C. (2015). New data on the rare deep-sea skate Amblyraja jenseni (Rajidae) from the North Atlantic Ocean. *Journal of ichthyology, 55*(4), 478-496.

Ozhigin, V. K., Ingvaldsen, R. B., Loeng, H., Boitsov, V. D., & Karsakov, A. L. (2011). The Barents Sea. In T. Jakobsen & V. K. Ozhigin (Eds.), *The Barents Sea – Ecosystems, resources, management*: Tapir Academic Press.

Palacios-Abrantes, J., Reygondeau, G., Wabnitz, C. C. C., & Cheung, W. W. L. (2020). The transboundary nature of the world's exploited marine species. *Scientific Reports, 10*(1), 17668. doi:10.1038/s41598-020-74644-2

Panayotova, I. N., & Horth, L. (2018). Modeling the impact of climate change on a rare color morph in fish. *Ecological Modelling, 387*, 10-16. doi:https://doi.org/10.1016/j.ecolmodel.2018.08.008

Peklova, I., Hussey, N., Hedges, K., Treble, M., & Fisk, A. (2014). Movement, depth and temperature preferences of an important by catch species, Arctic skate Amblyraja hyperborea, in Cumberland Sound, Canadian Arctic. *Endangered Species Research, 23*, 229-240. doi:10.3354/esr00563

Protas, M. E., & Patel, N. H. (2008). Evolution of coloration patterns. *Annual review of cell and developmental biology, 24*, 425-446.

R Core Team. (2020). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Ramesh, N., Rising, J. A., & Oremus, K. L. (2019). The small world of global marine fisheries: The cross-boundary consequences of larval dispersal. *Science, 364*(6446), 1192. doi:10.1126/science.aav3409

Reiertsen, T. K., Erikstad, K. E., Barrett, R. T., Sandvik, H., & Yoccoz, N. G. (2012). Climate fluctuations and differential survival of bridled and non-bridled Common Guillemots Uria aalge. *Ecosphere, 3*(6), art52. doi:https://doi.org/10.1890/ES12-00031R

Roa, R., Ernst, B., & Tapia, F. (1999). Estimation of size at sexual maturity: an evaluation of analytical and resampling procedures. *Fishery Bulletin, 97*, 570-580.

Ruxton, G. D., Speed, M. P., & Kelly, D. J. (2004). What, if anything, is the adaptive function of countershading? *Animal Behaviour, 68*(3), 445-451.

Schaefer, J. T., & Summers, A. P. (2005). Batoid wing skeletal structure: Novel morphologies, mechanical implications, and phylogenetic patterns. *Journal of Morphology, 264*(3), 298-313. doi:https://doi.org/10.1002/jmor.10331

Schrank, W. E. (2007). The ACIA, climate change and fisheries. *Marine Policy, 31*(1), 5-18. doi:https://doi.org/10.1016/j.marpol.2006.05.003

Somerton, D. (2011). A Computer Technique for Estimating the Size of Sexual Maturity in Crabs. *Canadian Journal of Fisheries and Aquatic Sciences, 37*, 1488-1494. doi:10.1139/f80-192

Stehmann, M. F. (2002). Proposal of a maturity stages scale for oviparous and viviparous cartilaginous fishes (Pisces, Chondrichthyes). *Archive of Fishery and Marine Research, 50*(1), 23-48.

Sulak, K., Macwhirter, P., Luke, K., Norem, A., Miller, J., Cooper, J., & Harris, L. (2009). Identification guide to skates (Family Rajidae) of the Canadian Atlantic and adjacent regions. *Canadian Manuscript Report of Fisheries and Aquatic Sciences*, 1-34.

Templeman, W. (1987). Differences in sexual maturity and related characteristics between populations of thorny skate (Raja radiata) in the Northwest Atlantic. *Journal of Northwest Atlantic Fisheries Science, 7*, 155-167.

Torrejón-Magallanes, E. (2016). *'sizeMat': An R package to Estimate Size at Sexual Maturity*.

True, J. R., Edwards, K. A., Yamamoto, D., & Carroll, S. B. (1999). Drosophila wing melanin patterns form by vein-dependent elaboration of enzymatic prepatterns. *Current Biology, 9*(23), 1382-1391.

Valetta, M. (2010). Report of the Workshop on Sexual Maturity Staging of Elasmobranchs (WKMSEL).

Vihtakari, M. (2021). *ggOceanMaps: Plot Data on Oceanographic Maps using 'ggplot2'*.

Whitehead, P. J. P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., & Tortonese, E. (1984). *Fishes of the north-eastern Atlantic and the Mediterranean. v. 1*.

Wienerroither, R., Johannesen, E., Dolgov, A., Byrkjedal, I., Bjelland, O., Drevetnyak, K., . . . Wenneck, T. (2011). Atlas of the Barents Sea Fishes. *IMR/PINRO Joint Report Series*(1-2011).

Williams, T., Helle, K., & Aschan, M. (2008). The distribution of chondrichthyans along the northern coast of Norway. *ICES Journal of Marine Science, 65*(7), 1161-1174.

Appendix I. Complementary figures

Visual aid for colouration categorization

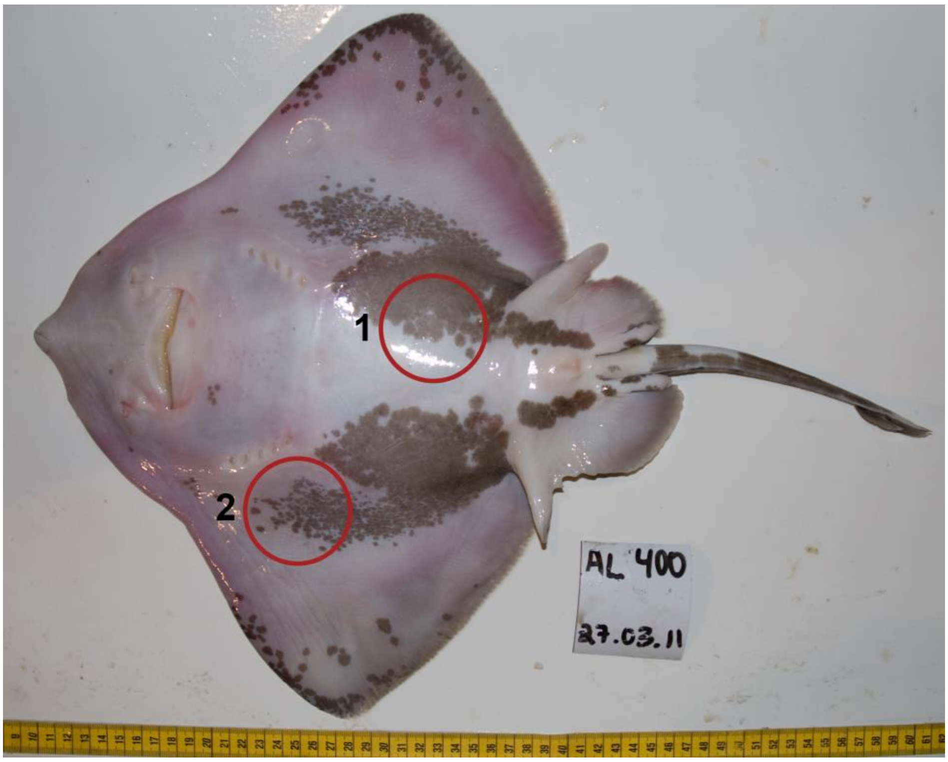


Figure I1. *Visual example of (1) large and dense, and (2) small and dense blotches. Individual 65 (400).*

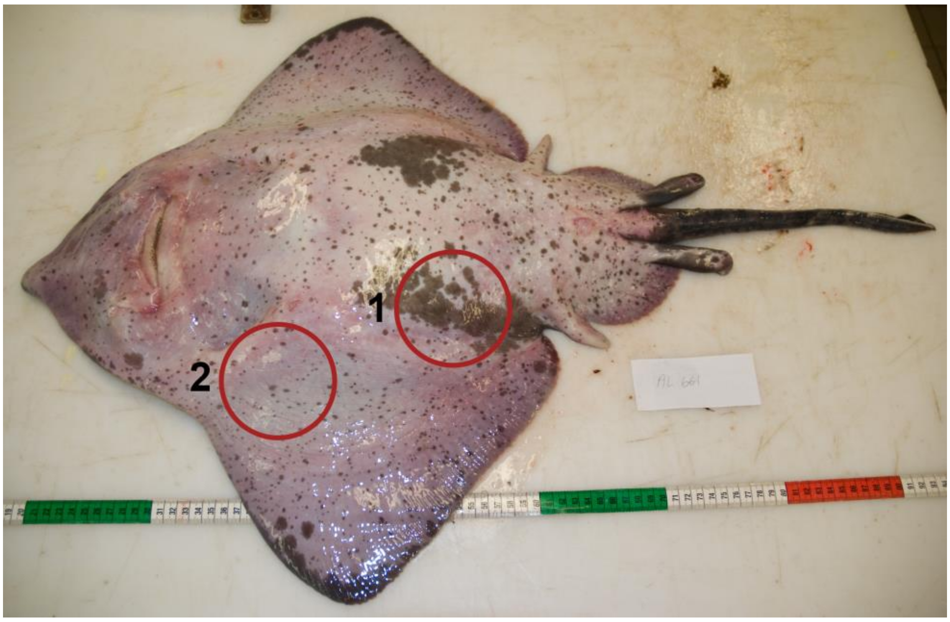


Figure I2. *Visual example of (1) large and dense, and (2) small and scattered blotches. Individual 114 (661).*

Figure I3. *Visual example of (1) large and scattered blotches. Individual 35 (313).*

Reproductive ecology

Table I1. *Parameters from the Bayesian logistic regression and estimation of L_{50} for female and male individuals of* A. hyperborea *from Iceland.* A*: intercept;* B*: slope;* R^2*: coefficient of determination; and* CI*: confidence interval. For explanation on estimation of the parameters, refer to equations **(1)** and **(2)**.*

	FEMALES	MALES
	Bootstrap (median)	**Bootstrap (median)**
A	-9.81	-12.38
B	0.16	0.19
L_{50}	62	65.4
R^2	0.69	0.54
CI	58.2 – 66.3	63.6 – 68

Table I2, *Parameters from the Bayesian logistic regression and estimation of L_{50} for female and male individuals of* A. hyperborea *from the Barents Sea.* A*: intercept;* B*: slope;* R^2*: coefficient of determination; and* CI*: confidence interval. For explanation on estimation of the parameters, refer to **(1)** and **(2)**.*

	FEMALES	MALES
	Bootstrap (median)	**Bootstrap (median)**
A	-17.38	-12.22
B	0.23	0.18
L_{50}	75.1	68
R^2	0.6	0.47
CI	72.1 – 79.2	66 – 70.1

Appendix II. Colouration categorization

Table II1. *Specimens of* A. hyperborea *examined for the analysis of the colouration.*

No	Specimen No	TL (mm)	Sex	Survey
1	2	610	m	Ecosystem (A)
2	58	705	m	TUNU
3	64	790	f	TUNU
4	67	595	f	TUNU
5	68	430	m	TUNU
6	69	420	m	TUNU
7	70	780	f	TUNU
8	133	662	m	Ecosystem (A)
9	158	442	f	TUNU
10	159	590	f	TUNU
11	160	325	m	TUNU
12	161	227	f	TUNU
13	162	232	m	TUNU
14	163	162	f	TUNU
15	164	223	m	TUNU
16	165	166	m	TUNU
17	166	302	f	TUNU
18	167	195	m	TUNU
19	168	562	f	TUNU
20	169	505	f	TUNU
21	170	387	f	TUNU
22	171	223	f	TUNU
23	172	236	f	TUNU
24	173	317	f	TUNU
25	174	195	f	TUNU

Table II1. *(Continuation)*

No	Specimen No	TL (mm)	Sex	Survey
26	175	225	m	TUNU
27	176	177	f	TUNU
28	180	275	m	TUNU
29	185	680	f	Ecosystem (S)
30	187	665	m	Ecosystem (S)
31	291	690	f	Ecosystem (A)
32	292	500	m	Ecosystem (A)
33	309	715	m	Ecosystem (S)
34	310	675	m	Ecosystem (S)
35	313	760	m	Ecosystem (S)
36	314	718	m	Ecosystem (S)
37	318	700	m	Ecosystem (S)
38	333	650	m	Ecosystem (S)
39	334	694	m	Ecosystem (S)
40	335	255	m	Ecosystem (S)
41	336	352	m	Ecosystem (S)
42	375	170	m	Egga
43	376	455	m	Egga
44	377	510	m	Egga
45	378	448	f	Egga
46	379	585	m	Egga
47	380	410	f	Egga
48	381	595	m	Egga
49	382	192	f	Egga
50	385	492	f	Egga

Table II1. (Continuation)

No	Specimen No	TL (mm)	Sex	Survey
51	386	650	m	Egga
52	387	455	f	Egga
53	388	805	m	Egga
54	389	730	m	Egga
55	390	578	m	Egga
56	391	563	m	Egga
57	392	640	m	Egga
58	393	750	m	Egga
59	394	760	f	Egga
60	395	764	m	Egga
61	396	720	m	Egga
62	397	707	m	Egga
63	398	660	m	Egga
64	399	670	m	Egga
65	400	508	m	Egga
66	401	610	m	Egga
67	402	672	m	Egga
68	403	605	m	Egga
69	404	598	m	Egga
70	405	612	m	Egga
71	406	700	m	Egga
72	457	560	m	MarBank
73	458	780	f	MarBank
74	459	610	m	MarBank
75	460	650	m	MarBank

Table II1. (Continuation)

No	Specimen No	TL (mm)	Sex	Survey
76	461	640	m	MarBank
77	462	730	f	MarBank
78	463	815	f	MarBank
79	23305-1	310	f	Jan Mayen
80	23305-10	160	f	Jan Mayen
81	23305-2	290	m	Jan Mayen
82	23305-3	260	m	Jan Mayen
83	23305-4	220	f	Jan Mayen
84	23305-5	210	m	Jan Mayen
85	23305-6	180	f	Jan Mayen
86	23305-7	180	f	Jan Mayen
87	23305-8	190	f	Jan Mayen
88	23305-9	170	f	Jan Mayen
89	23307-1	530	m	Jan Mayen
90	23307-2	420	f	Jan Mayen
91	23307-3	300	m	Jan Mayen
92	23307-4	170	m	Jan Mayen
93	23308-1	190	m	Jan Mayen
94	23310-1	690	m	Jan Mayen
95	23310-2	490	m	Jan Mayen
96	23310-3	300	f	Jan Mayen
97	84016-1	180	m	Egga
98	84017-1	440	f	Egga
99	84024-1	180	m	Egga
100	84024-2	670	f	Egga

Table II1. (Continuation)

No	Specimen No	TL (mm)	Sex	Survey
101	84024-3	610	f	Egga
102	84024-4	490	m	Egga
103	84024-5	390	f	Egga
104	84024-6	480	f	Egga
105	84024-7	680	f	Egga
106	84024-8	460	f	Egga
107	84026-1	710	m	Egga
108	84029-1	690	m	Egga
109	84033-1	920	f	Egga
110	656	290	f	TUNU
111	658	735	m	TUNU
112	659	380	f	TUNU
113	660	745	f	TUNU
114	661	855	m	TUNU
115	TUNU-VII_033	318	m	TUNU
116	TUNU-VII_090	250	m	TUNU
117	SKT-003	740	f	SW Uummannaq
118	SKT-010	680	f	SW Uummannaq
119	SKT-011	730	f	SW Uummannaq
120	SKT-012	580	f	SW Uummannaq
121	SKT-034	605	f	SW Uummannaq
122	SKT-035	511	f	SW Uummannaq
123	SKT-036	500	f	SW Uummannaq
124	SKT-038	593	f	SW Uummannaq
125	SKT-039	733	f	SW Uummannaq

Table II1. (Continuation)

No	Specimen No	TL (mm)	Sex	Survey
126	SKT-040	630	m	SW Uummannaq
127	SKT-041	521	f	SW Uummannaq
128	SKT-042	734	m	SW Uummannaq
129	SKT-045	781	m	SW Uummannaq
130	SKT-047	736	m	SW Uummannaq
131	SKT-048	494	f	SW Uummannaq
132	783	680	m	Ecosystem (A)
133	784	725	m	Ecosystem (A)
134	785	630	m	Ecosystem (A)
135	786	700	m	Ecosystem (A)
136	787	735	m	Ecosystem (A)
137	788	735	m	Ecosystem (A)
138	789	720	m	Ecosystem (A)
139	790	680	m	Ecosystem (A)

Table II2. *Variation in colouration patterns on the ventral surface of* A. hyperborea. *Refer to* ***Figure 4***, ***Figure I1***, ***Figure I2***, ***Figure I3***, *and* ***Table 5*** *for visual and abbreviations reference.*

Appearance and area (individuals with expressed character, %)		**Individuals examined** (CC, %)														
		1 (18.6)	**2** (30.4)	**3** (29.1)	**4** (64.5)	**5** (26.7)	**6** (5.7)	**7** (5.6)	**8** (16.3)	**9** (90.4)	**10** (0)	**11** (89.5)	**12** (81.7)	**13** (52.9)	**14** (79.5)	**15** (56.3)
Scattering of the blotches		D	D	D	D	D	Sc	D	D	D	N	D	D	D	D	D
Size of the blotches		L	L	L	L	Sm	Sm	L	L	L	N	L	L	S	L	L
Snout	**SO** (46.04)	I	I	I	I	I	X	I	I	II	X	II	II	I	I	X
	SI (27.34)	X	X	X	X	X	X	X	I	I	X	II	I	X	X	I
Thorax	**TO** (41.01)	I	X	I	I	X	X	X	X	III	X	III	III	X	III	X
	TM (47.83)	X	X	II	III	I	X	X	X	III	X	III	III	II	III	II
	TI-A (33.81)	X	X	X	II	X	X	X	II	III	X	II	X	X	X	II
	TI-P (62.59)	X	X	I	III	II	X	X	I	III	X	II	III	II	III	I
Abdomen	**AO** (92.81)	II	II	III	III	II	I	I	I	III	X	III	III	III	III	III
	AI (56.12)	X	X	X	II	I	X	X	X	II	X	II	II	X	II	II
Wings	**WO** (89.93)	II	II	III	II	II	I	I	I	III	X	III	III	III	III	II
	WM (46.76)	X	X	X	X	X	X	X	X	III	X	III	II	I	III	I
	WI (76.26)	I	I	I	II	X	X	X	I	III	X	III	III	III	III	III
Pelvic fins	**PO** (63.31)	I	II	I	III	I	X	X	X	III	X	III	III	I	III	II
	PM (37.41)	X	X	I	II	X	X	X	X	III	X	III	II	X	X	X
	PI (82.01)	I	III	III	III	II	X	X	III	III	X	III	III	III	III	III
Tail (91.37)		III	III	III	III	III	III	III	III	III	X	III	III	III	III	III
Claspers* (86.42)		II	II	–	–	I	X	–	II	–	–	III	–	X	–	I

Sc: scattered; D: dense; Sm: small; L: large; B: both; N: none; X: 0 CC: colouration coverage; I: 0-33%; II: 33-66%; III: 66-100% of coverage.
**Claspers were only assessed on males, and for females, the symbol " –" was used.*

Table II2. *(Continued)*

Appearance and areas (individuals with expressed character, %)		**Individuals examined** (CC, %)														
		16 (0)	**17** (83.8)	**18** (6.5)	**19** (68)	**20** (93.1)	**21** (94.3)	**22** (94.8)	**23** (90.3)	**24** (82.0)	**25** (0)	**26** (88)	**27** (0)	**28** (91.1)	**29** (16.2)	**30** (26.9)
Scattering of the blotches		N	D	D	D	D	D	D	D	D	N	D	N	D	D	D
Size of the blotches		N	L	Sm	L	L	L	L	L	L	N	L	N	L	Sm	L
Snout	**SO** (46.04)	X	I	X	X	I	III	III	I	X	X	II	X	III	X	I
	SI (27.34)	X	X	X	X	I	III	III	I	X	X	X	X	III	X	X
Thorax	**TO** (41.01)	X	III	X	III	III	III	III	III	II	X	III	X	II	X	I
	TM (47.83)	X	III	X	III	III	III	III	III	III	X	III	X	III	I	X
	TI-A (33.81)	X	I	X	I	I	III	II	I	X	X	I	X	III	I	X
	TI-P (62.59)	X	II	I	II	III	III	III	III	II	X	III	X	III	I	X
Abdomen	**AO** (92.81)	X	III	II	III	III	III	III	III	III	X	III	X	III	II	II
	AI (56.12)	X	II	X	I	III	III	III	III	II	X	II	X	II	I	I
Wings	**WO** (89.93)	X	III	X	III	III	III	III	III	III	X	III	X	III	I	I
	WM (46.76)	X	II	X	X	III	III	III	III	III	X	II	X	II	X	X
	WI (76.26)	X	III	X	III	III	III	III	III	III	X	III	X	III	X	I
Pelvic fins	**PO** (63.31)	X	III	X	II	III	III	III	III	III	X	III	X	III	I	I
	PM (37.41)	X	III	X	I	III	III	III	III	II	X	III	X	III	X	X
	PI (82.01)	X	III	II	III	III	III	III	III	III	X	III	X	III	I	X
Tail (91.37)		X	III	X	III	III	III	III	III	III	X	III	X	III	III	III
Claspers* (86.42)		X	–	X	–	–	–	–	–	–	–	III	–	III	–	I

Sc: scattered; D: dense; Sm: small; L: large; B: both; N: none; X: 0 CC: colouration coverage; I: 0-33%; II: 33-66%; III: 66-100% of coverage.
**Claspers were only assessed on males, and for females, the symbol " –" was used.*

Table II2. *(Continued)*

Appearance and areas (individuals with expressed character, %)		**Individuals examined** (CC, %)														
		31 (33.3)	**32** (9.4)	**33** (23.2)	**34** (17.3)	**35** (19.8)	**36** (17.2)	**37** (3.9)	**38** (17.2)	**39** (67.9)	**40** (10.3)	**41** (48.4)	**42** (56.6)	**43** (12.2)	**44** (21.8)	**45** (2)
Scattering of the blotches		D	D	D	D	D	B	Sc	B	D	D	Sc	D	Sc	Sc	Sc
Size of the blotches		L	L	L	L	Sm	B	L	B	L	B	Sm	L	L	L	L
Snout	**SO** (46.04)	I	I	X	X	X	X	X	X	I	I	X	X	X	I	X
	SI (27.34)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Thorax	**TO** (41.01)	I	X	I	X	X	I	X	X	I	X	X	X	X	X	X
	TM (47.83)	X	X	X	X	X	X	X	X	II	X	I	X	X	X	X
	TI-A (33.81)	X	X	X	X	X	X	X	X	X	I	X	X	X	X	X
	TI-P (62.59)	X	X	X	X	X	X	X	X	II	X	I	I	X	I	X
Abdomen	**AO** (92.81)	I	I	II	I	I	I	I	II	III	I	III	III	I	II	I
	AI (56.12)	X	X	I	X	X	I	X	X	II	X	I	II	X	X	X
Wings	**WO** (89.93)	II	X	I	II	II	I	I	I	III	I	III	III	I	II	X
	WM (46.76)	X	X	X	X	I	I	X	X	II	X	I	III	X	X	X
	WI (76.26)	II	X	X	X	X	X	X	I	III	X	I	II	X	II	X
Pelvic fins	**PO** (63.31)	II	X	I	X	X	I	X	I	III	X	I	X	X	X	X
	PM (37.41)	II	X	X	X	X	I	X	X	II	X	X	X	X	X	X
	PI (82.01)	III	X	III	II	II	I	X	II	III	II	III	II	II	II	I
Tail (91.37)		III	III	III	III	III	III	III	III	III	III	II	III	III	III	III
Claspers* (86.42)		–	I	II	I	II	I	I	I	III	X	II	III	I	II	–

Sc: scattered; D: dense; Sm: small; L: large; B: both; N: none; X: 0 CC: colouration coverage; I: 0-33%; II: 33-66%; III: 66-100% of coverage.
**Claspers were only assessed on males, and for females, the symbol " –" was used.*

Table II2. *(Continued)*

Appearance and areas (individuals with expressed character, %)		**Individuals examined** (CC, %)														
		46 (55.4)	**47** (8.3)	**48** (17.2)	**49** (29.8)	**50** (13.9)	**51** (63.9)	**52** (7.9)	**53** (22.6)	**54** (18.2)	**55** (59.8)	**56** (18.6)	**57** (19)	**58** (30.3)	**59** (56)	**60** (25.5)
Scattering of the blotches		D	Sc	D	D	Sc	D	Sc	Sc	Sc	B	B	D	B	B	D
Size of the blotches		Sm	L	L	L	L	Sm	Sm	L	L	B	Sm	L	B	L	L
Snout	**SO** (46.04)	X	X	X	X	X	X	X	X	I	I	X	I	X	X	X
	SI (27.34)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Thorax	**TO** (41.01)	I	X	X	X	X	X	X	X	X	X	X	I	X	X	X
	TM (47.83)	II	X	X	X	X	II	X	X	X	II	X	X	X	X	X
	TI-A (33.81)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
	TI-P (62.59)	I	X	X	X	I	II	X	X	I	II	X	X	X	X	I
Abdomen	**AO** (92.81)	III	I	II	II	I	III	I	II	I	III	I	II	II	II	I
	AI (56.12)	X	X	X	X	X	II	X	X	X	I	X	I	II	X	I
Wings	**WO** (89.93)	III	I	I	II	I	III	I	II	II	III	II	I	II	III	I
	WM (46.76)	X	X	X	II	X	II	X	X	X	III	X	X	X	II	X
	WI (76.26)	III	X	X	I	X	III	X	II	X	III	X	I	I	III	I
Pelvic fins	**PO** (63.31)	III	X	II	X	X	III	X	I	X	III	I	X	I	III	I
	PM (37.41)	I	X	X	X	X	X	X	X	X	X	X	X	X	II	X
	PI (82.01)	III	X	X	X	I	III	X	I	I	III	X	X	II	III	III
Tail (91.37)		III	III	III	III	III	II	I	III	III	III	III	III	III	III	III
Claspers* (86.42)		II	–	II	–	–	II	–	I	III	II	I	II	II	–	III

Sc: scattered; D: dense; Sm: small; L: large; B: both; N: none; X: 0 CC: colouration coverage; I: 0-33%; II: 33-66%; III: 66-100% of coverage.
**Claspers were only assessed on males, and for females, the symbol " –" was used.*

Table II2. *(Continued)*

Appearance and areas (individuals with expressed character, %)		**Individuals examined** (CC, %)														
		61 (9.7)	**62** (15.1)	**63** (19.4)	**64** (55.6)	**65** (21.8)	**66** (18.8)	**67** (36.5)	**68** (17.2)	**69** (15.9)	**70** (13.2)	**71** (42.7)	**72** (34.7)	**73** (50.7)	**74** (47.8)	**75** (23.4)
Scattering of the blotches		D	D	D	D	B	D	B	D	B	B	D	B	B	D	B
Size of the blotches		L	L	L	L	B	L	B	L	L	B	L	B	B	L	B
Snout	**SO** (46.04)	X	X	X	I	X	I	X	X	X	X	X	X	X	I	I
	SI (27.34)	X	X	X	X	X	X	X	X	X	I	X	X	X	X	X
Thorax	**TO** (41.01)	X	X	I	I	X	X	X	X	X	X	I	I	X	I	X
	TM (47.83)	X	X	I	X	X	X	X	X	X	X	X	X	II	II	I
	TI-A (33.81)	X	X	I	X	X	X	X	X	X	I	X	I	X	X	X
	TI-P (62.59)	X	I	I	I	I	X	X	I	I	I	I	I	II	X	I
Abdomen	**AO** (92.81)	II	II	I	III	III	I	X	I	II	I	III	II	III	III	II
	AI (56.12)	X	X	X	I	I	I	I	I	I	X	I	X	I	I	X
Wings	**WO** (89.93)	I	I	I	III	I	II	III	II	I	I	III	II	III	II	I
	WM (46.76)	X	X	X	X	X	X	I	X	X	X	X	I	I	X	X
	WI (76.26)	I	I	I	II	II	I	II	I	II	I	II	III	II	III	II
Pelvic fins	**PO** (63.31)	X	X	X	III	X	I	I	I	X	I	I	I	III	III	X
	PM (37.41)	X	X	X	I	X	X	X	X	X	X	X	X	X	III	I
	PI (82.01)	I	II	I	III	II	I	II	X	X	X	II	III	III	III	III
Tail (91.37)		III	III	III	III	II	III	III	III	III	III	III	III	III	III	III
Claspers* (86.42)		I	I	II	III	I	II	III	II	I	II	III	I	–	III	X

Sc: scattered; D: dense; Sm: small; L: large; B: both; N: none; X: 0 CC: colouration coverage; I: 0-33%; II: 33-66%; III: 66-100% of coverage.
**Claspers were only assessed on males, and for females, the symbol " –" was used.*

Table II2. *(Continued)*

Appearance and areas (individuals with expressed character, %)		**Individuals examined** (CC, %)														
		76 (4.5)	**77** (19)	**78** (14.6)	**79** (36.3)	**80** (0)	**81** (90)	**82** (72.7)	**83** (16.3)	**84** (45.7)	**85** (54.9)	**86** (0)	**87** (92.3)	**88** (68.5)	**89** (85.1)	**90** (64)
Scattering of the blotches		D	B	D	D	N	D	D	D	D	D	N	D	D	D	D
Size of the blotches		Sm	L	L	L	N	L	L	L	L	L	N	L	B	L	B
Snout	**SO** (46.04)	X	I	I	X	X	X	I	I	X	I	X	I	X	X	X
	SI (27.34)	X	X	X	X	X	I	I	I	X	X	X	II	X	I	I
Thorax	**TO** (41.01)	X	X	X	I	X	III	X	X	X	II	X	III	X	III	X
	TM (47.83)	X	X	X	X	X	III	III	I	X	I	X	III	III	III	III
	TI-A (33.81)	X	I	X	X	X	II	II	I	II	X	X	I	X	I	I
	TI-P (62.59)	X	I	X	I	X	III	II	I	I	I	X	III	I	II	I
Abdomen	**AO** (92.81)	I	II	I	II	X	III	III	III	III	III	X	III	III	III	III
	AI (56.12)	X	X	I	I	X	II	II	X	II	I	X	II	I	II	X
Wings	**WO** (89.93)	I	I	II	II	X	III	III	I	III	III	X	III	III	III	III
	WM (46.76)	X	X	X	I	X	III	II	X	I	I	X	III	I	III	III
	WI (76.26)	I	II	I	II	X	III	III	X	II	I	X	III	III	III	II
Pelvic fins	**PO** (63.31)	X	I	II	X	X	III	III	X	I	II	X	III	III	III	III
	PM (37.41)	X	X	X	X	X	III	I	X	X	X	X	III	X	III	II
	PI (82.01)	X	II	II	II	X	III	III	II	III	III	X	III	III	III	III
Tail (91.37)		II	III	III	III	X	III	III	X	III	III	X	III	III	III	III
Claspers* (86.42)		X	–	–	–	–	III	II	–	I	–	–	–	–	III	–

Sc: scattered; D: dense; Sm: small; L: large; B: both; N: none; X: 0 CC: colouration coverage; I: 0-33%; II: 33-66%; III: 66-100% of coverage.
**Claspers were only assessed on males, and for females, the symbol " –" was used.*

Table II2. *(Continued)*

Appearance and areas (individuals with expressed character, %)		**Individuals examined** (CC, %)														
		91 (46.6)	**92** (25.3)	**93** (78.8)	**94** (29.8)	**95** (92.5)	**96** (17.4)	**97** (6.2)	**98** (4.6)	**99** (11.2)	**100** (8.6)	**101** (49.7)	**102** (8.1)	**103** (63.3)	**104** (63.1)	**105** (49)
Scattering of the blotches		B	D	D	B	B	B	D	B	D	B	B	D	B	D	D
Size of the blotches		B	L	L	L	L	B	L	B	L	B	L	L	Sm	L	L
Snout	**SO** (46.04)	X	X	X	I	I	X	X	X	X	I	X	X	III	I	I
	SI (27.34)	X	X	X	I	I	X	X	X	X	X	X	X	II	I	II
Thorax	**TO** (41.01)	X	X	III	X	X	X	X	X	X	X	X	X	III	I	I
	TM (47.83)	II	X	III	X	X	X	I	X	I	X	X	X	III	II	I
	TI-A (33.81)	I	X	X	X	X	X	X	X	X	X	X	I	X	X	II
	TI-P (62.59)	I	II	II	I	I	X	X	X	X	X	I	X	X	II	II
Abdomen	**AO** (92.81)	III	II	III	I	I	II	I	X	II	I	II	I	III	III	III
	AI (56.12)	X	X	II	I	I	X	X	X	X	X	X	X	I	II	II
Wings	**WO** (89.93)	III	X	III	II	II	I	X	I	I	I	III	I	III	III	III
	WM (46.76)	I	X	III	I	I	X	X	X	X	X	I	X	II	I	X
	WI (76.26)	II	III	III	II	II	I	I	I	X	I	III	I	III	II	II
Pelvic fins	**PO** (63.31)	X	X	III	X	X	X	X	X	X	X	III	X	III	II	I
	PM (37.41)	X	X	II	X	X	X	X	X	X	X	I	X	III	II	I
	PI (82.01)	II	III	III	II	II	I	I	X	I	I	II	I	II	III	III
Tail (91.37)		III	III	III	III	III	III	II	II	I	III	II	III	II	III	III
Claspers* (86.42)		II	X	II	II	II	–	X	–	X	–	–	I	–	–	–

Sc: scattered; D: dense; Sm: small; L: large; B: both; N: none; X: 0 CC: colouration coverage; I: 0-33%; II: 33-66%; III: 66-100% of coverage.
**Claspers were only assessed on males, and for females, the symbol " –" was used.*

Table II2. *(Continued)*

Appearance and areas (individuals with expressed character, %)		**Individuals examined** (CC, %)														
		106 (49.8)	**107** (34.4)	**108** (10.2)	**109** (3.7)	**110** (30)	**111** (11.8)	**112** (78.4)	**113** (70.1)	**114** (17.7)	**115** (4)	**116** (93.5)	**117** (96.6)	**118** (90.7)	**119** (41.2)	**120** (82.5)
Scattering of the blotches		D	D	B	B	B	B	D	D	B	D	D	D	D	D	D
Size of the blotches		B	L	B	B	B	L	L	L	B	L	L	L	L	L	L
Snout	**SO** (46.04)	X	X	X	X	I	I	I	X	I	X	III	III	II	I	I
	SI (27.34)	X	X	X	X	I	X	II	X	I	X	III	III	II	X	I
Thorax	**TO** (41.01)	X	X	X	X	I	X	I	X	I	X	III	III	III	I	I
	TM (47.83)	II	X	X	X	I	X	III	III	I	X	III	III	III	X	III
	TI-A (33.81)	X	X	X	X	X	X	II	X	I	X	III	III	II	I	II
	TI-P (62.59)	X	X	I	X	I	I	III	II	I	X	III	III	III	III	II
Abdomen	**AO** (92.81)	II	II	I	I	II	II	III	III	II	I	III	III	III	III	III
	AI (56.12)	X	I	I	X	X	X	I	I	I	X	III	III	II	I	II
Wings	**WO** (89.93)	III	III	I	I	I	I	III	III	I	I	III	III	II	I	III
	WM (46.76)	I	X	I	X	X	X	I	I	I	X	III	III	III	X	III
	WI (76.26)	III	I	X	I	III	I	III	III	I	X	III	III	III	II	III
Pelvic fins	**PO** (63.31)	III	I	I	X	X	X	III	III	I	X	III	III	III	I	III
	PM (37.41)	X	X	X	X	X	X	I	I	I	X	III	III	III	X	III
	PI (82.01)	III	II	I	I	II	X	III	III	I	I	III	III	III	III	III
Tail (91.37)		III	III	III	I	III	III	III	III	III	X	III	III	III	III	III
Claspers* (86.42)		–	III	I	–	–	I	–	–	II	X	III	III	–	–	–

Sc: scattered; D: dense; Sm: small; L: large; B: both; N: none; X: 0 CC: colouration coverage; I: 0-33%; II: 33-66%; III: 66-100% of coverage.
**Claspers were only assessed on males, and for females, the symbol " –" was used.*

Table II2. *(Continued)*

Appearance and areas (individuals with expressed character, %)		**Individuals examined** (CC, %)														
		121 (92.6)	**122** (2.1)	**123** (80.5)	**124** (96.2)	**125** (65.1)	**126** (91.1)	**127** (0)	**128** (95.3)	**129** (30.6)	**130** (95.8)	**131** (0.1)	**132** (68.8)	**133** (34.3)	**134** (39.1)	**135** (32.3)
Scattering of the blotches		D	B	D	D	D	D	N	D	B	D	D	D	B	D	D
Size of the blotches		L	L	L	L	L	L	N	L	B	L	L	L	L	L	L
Snout	**SO** (46.04)	III	X	I	III	I	I	X	III	I	II	X	X	X	X	X
	SI (27.34)	I	X	I	II	I	I	X	II	X	II	X	X	X	X	X
Thorax	**TO** (41.01)	III	X	III	III	I	III	X	III	X	III	X	III	X	X	X
	TM (47.83)	III	X	II	III	II	III	X	III	I	III	X	II	X	X	X
	TI-A (33.81)	II	X	II	II	II	I	X	II	X	III	X	X	X	X	X
	TI-P (62.59)	III	X	II	III	II	III	X	III	I	III	X	I	I	X	I
Abdomen	**AO** (92.81)	III	II	III	III	III	III	X	III	III	III	X	III	II	II	III
	AI (56.12)	III	X	II	III	III	III	X	III	I	III	X	I	I	I	I
Wings	**WO** (89.93)	III	X	III	III	III	III	X	III	II	III	X	III	II	III	I
	WM (46.76)	III	X	III	III	X	III	X	III	I	III	X	I	X	I	I
	WI (76.26)	III	X	III	III	III	III	X	III	I	III	X	III	II	I	III
Pelvic fins	**PO** (63.31)	III	X	III	III	III	III	X	III	X	III	I	III	I	I	X
	PM (37.41)	III	X	I	III	III	III	X	III	I	III	X	X	X	X	X
	PI (82.01)	III	I	III	III	III	III	X	III	III	III	X	III	II	III	III
Tail (91.37)		III	X	III	III	III	III	X	III	III	III	X	III	III	III	III
Claspers* (86.42)		–	–	–	–	–	III	–	III	II	III	–	III	I	III	II

Sc: scattered; D: dense; Sm: small; L: large; B: both; N: none; X: 0 CC: colouration coverage; I: 0-33%; II: 33-66%; III: 66-100% of coverage.
**Claspers were only assessed on males, and for females, the symbol " –" was used.*

Table II2. *(Continued)*

Appearance and areas (individuals with expressed character, %)		**Individuals examined** (CC, %)			
		136 (90.4)	**137** (63.5)	**138** (63.2)	**139** (85.8)
Scattering of the blotches		D	B	D	D
Size of the blotches		L	B	L	L
Snout	**SO** (46.04)	III	X	II	I
	SI (27.34)	I	X	X	I
Thorax	**TO** (41.01)	III	X	II	III
	TM (47.83)	III	II	II	III
	TI-A (33.81)	II	X	II	I
	TI-P (62.59)	III	I	I	III
Abdomen	**AO** (92.81)	III	III	III	III
	AI (56.12)	II	I	I	II
Wings	**WO** (89.93)	III	III	III	III
	WM (46.76)	III	I	I	III
	WI (76.26)	III	III	III	III
Pelvic fins	**PO** (63.31)	III	III	III	II
	PM (37.41)	III	I	II	II
	PI (82.01)	III	III	III	III
Tail (91.37)		III	III	III	III
Claspers* (86.42)		III	III	III	III

The explanation of the terminology can be found on the previous page.

Appendix III. R script

###North Atlantic distribution and L50 analysis

```
setwd("~/Tromsø/UiT/Isskate Masteroppgaver/Analysis/N-Atlantic
distribution data")

nadah = read.delim("nadah_nou.txt")

summary(nadah)

names(nadah)
attach(nadah)
attach(mat)

library(ggOceanMaps)
library(ggplot2, ggspatial)

#
##### Creating a map with the entirety of the data #####
#Plain map
basemap(limits = c(-45,35,55,90), bathymetry = TRUE)

#
basemap(limits = c(-45,35,55,90), bathymetry = TRUE) +
  geom_spatial_point(data=nadah, aes(x = LONG, y = LAT), size =
1, color = pal_all)

#"Real" base data
nadah_ <- subset(nadah, YEAR > 2008)
#
##### Subsetting the data for the distribution analysis -->
TL>92, Year > 2008, and extra surveys #####
nadah_dis <- subset(nadah, SURVEY != "Jan Mayen" & SURVEY !=
"MarBank" & SURVEY != "SW Ummanaq" &
                    SURVEY != "TUNU")
nadah_dis <- subset(nadah_dis, TL <= 92)
nadah_dis <- subset(nadah_dis, YEAR > 2008 & YEAR <= 2019)

#
##### Creating a new variable "AREA2" and reordering the levels
from W-E #####
#New variable
nadah_dis$AREA2       <-       plyr::revalue(nadah_dis$SURVEY,
c("Ecosystem" = "Barents Sea", "Egga Nor" = "Norway",
                                                "Egga  Sor"  =
"Norway", "NORRUS" = "Barents Sea"))
#Reordering the levels
nadah_dis$AREA2    <-    factor(nadah_dis$AREA2,    levels    =
c("Greenland", "Iceland", "Faroe Islands",
```

```
"Norway", "Barents Sea"))

#
##### Transforming Year into a factor #####
nadah_dis$YEAR <- as.factor(nadah_dis$YEAR)

#
##### Creating a new variable "TL2": TL classes #####
nadah_dis$TL2 <- cut(nadah_dis$TL, breaks = c(0, 20, 40, 60, 80, 100), labels = c("<20", "20-40", "40-60", "60-80", ">80"),
                 include.lowest = TRUE)

nadah_dis$TL3 <- cut(nadah_dis$TL, breaks = c(0, 10, 20, 30, 40, 50, 60, 70, 80, 100),
                     labels = c("<10", "10-20", "20-30", "30-40", "40-50", "50-60", "60-70", "70-80", ">80"),
                     include.lowest = TRUE)

#
##### Creating a new variable "DEPTH2": DEPTH classes #####
nadah_dis$DEPTH2 <- cut(nadah_dis$DEPTH, breaks = c(0, 200, 400, 600, 800, 1000, 1200, 1400, 1600),
                        labels = c("<200", "200-400", "400-600", "600-800", "800-1000", "1000-1200", "1200-1400", ">1400"), include.lowest = TRUE)
#
##### Creating palettes #####
library(ggplot2)
library(ggsci) #Scientific Journal and Sci-Fi Themed Color Palettes for 'ggplot2'
library(RColorBrewer)
library(scales)
show_col(hue_pal()(5)) #We only need 5 colors since there is only 5 areas
#This colors are too bright. We will mute them
pal_area <- c(muted("#00BF7D", l = 70), muted("#00B0F6", l = 70), muted("#F8766D", l = 70),
              muted("#E76BF3", l = 70), muted("#A3A500", l = 70)) #Ordering the colors

Dark2 <- brewer.pal(8, "Dark2") #Looking for colors to use in our pal_nur
show_col(Dark2)
Set1 <- brewer.pal(10, "Set1") #Looking for colors to use in our pal_nur
show_col(Set1)
pal_nur <- c("#1B9E77", "#D95F02", "#999999")
show_col(pal_nur)

pal_all <- c("#FF6F00FF")
```

```
#
##### Plotting nadah_dis on a map #####
library(ggOceanMaps)
basemap(limits = c(-45,35,55,90), bathymetry = TRUE) +
  geom_spatial_point(data=nadah_dis, aes(x = LONG, y = LAT),
size = 1, color = pal_all)

#by area
basemap(limits = c(-45,35,55,90), bathymetry = TRUE) +
  geom_spatial_point(data=nadah_dis, aes(x = LONG, y = LAT,
color = AREA2), size = 1) +
  scale_color_manual(values = pal_area) + labs(color = "Area")

#by year
#2009
nadah_2009 <- subset(nadah_dis, YEAR == "2009")
y09 = basemap(limits = c(-45,35,55,90), bathymetry = TRUE,
legends = FALSE) +
  geom_spatial_point(data = nadah_2009, aes(x = LONG, y = LAT,
color = AREA2), size = 0.9) +
  scale_color_manual(values = pal_area) + theme(legend.position
= "none") + labs(title= "2009")

#2010
nadah_2010 <- subset(nadah_dis, YEAR == "2010")
y10 = basemap(limits = c(-45,35,55,90), bathymetry = TRUE,
legends = FALSE) +
  geom_spatial_point(data = nadah_2010, aes(x = LONG, y = LAT,
color = AREA2), size = 0.9) +
  scale_color_manual(values = c("#1FC382", "#56B4EF",
"#AFB133")) + theme(legend.position = "none") + labs(title=
"2010")

#2011
nadah_2011 <- subset(nadah_dis, YEAR == "2011")
y11 = basemap(limits = c(-45,35,55,90), bathymetry = TRUE,
legends = FALSE) +
  geom_spatial_point(data = nadah_2011, aes(x = LONG, y = LAT,
color = AREA2), size = 0.9) +
  scale_color_manual(values = pal_area) + theme(legend.position
= "none") + labs(title= "2011")

#2012
nadah_2012 <- subset(nadah_dis, YEAR == "2012")
y12 = basemap(limits = c(-45,35,55,90), bathymetry = TRUE,
legends = FALSE) +
  geom_spatial_point(data = nadah_2012, aes(x = LONG, y = LAT,
color = AREA2), size = 0.9) +
```

```
  scale_color_manual(values    =    c("#1FC382",    "#56B4EF",
"#DE8EE7", "#AFB133")) +
  theme(legend.position = "none") + labs(title= "2012")

#2013
nadah_2013 <- subset(nadah_dis, YEAR == "2013")
y13  =  basemap(limits  =  c(-45,35,55,90),  bathymetry  =  TRUE,
legends = FALSE) +
  geom_spatial_point(data = nadah_2013, aes(x = LONG, y = LAT,
color = AREA2), size = 0.9) +
  scale_color_manual(values    =    c("#1FC382",    "#56B4EF",
"#DE8EE7", "#AFB133")) +
  theme(legend.position = "none") + labs(title= "2013")

#2014
nadah_2014 <- subset(nadah_dis, YEAR == "2014")
y14  =  basemap(limits  =  c(-45,35,55,90),  bathymetry  =  TRUE,
legends = FALSE) +
  geom_spatial_point(data = nadah_2014, aes(x = LONG, y = LAT,
color = AREA2), size = 0.9) +
  scale_color_manual(values = pal_area) + theme(legend.position
= "none") + labs(title= "2014")

#2015
nadah_2015 <- subset(nadah_dis, YEAR == "2015")
y15  =  basemap(limits  =  c(-45,35,55,90),  bathymetry  =  TRUE,
legends = FALSE) +
  geom_spatial_point(data = nadah_2015, aes(x = LONG, y = LAT,
color = AREA2), size = 0.9) +
  scale_color_manual(values = pal_area) + theme(legend.position
= "none") + labs(title= "2015")

#2016
nadah_2016 <- subset(nadah_dis, YEAR == "2016")
y16  =  basemap(limits  =  c(-45,35,55,90),  bathymetry  =  TRUE,
legends = FALSE) +
  geom_spatial_point(data = nadah_2016, aes(x = LONG, y = LAT,
color = AREA2), size = 0.9) +
  scale_color_manual(values = pal_area) + theme(legend.position
= "none") + labs(title= "2016")

#2017
nadah_2017 <- subset(nadah_dis, YEAR == "2017")
y17  =  basemap(limits  =  c(-45,35,55,90),  bathymetry  =  TRUE,
legends = FALSE) +
  geom_spatial_point(data = nadah_2017, aes(x = LONG, y = LAT,
color = AREA2), size = 0.9) +
  scale_color_manual(values = pal_area) + theme(legend.position
= "none") + labs(title= "2017")

#2018
```

```
nadah_2018 <- subset(nadah_dis, YEAR == "2018")
y18 = basemap(limits = c(-45,35,55,90), bathymetry = TRUE,
legends = FALSE) +
  geom_spatial_point(data = nadah_2018, aes(x = LONG, y = LAT,
color = AREA2), size = 0.9) +
  scale_color_manual(values = pal_area) + theme(legend.position
= "none") + labs(title= "2018")

#2019
nadah_2019 <- subset(nadah_dis, YEAR == "2019")
y19 = basemap(limits = c(-45,35,55,90), bathymetry = TRUE,
legends = FALSE) +
  geom_spatial_point(data = nadah_2019, aes(x = LONG, y = LAT,
color = AREA2), size = 0.9) +
  scale_color_manual(values = pal_area) + theme(legend.position
= "none") + labs(title= "2019")

library(gridExtra)
grid.arrange(y09, y10, y11, y12, ncol = 2)
grid.arrange(y13, y14, y15, y16, ncol = 2)
grid.arrange(y17, y18, y19, ncol = 2)
#

##### Summary figures #####
#Area2
ggplot(nadah_dis, aes(AREA2, fill = AREA2)) +
  geom_bar(stat = "count", color = "gray0", fill = pal_area,
width = 0.7) +
  scale_fill_manual(values = pal_area) + theme_classic() +
xlab("Areas") + ylab("Number of individuals") #Fet!

ggplot(nadah_dis, aes(AREA2, fill = SEX)) + geom_bar(stat =
"count", color = "gray0", width = 0.7, position = "dodge") +
  theme_classic() + xlab("Areas") + ylab("Number of
individuals") + labs(fill = "Sex") #Fet!

ggplot(nadah_dis, aes(TL2)) + geom_bar(position="dodge",
stat="count", fill = "gray0", width = 0.8) +
  facet_wrap(~AREA2) + theme_bw() + xlab("Total Length (cm)") +
ylab("Number of individuals") #Fet!

ggplot(nadah_dis, aes(YEAR)) + geom_bar(position="dodge",
stat="count", fill = "gray0", width = 0.8) +
  facet_wrap(~AREA2) + theme_bw() + theme(axis.text.x =
element_text(angle = 45, hjust = 1)) +
  xlab("Total Length (cm)") + ylab("Number of individuals")
#Fet!


#TL2
```

```
ggplot(nadah_dis, aes(TL2)) + geom_bar(stat = "count", fill =
"gray0", width = 0.7) +
  theme_classic() + xlab("Total Length (cm)") + ylab("Number of
individuals") #Fet!

ggplot(nadah_dis, aes(TL3)) + geom_bar(stat = "count", fill =
"gray0", width = 0.7) +
  theme_classic() + xlab("Total Length (cm)") + ylab("Number of
individuals") #Fet!


#Year
ggplot(nadah_dis, aes(YEAR, fill = YEAR)) + geom_bar(stat =
"count", fill = "gray0", width = 0.7) +
  theme_classic() + theme(legend.position = "none") +
xlab("Year") + ylab("Number of individuals") #Fet!


#TL(mean)xYear (xArea2)
library(tidyr)
library(dplyr)
nadah.means <- nadah_dis %>% group_by(YEAR) %>% summarize(TLmean
= mean(TL))
nadah.means2 <- nadah_dis %>% group_by(YEAR, AREA2) %>%
summarize(TLmean = mean(TL))


ggplot(nadah.means, aes(x=YEAR, y=TLmean)) + geom_col(fill =
"gray0", width = 0.7) +
  theme_classic() + xlab("Year") + ylab("Mean total length
(cm)") #Fet!

p <- ggplot(nadah.means2, aes(x =
as.numeric(as.character(YEAR)), y = TLmean, color = AREA2)) +
  scale_color_manual(values = pal_area) + theme_classic() +
geom_point() + geom_line() +
  xlab("Year") + ylab("Mean total length (cm)") + labs(color =
"Areas") #Fet!

p + scale_x_continuous(limits = c (2009, 2019),
                       breaks = c(2009, 2010, 2011, 2012, 2013,
2014, 2015, 2016, 2017, 2018, 2019)) #Fet!

##Summaries
n_sexTL2 <- nadah_dis %>% group_by(SEX, TL2) %>% summarize(n =
n())
n_areaTL2 <- nadah_dis %>% group_by(AREA2, TL2) %>% summarize(n
= n())

#
##### Depth distribution #####
```

```
ggplot(nadah_dis,    aes(DEPTH2))    +    geom_bar(stat="count",
fill="black", width = 0.5) +
 theme_classic()  +    xlab("Depth  (m)")  +  ylab("Number  of
individuals")

ggplot(nadah_dis, aes(x = TL, y = DEPTH)) + geom_point(size =
0.9) +
  scale_y_reverse()  +  theme_classic()  +  xlab("Total  length
(cm)") +  ylab("Depth (m)")

#TLxSex
df <- ggplot(subset(nadah_dis, SEX == "f"), aes(x = TL, y =
DEPTH)) + geom_point(color = "#F8766D") +
  scale_y_reverse() + geom_smooth(method = "loess", alpha = 0.2,
size = 1, span = 1, color = "#F8766D") +
  theme_classic() + xlab("Total length (cm)") +  ylab("Depth
(m)") + labs(title = "Females")

dm <- ggplot(subset(nadah_dis, SEX == "m"), aes(x = TL, y =
DEPTH)) + geom_point(color = "#00BFC4") +
  scale_y_reverse() + geom_smooth(method = "loess", alpha = 0.2,
size = 1, span = 1, color = "#00BFC4") +
  theme_classic() + xlab("Total length (cm)") +  ylab("Depth
(m)") + labs(title = "Males")

library(gridExtra)
grid.arrange(df, dm, ncol = 2)

#TLxArea2
gl <- ggplot(subset(nadah_dis, AREA2 == "Greenland"), aes(x =
TL, y = DEPTH)) + geom_point(color = "#00BF7D") +
  scale_y_reverse() + geom_smooth(method = "loess", alpha = 0.2,
size = 1, span = 1, color = "#00BF7D") +
  xlim(0,100) + ylim(1500, 0) + theme_classic() +
  xlab("Total length (cm)") +  ylab("Depth (m)") + labs(title =
"Greenland")

is <- ggplot(subset(nadah_dis, AREA2 == "Iceland"), aes(x = TL,
y = DEPTH)) + geom_point(color = "#00B0F6") +
  scale_y_reverse() + geom_smooth(method = "loess", alpha = 0.2,
size = 1, span = 1, color = "#00B0F6") +
  xlim(0,100) + ylim(1500, 0) + theme_classic() +
  xlab("Total length (cm)") +  ylab("Depth (m)") + labs(title =
"Iceland")

fo <- ggplot(subset(nadah_dis, AREA2 == "Faroe Islands"), aes(x
= TL, y = DEPTH)) + geom_point(color = "#F8766D") +
  scale_y_reverse() + geom_smooth(method = "loess", alpha = 0.2,
size = 1, span = 1, color = "#F8766D") +
  xlim(0,100) + ylim(1500, 0) + theme_classic() +
```

```
  xlab("Total length (cm)") +  ylab("Depth (m)") + labs(title =
"Faroe Islands")

no <- ggplot(subset(nadah_dis, AREA2 == "Norway"), aes(x = TL,
y = DEPTH)) + geom_point(color = "#E76BF3") +
  scale_y_reverse() + geom_smooth(method = "loess", alpha = 0.2,
size = 1, span = 1, color = "#E76BF3") +
  xlim(0,100) + ylim(1500, 0) + theme_classic() +
  xlab("Total length (cm)") +  ylab("Depth (m)") + labs(title =
"Norway")

bs <- ggplot(subset(nadah_dis, AREA2 == "Barents Sea"), aes(x =
TL, y = DEPTH)) + geom_point(color = "#A3A500") +
  scale_y_reverse() + geom_smooth(method = "loess", alpha = 0.2,
size = 1, span = 1, color = "#A3A500") +
  xlim(0,100) + ylim(1500, 0) + theme_classic() +
  xlab("Total length (cm)") +  ylab("Depth (m)") + labs(title =
"Barents Sea")


grid.arrange(gl, is, ncol = 2, nrow = 2)
grid.arrange(fo, no, bs, ncol = 2)

#Boxplot for sex
ggplot(subset(nadah_dis,   SEX   !=   is.na(SEX)),   aes(x=SEX,
y=DEPTH)) + geom_boxplot() + theme_classic() +
  xlab("Sex") +  ylab("Depth (m)")

#

##### Subsetting nadah for the L50 analysis #####
mat <- subset(nadah, MATURITY != is.na(nadah$MATURITY) & SEX !=
is.na(nadah$SEX))
#Adding the same new variables as in nadah_dis
mat$AREA2 <- cut(mat$LONG, breaks = c (-28.0612, 0, 85.7833),
labels = c("West NAO", "East NAO"),
                 include.lowest = TRUE)


mat$YEAR <- as.factor(mat$YEAR)

mat$TL2 <- cut(mat$TL, breaks = c(0, 20, 40, 60, 80, 100), labels
= c("<20", "20-40", "40-60", "60-80", ">80"),
                     include.lowest = TRUE)



#
##### Plotting mat into a map #####
basemap(limits = c(-45,35,55,90), bathymetry = TRUE) +
  geom_spatial_point(data=mat, aes(x = LONG, y = LAT), size =
1, color = pal_all)
```

```
#
##### L50 General #####
library(sizeMat)

#Females
mat_f <- subset(mat, SEX == "f")
f_ogive_bayes   =   gonad_mature(mat_f,   varNames   =   c("TL",
"MATURITY"), inmName = c("1", "2"),
                             matName  =  c("3a",  "3b",  "4a"),
method = "bayes", niter = 999)
print(f_ogive_bayes)

plot(f_ogive_bayes,  xlab  =  "Total  length  (cm)",  ylab  =
"Proportion mature", col = c("dodgerblue4", "firebrick3"),
     onlyOgive = TRUE)

#Males
mat_m <- subset(mat, SEX == "m")
m_ogive_bayes   =   gonad_mature(mat_m,   varNames   =   c("TL",
"MATURITY"), inmName = c("1", "2"),
                             matName   =   c("3a",   "3b","4a"),
method = "bayes", niter = 999)
print(m_ogive_bayes)
plot(m_ogive_bayes,  xlab  =  "Total  length  (cm)",  ylab  =
"Proportion mature", col = c("dodgerblue4", "firebrick3"),
     onlyOgive = TRUE)

#
##### L50 Iceland #####
#Females
mat_f_I <- subset(mat_f, AREA == "Iceland")
f_ogive_bayes_I  =  gonad_mature(mat_f_I,  varNames  =  c("TL",
"MATURITY"), inmName = c("1", "2"),
                               matName = c( "3a", "3b", "4a"),
method = "bayes", niter = 999)
print(f_ogive_bayes_I)
plot(f_ogive_bayes_I,  xlab  =  "Total  length  (cm)",  ylab  =
"Proportion mature", col = c("dodgerblue4", "firebrick3"),
     onlyOgive = TRUE)

#Males
mat_m_I <- subset(mat_m, AREA == "Iceland")
m_ogive_bayes_I  =  gonad_mature(mat_m_I,  varNames  =  c("TL",
"MATURITY"), inmName = c("1", "2"),
                               matName  = c("3a",  "3b",  "4a"),
method = "bayes", niter = 999)
print(m_ogive_bayes_I)
plot(m_ogive_bayes_I,  xlab  =  "Total  length  (cm)",  ylab  =
"Proportion mature", col = c("dodgerblue4", "firebrick3"),
     onlyOgive = TRUE)
```

```
#
##### L50 Barents Sea #####
#Females
mat_f_ENAO <- subset(mat_f, AREA2 == "East NAO")
mat_f_B <- subset(mat_f_ENAO, LAT >= 70)

f_ogive_bayes_B  =  gonad_mature(mat_f_B,  varNames  =  c("TL",
"MATURITY"), inmName = c("1", "2"),
                               matName = c( "3a", "3b", "4a"),
method = "bayes", niter = 999)
print(f_ogive_bayes_B)
plot(f_ogive_bayes_B,  xlab  =  "Total  length  (cm)",  ylab  =
"Proportion mature", col = c("dodgerblue4", "firebrick3"),
     onlyOgive = TRUE)

#Males
mat_m_ENAO <- subset(mat_m, AREA2 == "East NAO")
mat_m_B <- subset(mat_m_ENAO, LAT >= 70)

m_ogive_bayes_B  =  gonad_mature(mat_m_B,  varNames  =  c("TL",
"MATURITY"), inmName = c("1", "2"),
                               matName  =  c("3a",  "3b",  "4a"),
method = "bayes", niter = 999)
print(m_ogive_bayes_B)
plot(m_ogive_bayes_B,  xlab  =  "Total  length  (cm)",  ylab  =
"Proportion mature", col = c("dodgerblue4", "firebrick3"),
     onlyOgive = TRUE)

#
##### Plotting the ogives together #####
par(mfrow = c(2,3))
plot(f_ogive_bayes,  xlab  =  "Total  length  (cm)",  ylab  =
"Proportion mature (%)",
     col = c("dodgerblue4", "firebrick3"), onlyOgive = TRUE) +
title( main = "A", adj = 0) +
  plot(f_ogive_bayes_I,  xlab  =  "Total  length  (cm)",  ylab  =
"Proportion mature (%)",
       col = c("dodgerblue4", "firebrick3"), onlyOgive = TRUE)+
title( main = "C", adj = 0) +
  plot(f_ogive_bayes_B,  xlab  =  "Total  length  (cm)",  ylab  =
"Proportion mature (%)",
       col  =  c("dodgerblue4",  "firebrick3"),  onlyOgive  =  TRUE)
+ title( main = "E", adj = 0) +
  plot(m_ogive_bayes,  xlab  =  "Total  length  (cm)",  ylab  =
"Proportion mature (%)",
       col  =  c("dodgerblue4",  "firebrick3"),  onlyOgive  =  TRUE)
+ title( main = "B", adj = 0) +
  plot(m_ogive_bayes_I,  xlab  =  "Total  length  (cm)",  ylab  =
"Proportion mature (%)",
```

```
       col = c("dodgerblue4", "firebrick3"), onlyOgive = TRUE)
+ title( main = "D", adj = 0) +
  plot(m_ogive_bayes_B, xlab = "Total length (cm)", ylab =
"Proportion mature (%)",
       col = c("dodgerblue4", "firebrick3"), onlyOgive = TRUE)
+ title( main = "F", adj = 0)




#
##### Extrapolating L50 to nadah_dis #####
library(dplyr)
#Converting MATURITY into a binomial factor -> MAT2
nadah_dis$MAT2 <- case_when(nadah_dis$MATURITY == "1" ~
"Immature", nadah_dis$MATURITY == "2" ~ "Immature",
                            nadah_dis$MATURITY == "3a" ~
"Mature", nadah_dis$MATURITY == "3b" ~ "Mature",
                            nadah_dis$MATURITY == "4a" ~
"Mature")

#Extrapolating L50 to the rest of observations which have
information on SEX -> MAT3
nadah_dis$MAT3 <- case_when(nadah_dis$MAT2 == "Immature" ~
"Immature",
                            nadah_dis$MAT2 == "Mature" ~
"Mature",
                            nadah_dis$SEX == "f" & nadah_dis$TL
>= 70.5 ~ "Mature",
                            nadah_dis$SEX == "f" & nadah_dis$TL
< 70.5 ~ "Immature",
                            nadah_dis$SEX == "m" & nadah_dis$TL
>= 66.8 ~ "Mature",
                            nadah_dis$SEX == "m" & nadah_dis$TL
< 66.8 ~ "Immature")


#Classifying hatchlings, mature females and the rest of the data
from MAT3 -> MAT4
nadah_dis$MAT4 <- case_when(nadah_dis$MAT3 == "Immature" &
nadah_dis$TL <= 20 ~ "Hatchlings",
                            nadah_dis$MAT3 == "Immature" &
nadah_dis$TL > 20 ~ "Others",
                            nadah_dis$MAT3 == "Mature" &
nadah_dis$SEX == "f" ~ "Mature females",
                            nadah_dis$MAT3 == "Mature" &
nadah_dis$SEX == "m" ~ "Others")

#Plottiong on a map
nadah_nurs <- subset(nadah_dis, MAT4 != is.na(MAT4))
nadah_nurs1 <- subset(nadah_nurs, MAT4 != "Others")
```

```
nadah_nurs2 <- subset(nadah_nurs, MAT4 == "Others")

#This map has the grey dots on the background and the relevant
dots (hatchlings and mature females) on the foreground
basemap(limits = c(-45,35,55,90), bathymetry = TRUE) +
  geom_spatial_point(data=nadah_nurs2, aes(x = LONG, y = LAT),
size = 1, color = pal_nurs2) +
  geom_spatial_point(data=nadah_nurs1, aes(x = LONG, y = LAT,
color = MAT4), size = 1) +
  scale_color_manual(values = pal_nurs1) + labs(color =
"Individuals")

#This map was used to get the right legend for the colors and
was later pasted into the map above.
basemap(limits = c(-45,35,55,90), bathymetry = TRUE) +
  geom_spatial_point(data=nadah_nurs, aes(x = LONG, y = LAT,
color = MAT4), size = 1) +
  scale_color_manual(values = pal_nur) + labs(color =
"Individuals")
#
```

<u>###Venrtal colouration analysis</u>

```
setwd("~/Tromsø/UiT/Isskate Masteroppgaver/Analysis")
#Upload/read the data file
issk=read.delim("issk.txt")

summary(issk)
attach(issk)
library(ggplot2)
library(ggOceanMaps)
library(ggpubr)

#
##### Plotting the data on a map #####
basemap(limits = c(-45,35,55,90), bathymetry = TRUE) +
        geom_spatial_point(data=issk, aes(x = Longitude, y =
Latitude), size = 1, color ="#FF6F00FF")

#
##### Creating new variables #####
issk$Coverage2 <- cut(issk$Coverage, breaks = c(0, 0.2, 0.4,
0.6, 0.8, 1), include.lowest = TRUE,
                      labels = c("<0.2","0.2-0.4","0.4-
0.6","0.6-0.8",">0.8"))

issk$TL2 <- cut(issk$TL, breaks = c(0, 200, 400, 600, 800, 1000),
include.lowest = TRUE,
                labels = c("<20","20-40","40-60","60-
80",">80"))
```

```
issk$AREA2 <- cut(issk$Longitude, breaks = c (-52.337 , 0, 
42.45), labels = c("West NAO", "East NAO"),
                  include.lowest = TRUE)

issk$Depth2 <- cut(issk$Depth, breaks = c(92, 200, 400, 600, 
800, 1000, 1200, 1400), include.lowest = TRUE,
                   labels = c("<200", "200-400", "400-600", 
"600-800", "800-1000", "1000-1200", "1200-1400"))

#
##### Chi-square test #####
##Coverage2 x Sex
#Contingency table
table(issk$Coverage2, issk$Sex)
##Coverage2 x Sex
chisq.test(table(issk$Coverage2, issk$Sex)) #Chisq = 8.632, df 
= 4, p-value = 0.07099 --> INDEPENDENT
summary(table(issk$Coverage2, issk$Sex))

##Coverage2 x TL2
table(issk$Coverage2, issk$TL2)
chisq.test(table(issk$Coverage2, issk$TL2)) #IT DOESN'T WORK BC 
THERE ARE GROUPS THAT DON'T HAVE ENOUGH EXPECTED COUNTS -> 
FISHER.TEST()
fisher.test(table(issk$Coverage2, issk$TL2), workspace = 2e7, 
simulate.p.value=TRUE) #p-value = 0.09245 --> INDEPENDENT

##Coverage2 x Area2
table(issk$Coverage2, issk$AREA2)
chisq.test(table(issk$Coverage2, issk$AREA2)) #X-squared = 
37.91, df = 4, p-value = 1.169e-07 --> DEPENDENT!!

ggplot(issk) + aes(x = AREA2, fill = Coverage2) + 
geom_bar(position = "fill", width = 0.6) +
        scale_fill_manual(values = c("#d9d9d9", "#bdbdbd", 
"#969696", "#636363", "#252525")) +
        xlab("Areas") + ylab("Number of individuals (%)") + 
labs(fill = "Coverage \npercentage") + theme_classic()

##Coverage2 x Depth2
table(issk$Coverage2, issk$Depth2)
fisher.test(table(issk$Coverage2, issk$Depth2), workspace = 
2e7, simulate.p.value=TRUE) #p-value = 0.2179 --> INDEPENDENT
```