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Maturation patterns and genetic diversity of the spinytail skate *Bathyraja spinicauda*

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Abstract

With the expansion of fisheries into deeper waters and climate change, it is increasingly important to determine the status of the species affected by these changes. One of these species is the spinytail skate *Bathyraja spinicauda*, an understudied skate species with vulnerable life history traits such as slow maturation and a low number of offspring. To address the lack of basic knowledge about the species, this thesis utilized individuals collected during multiple surveys in Norwegian and other waters over the past 15 years, and focused on morphometric and genetic analyses as well as reviewing the existing literature on the target species and its genus. The morphometric analyses were performed to identify patterns in sexual dimorphism, maturation, and spatial distribution. The genetic analysis was carried out using the mitochondrial NADH2 marker for samples from the Barents Sea, the North Norwegian Sea, the South Norwegian Sea, the Faroes, and Greenland. Significant morphometric differences were found between the sexes and throughout growth. No direct correlation was found between depth and total length; however, there was a link in distribution wherein larger individuals were found on the Barents Shelf compared to the Norwegian Sea. Notably, there were no mature females in the collected samples. The estimated size at maturity (L50) for males was determined to be 131 cm. This suggests that maturity is reached at approximately 72% of the maximum total length for the species, which is within the range 41.9-90.9% for comparable sized *Bathyraja* species. There was no clear genetic population structure found between the study regions, indicating either high genetic connectivity or limitations of the chosen markers, or potentially both. This study identified the knowledge gaps that should be further investigated for the species, such as the total population size and the scarcity of mature females. Additionally, the study emphasizes the necessity of employing more fine-scale genetic methods to better assess the population structure.

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1. Introduction

1.1. Chondrichthyans: a vulnerable group

As climate change and human interference continue to reshape our planet, we are facing a rise in the number of present and potential future species extinctions (Di Marco et al., 2018). Chondrichthyans (sharks, skates, rays and chimaeras) are particularly sensitive to climate change and human activities (Simpfendorfer & Kyne, 2009), due to their K-strategist life history traits such as slow development and low fecundity (Stevens et al., 2000; Elliott et al., 2020). Consequently, they are slow to recover from disturbances and thus more vulnerable to extinction compared to many other species (Reynolds et al., 2005; Baker et al., 2009). Due to their ecological and economic importance (Stevens et al., 2000), as well as the observed decrease in population size, chondrichthyans are receiving increased interest in research (Ferretti et al., 2010; Shiffman et al., 2020). Nevertheless, larger coastal and pelagic chondrichthyans such as the great white shark *Carcharodon carcharias* dominate research efforts compared to deep-sea chondrichthyans, possibly due to accessibility and public interest (Shiffman et al., 2020); however, a change may be in motion (Veríssimo et al., 2012; Finucci et al., 2021; Jac et al., 2022). While deep-sea chondrichthyans such as deep-sea skates might benefit from being less accessible to most fisheries (Finucci et al., 2024), their vulnerable life history traits are even more extreme than those of their shallower relatives (García et al., 2008). As fisheries are continuing to go deeper and into areas that were previously not as accessible for them, some of these deep-sea bottom-dwelling species will be affected by fisheries, either as catch or bycatch. As mesopredators, skates play an important ecological role, influencing prey abundance and serving as prey for other species (Ebert & Bizzarro, 2007), making their conservation vital for maintaining ecosystem balance (Dulvy et al., 2014). For this reason, urgent knowledge gaps on their life histories and distribution dynamics must be addressed and conservation measures implemented where needed, by both national and local governments. This is essential in order to prevent a potential irreversible loss of biodiversity (Hoffmann et al., 2015; Luther et al., 2016). To undertake conservation actions, it is necessary to identify which species are most vulnerable to extinction through periodic assessments such as those of the Red List of Threatened Species by the International Union for Conservation of Nature (IUCN), which classifies the conservation status of the

species. Recent IUCN assessments estimate that approximately one quarter of chondrichthyans globally are threatened and the majority of data deficient elasmobranchs (57.6%) are located on deep-sea slopes (Dulvy et al., 2014).

1.2. The spinytail skate - distribution and population trends

The spinytail skate *Bathyraja spinicauda* belongs to the family of softnose skates (Arhynchobatidae) within the Rajiformes order. There are 56 recognized species within the genus *Bathyraja* today, of which 17 are found in the Atlantic Ocean. The spinytail skate's distribution range extends from the Northwest to the Northeast Atlantic and to the Arctic Ocean (Mecklenburg et al., 2018) (Figure 1), with a documented preference for depths between 140 m and 1650 m (Last et al., 2016) and a temperature range of -1.5 to 7.5°C (Moller et al., 2018).

Due to the relatively small number of individuals that have been caught or documented by scientific surveys, there is limited knowledge on the species' abundance (Pollom et al., 2020a). For example, between 1996 and 2003, the quantity of spinytail skate catches made up less than 1% of the total skate catches by the Polar Research Institute of Marine Fisheries and Oceanography (PINRO) in the Barents Sea (Drevetnyak et al., 2005). Furthermore, despite being of low commercial value, the species is vulnerable to fishing in the form of bycatch. The expansion of fisheries and climate change are currently considered to be the spinytail skate's two main threats (Devine et al., 2006; Pollom et al., 2020a). These factors give it the IUCN conservation status of being Near Threatened on a global level (Pollom et al., 2020a).

However, assessing the conservation status is difficult given that there are no true population size estimates, especially with skates and rays caught as bycatch often not being identified (Stevens et al., 2000). Despite these challenges, the spinytail skate is still considered a common species since it is regularly caught (Mecklenburg et al., 2018; Dolgov & Prozorkevich, 2022). Nevertheless, there is limited catch data, making the assessment of the population status challenging; however, some changes in abundance and distribution have already been observed in the Northwest Atlantic (Devine et al., 2006) and the Barents Sea (Dolgov & Prozorkevich, 2022). For instance, in the 1970s, the Northwest Atlantic saw an

increase in deep-water fishing due to lower fish availability in shallower water, resulting in an increase in by-catch and a decrease in prey availability. This led to a drastic population decline for the spinytail skate (Devine et al., 2006). In the Barents Sea, there have also been observations of a notable change in the distribution range of the spinytail skate between 2004 and 2021, with a northward shift and a slight shift of the eastern border to the west (Dolgov & Prozorkevich, 2022). Despite this shift in distribution, no negative population trend has been found in the Barents Sea between 2004 and 2016 (Knutsen et al., 2017). More research must be done on the behavior and life history of the species in order to comprehend how it will react to increasing temperatures (Doney et al., 2012) and the expansion of fisheries (Villasante et al., 2012), as well as to develop effective conservation strategies.

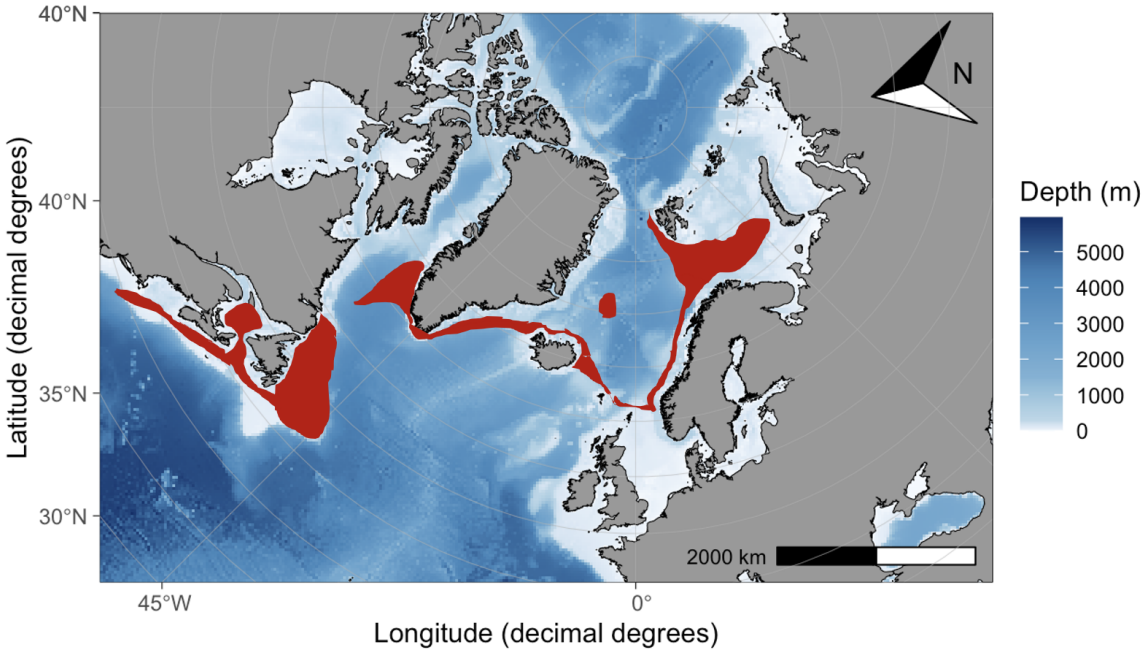

Figure 1: *Distribution range of* Bathyraja spinicauda

1.3. The spinytail skate - morphology and life history

The spinytail skate is characterized by a uniformly brown or grey dorsal side, and a white underside with a darker color on the posterior edge of the pectoral and pelvic fins, as well as the tail (Mecklenburg et al., 2018) (visualized in Figure 2). Furthermore, it has a pointed snout and a single row of 21-26 thorns on the median row of its tail (Bigelow & Schroeder, 1954; Sulak et al., 2009). The spinytail skate can grow to a total length of up to 182 cm

(Dolgov et al., 2005), though an unverified specimen of 330 cm was reported (Baranenkova et al., 1962), likely a misidentification. Despite the distinct morphological characteristics of the species, there have occasionally been misidentifications with other species, such as the blue skate *Dipturus batis* or the flapper skate *(Dipturus intermedius*) due to shared morphological features, leading to inaccuracies in distribution and size data (Dolgov & Prozorkevich, 2022).

Figure 2: *Dorsal and ventral views of a* Bathyraja spinicauda *female*

While skates undergo direct development, wherein juveniles closely resemble adults, there are notable differences in body proportions, such as the shorter tail length in adults relative to the body proportions (Bigelow & Schroeder, 1954). There is also a suspected disparity in distribution between immature and mature individuals, wherein mature individuals migrate to warmer waters in order to spawn (Krefft, 1956; Baranenkova, 1968). Much like other skate species, the spinytail skate exhibits sexual dimorphism, where males have claspers, a dent in the pectoral fin, and alar thorns near the disc edge (Figure 3).

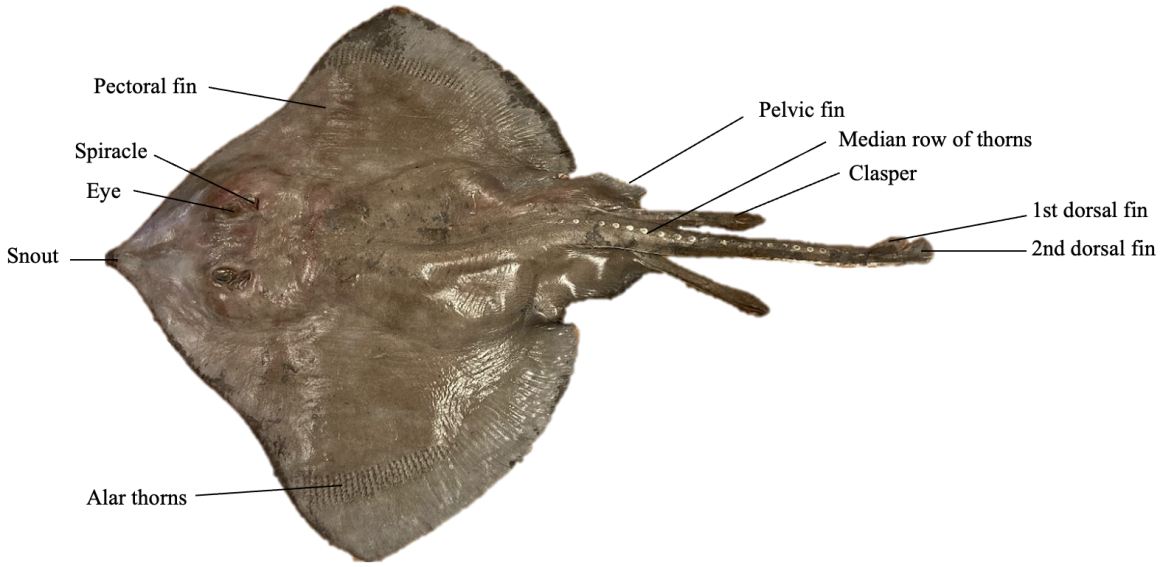

Figure 3: *Dorsal view of a mature male* Bathyraja spinicauda

There is still a lack of knowledge when it comes to the maturation of the spinytail skate since relatively few sexually mature female spinytail skates have been caught and reported in the past; however, one mature female of 164 cm was recorded in September 1956 in the Barents Sea at a depth of 200 meters (Koefoed, 1956). This could be explained by the low abundance of the species or by the uncertainties surrounding the species' development and behavior. This makes estimating the species' size and age at maturity, as well as understanding its reproductive behavior challenging. Insights on the maturation of the species can be gained through comparison with other species in the genus. For instance, the graytail skate *Bathyraja griseocauda* has an estimated size at maturity of 94.5 and 108.2 cm for males and females, respectively (Arkhipkin et al., 2008).

For the early life history stages of the spinytail skate, it is known that the egg cases have a maximum length of 160 mm (not including the horns), which is large compared to other Barents Sea skate species such as the Arctic skate *Amblyraja hyperborea* and the sailray *Rajella lintea*, which have a maximum egg capsule length of 133 and 116 mm, respectively (Forsberg et al., 2018). Upon hatching, the total length of a spinytail skate is around 21 cm (Last et al., 2016). It has been suggested that the period of embryonic development is 5-6 thousand degree-days, meaning 3.5-4 years in the Barents Sea with a 0-5 °C temperature range (Berestovskii, 1994). However, this study did not successfully incubate a spinytail skate

egg and is therefore based on extrapolation from incubation data of the thorny skate *Raja radiata*. The spinytail skate has also been reported to use egg nurseries, which can be identified as areas with high densities of deposited eggs (Lennon et al., 2021). Due to the destructive nature of identifying egg nurseries through trawling, little information is available. The median spinytail skate egg nursery depth was found to be 1825 m on the Mid-Atlantic ridge (Lennon et al., 2021), challenging the known depth distribution range of the species.

1.4. The spinytail skate - diet and behavior

Based on stomach sample studies, the spinytail skate predominantly feeds on chordates. These include haddock *Melanogrammus aeglefinus*, greater eelpout *Lycodes esmarkii*, cod *Gadus morhua*, Arctic rockling *Gaidropsarus argentatus*, and redfish *Sebastes* sp. (Koefoed, 1956; Baranenkova et al., 1968; Dolgov, 2005; Kleiven, Master thesis). Arthropods and polychaetes are also common prey for the species, with some variation depending on the size and location of the skate (Dolgov, 2005; Gonzales et al., 2006). The species undergoes an ontogenetic shift, leading to an increase in trophic level. For instance, the diet of juveniles consists of smaller prey such as the northern krill (*Meganyctiphnes norvegica*) (Kleiven, Master thesis), whereas adults feed preferentially on fish (Ebert & Stehmann, 2013). The preference for arthropods also increases with size in spinytail skates (Kleiven, Master thesis). Furthermore, skates exhibit opportunistic feeding behaviors. For example, spinytail skates have been found to feed on other skates, such as the round skate *Rajella fyllae* (Dolgov, 2005) and carcasses (Byrkjedal et al., 2014; Kleiven, Master thesis).

1.5. Population genetic diversity and migration

A population genetic analysis across the geographic range of a given species can provide information on its evolution, migration patterns and connectivity; that is, the movement of genes across time and space. A population can be defined as a group of individuals of the same species living in close enough proximity for any member of the group to be able to reproduce with another member of the group (Waples & Gaggiotti, 2006). However, the challenge lies in determining quantitative criteria to be able to distinguish between populations (Waples & Gaggiotti, 2006). Studying genetic diversity within and among defined populations is crucial when determining where conservation efforts should be

targeted (Larson et al., 2017; Marandel et al., 2017). This is because population decline can lead to a loss of genetic diversity through the increase of population fragmentation, which can increase a species' susceptibility to changes in environmental conditions (Frankham et al., 2019). Inversely, high connectivity could indicate a potential for recolonization if the species in question, here the spinytail skate, were to disappear from a region (Aurelle et al., 2020; Hemmingmoore et al., 2020)

To understand the genetic differences and the migration patterns of a species, it is important to study the barriers to migration. For instance, depth and currents can act as barriers to migration because of temperature preferences (Riginos & Liggins, 2013). For the spinytail skate, this could mean that there is a dispersal route between the eastern and western parts of its distribution range by crossing the Greenland-Scotland ridge (Hansen & Østerhus, 2000) instead of crossing the deeper waters. Additionally, temperature shifts can cause the species to migrate to more suitable areas (Baranenkova et al., 1962; Dolgov & Prozorkevich, 2022). Potential genetic differences between populations can also be a result of geographical isolation during the last ice age (Hewitt, 1996) or local adaptation to abiotic and biotic conditions (Savolainen et al., 2013). Currently, the potential migration patterns of the spinytail skate remain unknown, and estimating them is challenging due to the considerable variation in migration distances across skate species. For example, the blue skate *Dipturus batis* (Wearmouth & Sims, 2009) and the thorny skate *Amblyraja radiata* (Templeman, 1984) exhibit limited horizontal dispersal, while species such as the winter skate *Leucoraja ocellata* (Frisk et al., 2019) and the big skate *Raja binoculata* (Farrugia et al., 2016) undergo large-scale migrations.

One method of studying genetic diversity is by using mitochondrial DNA barcoding, which refers to the process of analyzing the variability in standardized DNA regions to determine the genetic "identity" of an individual (Casiraghi et al., 2010; Hubert & Hanner, 2015). It is most commonly used to differentiate between species, as it can be used for identifying species genetically that are more challenging to differentiate morphologically, as well as for identifying new species (Casiraghi et al., 2010); however, it has also been applied for intra-specific variation across larger regions (Veríssimo et al., 2010; Veríssimo et al., 2012).

Common markers used for this approach are the cytochrome *c* oxidase subunit I (CO1) and the nicotinamide adenine dinucleotide dehydrogenase subunit 2 (NADH2) mitochondrial genes. Both markers have been successfully used for identifying species and populations in chondrichthyans (Faria et al., 2013; Henderson et al., 2016; Loh et al., 2023). The NADH2 gene has an advantage over the CO1 marker in that it is longer and faster evolving in chondrichthyans, allowing it to detect more recent changes and differentiate between closely related species (Naylor et al., 2012).

1.6. Objectives and hypotheses

The overall aim of the thesis was to gather existing information while identifying the missing data required to assess the vulnerability of the species and the appropriate conservation strategies. Two approaches were used to gain insights into the species: a morphological and a genetic analysis.

1) Morphometrics were investigated for Norwegian waters to gain a better understanding of existing patterns in terms of life history traits like size at maturity and total length. The expectation was to find differences between sexes and potentially spatial distribution. Furthermore, existing life history knowledge on the species as well as new data from this thesis were compared to other relevant skate species of similar sizes and habitats, looking for pattern similarities and differences.

2) Genetic diversity and potential barriers to gene flow were investigated across the species' distribution range, i.e. also including Greenland and the Faroe Islands, using the NADH2 marker, a mitochondrial marker known to provide a decent resolution on an intraspecific level. The patterns were further investigated and compared by analyzing the genetic diversity among CO1 sequences from online databases. The aim of the genetic analysis was to identify the population structure, which could then aid in assessing the vulnerability of the species and informing conservation measures. The expectation was to find a gradient of genetic diversity across the species' distribution range, meaning that individuals further apart would be more genetically divergent than neighboring individuals.

2. Material and methods

2.1. Sampling

The samples used for measurements and DNA extractions were obtained from 20 different research cruises between 2008 and 2023 (for details, see Appendix A). They were obtained through bottom-trawling at depths ranging from 90 to 928 meters in three regions of Norway (Barents Sea Shelf "BSS", Continental Slope North "CSN" and Continental Slope South "CSS"), South-East Greenland ("Greenland"), and the Faroes ("Faroes"; Figure 4). The skates were caught in the months of January to April and August to November. The metadata for each individual is listed in Appendix B.

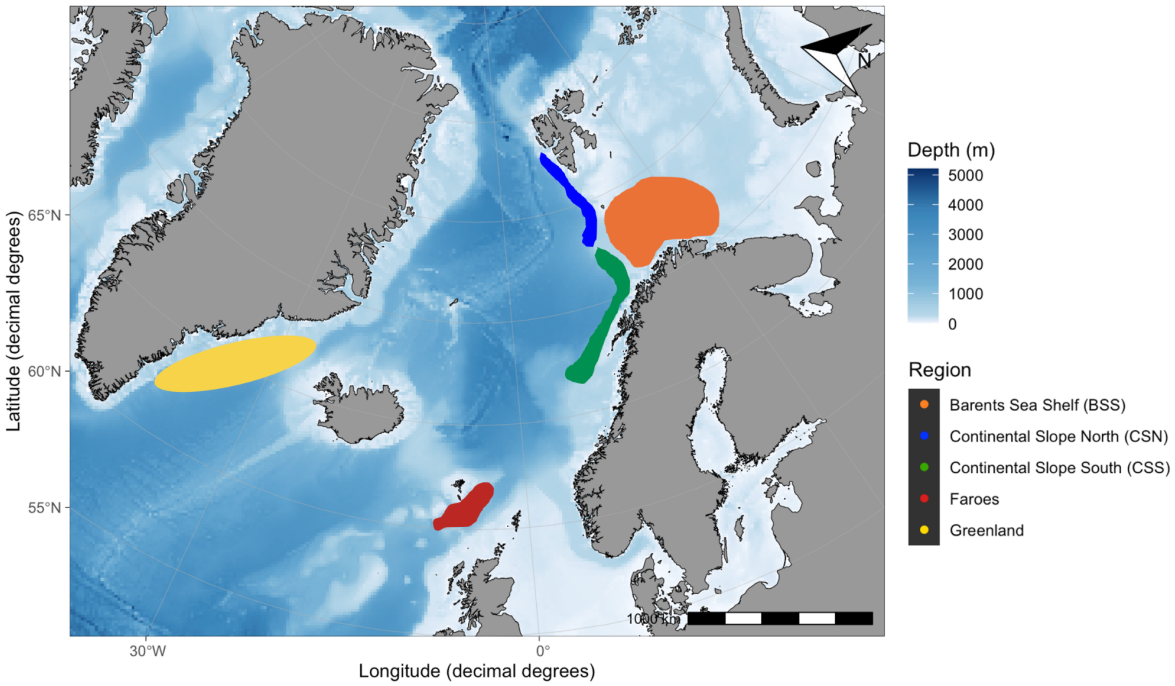

Figure 4: *Map of study regions for own* Bathyraja spinicauda *samples*

Own samples: out of the 104 individuals used, 72 were used for the full morphometric analysis and 60 for the genetic analysis. Only 72 individuals could be used for full morphometric analyses, as these required whole individuals. The number of individuals for genetic analyses was limited by sequencing costs, thus individuals were chosen as evenly as possible across all regions within the cost frame. In some cases, precise location information was unavailable, which made some individuals suitable for morphometric analysis but not genetic analysis, which contributed to the unequal sample sizes.

Additional samples: three NADH2 sequences collected in Greenland were received from Valentina Crobe at the University of Bologna (BOLD:AAA8060 and AAA8067). Eighty CO1 sequences from the Barcode of Life Data Systems (BOLD)(Ratnasingham & Hebert, 2007) were used for comparison across additional regions.

***Table 1**: Summary of the number of individuals used for each analysis per area. BSS = Barents Sea Shelf, CSN = Continental Slope North, CSS = Continental Slope South*

Category	Number of samples	Region							
		BSS	**CSN**	**CSS**	**Faroes**	**Greenland**	**Iceland**	**Canada**	**Unknown**
Tissue samples received (including misidentifications)	104	26	33	13	13	9	-	-	10
Full morphometric analysis	72	18	32	12	-	-	-	-	10
Morphometric analysis with total length and location (including one sample from Valentina Crobe)	87	26	33	13	7	8	-	-	-
Genetic analysis of own NADH2 sequences	60	14	14	10	13	9	-	-	-
NADH2 samples used in both full morphometric and genetic analysis	28	6	13	9	-	-	-	-	-
NADH2 sequences received from Valentina Crobe (also on BOLD)	3	-	-	-	-	3	-	-	-
Genetic analysis of CO1 sequences from BOLD	80	6	3	1	-	1	10	59	-
Misidentifications	11	-	-	-	6	2	-	3	-

2.2. Morphometric analysis

The whole specimens used for the full morphometric analysis could only be obtained from Norwegian cruises in the Norwegian Sea and the Barents Sea (Figure 5).

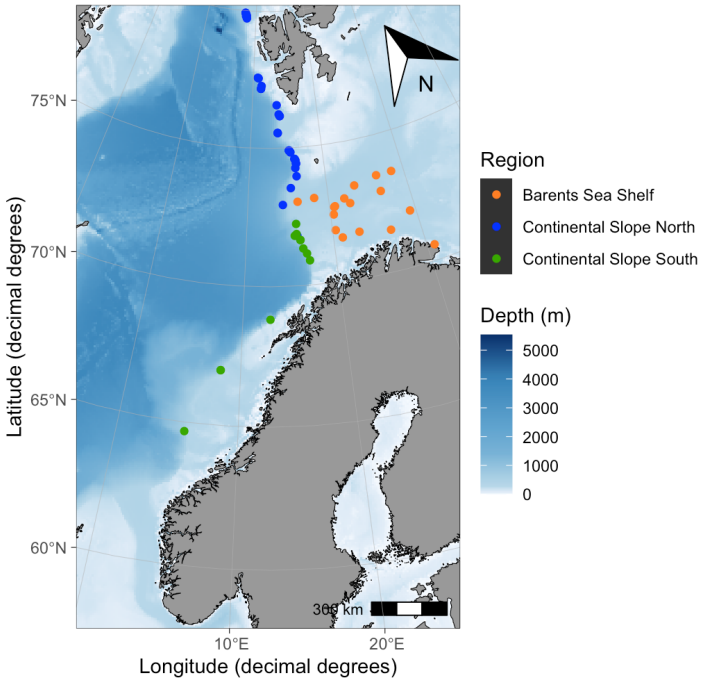

Figure 5: *Geographical distribution of the individuals used for morphometric analysis, n = 72*

2.2.1. Dissections and measurements

Out of the 72 whole individuals used for the morphometric analysis, 66 were frozen and 6 were fresh specimens. Each specimen was weighed and measured using the twenty measurements listed in Table 2. The measurements were conducted using a tape measure and a vernier caliper to the nearest 0.01 mm.

Table 2: *Descriptions of length and meristic measurements based on Clark (1926) and Heintz (1962). Measurements A-Z are dorsal and L-T are ventral.*

Measurement	Description
A: Total length	From tip of snout to tip of tail
B: Length of disc	From tip of snout to inner curve of pectoral fin, close to tail origin
C: Breadth of disc	From pectoral fin tip to pectoral fin tip
D: Length of snout	From tip of snout to an imaginary line just in front of eyeballs
E: Minimum interorbital length	From edge to edge of the cartilage between the eyes with the vernier caliper tightened gently
F: Longitudinal diameter of eye	Eyeballs measured with the vernier caliper
G: Length of eye and spiracle	From front of eye to hind part of spiracle, measured with the vernier caliper
H: Length from snout to vent	From tip of snout to posterior edge of posterior lobe of pelvic fin
I: Preorbital spines	Number of spines in front of eye center
J: Postorbital spines	Number of spines behind eye center
X: Number of spines in mid row	Number of spines from first dorsal fin and up the disc
Y: Scapular spines	Number of spines in the scapular area
Z: Interdorsal spines	Number of spines between dorsal fins
L: Preoral length	From tip of snout to lip border
M: Minimum internasal length	With vernier caliper gently tightened
N: Prenasal length	From tip of snout to an imaginary line in front of nasal apertures
P: Width of mouth	From corner to corner in the mouth the vernier caliper
R: Length of claspers	From tip of claspers to inner corner towards the tail
S: Preanal length	From tip of snout to center of anus
T: Postanal length	From center of anus to tip of tail

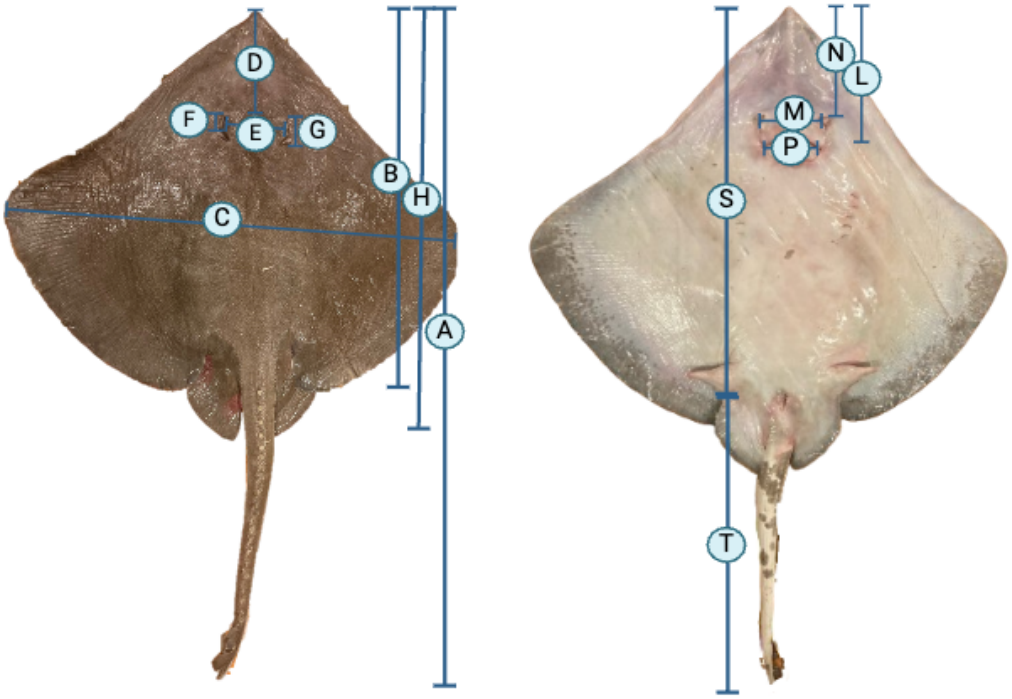

Figure 6: *Length measurements on an immature female* Bathyraja spinicauda *as detailed in Table 2*

Following the measurements, the individuals were dissected, and the liver and digestive tract were removed in order to examine the reproductive organs. Using maturation criteria from Table 3, the individuals were classified from maturity stage 1 to 4b. To re-evaluate potential measurement errors, photos were taken of each individual ventrally and dorsally, as well as their reproductive organs during dissection.

Table 3: *Macroscopic maturity scale for oviparous elasmobranchs based on ICES (2010)*

Females	Males	Maturity stage	Stage	Maturity
Ovaries barely visible or small, whitish; undistinguishable ovarian follicles. Oviducal (nidamental) gland not visible in skates and may be slightly visible in sharks. Uterus is thread-like and narrow.	Claspers flexible and shorter than pelvic fins. Testes small (in skates, sometimes with visible lobules). Sperm ducts straight and thread-like.	Immature	1	Immature
Ovaries enlarged with small follicles (oocytes) of different sizes. Some relatively larger yellow follicles may be present. Developing oviducal gland and uterus.	Claspers still flexible, and as long as or longer than pelvic fins. Testes enlarged, (in skates, lobules clearly visible but not occupying the whole surface). Sperm ducts developing and beginning to coil (meander).	Developing	2	Immature
Large ovaries with enlarged yolk follicles of different sizes. Oviducal gland and uterus fully developed.	Claspers fully formed, skeleton hardened, rigid and generally longer than pelvic fins. Testes greatly enlarged, (in skates, filled with developed lobules). Sperm ducts tightly coiled and filled with sperm.	Spawning capable	3a	Mature
Description similar to stage 3a, however with the presence of egg capsules	Description similar to stage 3a, however with clasper glands dilated, sometimes swollen and reddish. Sperm may be present in clasper groove or glands. On pressure sperm is observed flowing out of the cloaca or in the sperm ducts.	Actively spawning	3b	Mature
Ovaries shrunken with few follicles of different sizes. The oviducal glands diameter may be reducing. Uterus appears much enlarged (relative to stage 2), collapsed, empty and reddish	Claspers fully formed, similar to stage 3. Testes shrunken and flaccid, (in skates with few visible lobules). On pressure sperm does not flow. Sperm ducts empty and flaccid	Regressing	4a	Mature
Ovaries full of small follicles similar to stage 2, enlarged oviducal glands and uterus.	Stage 4b only for females	Regenerating	4b	Mature

2.2.2. Data analysis

All data analyses were performed using RStudio version 4.3.2. (R Core Team, 2023). To analyze body proportions, ratios of the measurements in Table 2 were used. The ratios were selected with particular emphasis on comparing body parts to total length, as that was most informative in identifying differences across maturity stages and sexes. To identify differences between sexes, either a Wilson Rank sum test (non-parametric) or a T test (parametric) was used, depending on the data's normality and variance homogeneity. Furthermore, to identify the link between maturity or size and the body proportion ratios, both Kruskal-Wallis and linear regression analyses were conducted. Additionally, the size at maturity for the species was estimated using the L50 model. Defined as the size at which an individual has a 50% chance of being mature, the L50 value was obtained using the "sizeMat" package version 1.1.2. (Torrejón-Magallanes, 2016) in RStudio.

Furthermore, the study explored the effect of depth and geographical distribution on morphometrics by comparing total length and depth through Kruskal-Wallis tests. There was also a comparison of slope and shelf individuals, with individuals in the Barents Sea being considered shelf individuals and individuals in the Norwegian Sea being considered slope individuals. The distinction between the slope and shelf group was made by looking at a bathymetry map, wherein individuals located on the shelf break and on the slope were considered slope individuals. The Barents Sea also has slopes however, only the individuals in the Norwegian Sea (CSN and CSS) defined in Figure 5 were considered to be slope individuals. There was also a regional comparison using the regions of the Continental Slope South (CSS), the Continental Slope North (CSN) and the Barents Shelf Sea (BSS).

2.3. Genetic analysis

The tissue samples for the genetic analysis were collected within the geographical coordinates of 60°N to 77°N and 37°W to 32°E. The study area was divided into five groups: Greenland, Faroes, the BSS, the CSS and the CSN, as illustrated in Figure 4 and Figure 7.

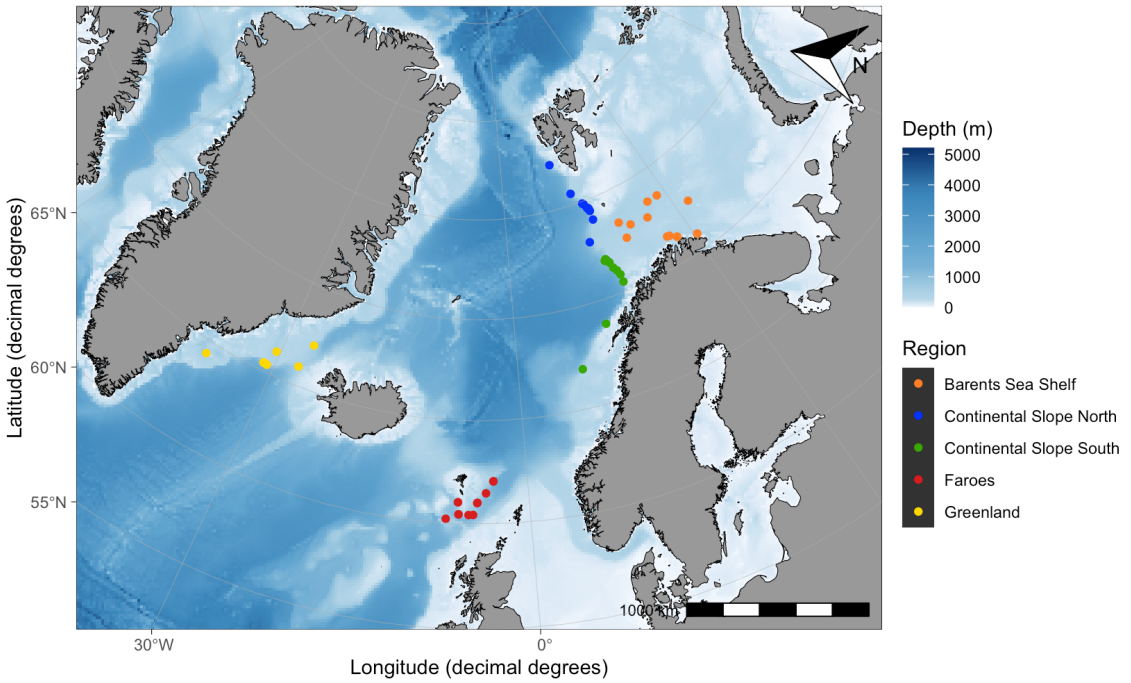

Figure 7: *Geographical distribution of the individuals used for the genetic population analysis, colour coded by region, n = 63*

2.3.1. DNA extraction and quality control

The tissue samples were stored in 96% ethanol at -20°C. For samples where the DNA could not be extracted immediately, the ethanol was replaced after a few days in order to avoid dilution of the ethanol coming from the sampling, which would in turn affect the quality of the tissue and the DNA. The DNA extraction was conducted with approximately 20 mg of tissue following the Qiagen DNA Blood and Tissue Kit and Protocol (Appendix A). The tools used, such as the scalpel and tweezers, were cleaned with 10% bleach, MilliQ water, and 70% ethanol in order to avoid contamination between samples. The type of tissue sample differed between individuals, with some being muscle samples while others were skin samples. The lysis for skin samples took longer and therefore needed a longer incubation time.

The quality and concentrations of the extracted DNA were analyzed using a NanoDrop spectrophotometer and gel electrophoresis. Extractions that produced low-quality results were re-extracted in order to assess whether the issue stemmed from laboratory errors or poor tissue quality. The samples of extracted DNA were then stored in the freezer until further processing.

2.3.2. Polymerase chain reaction (PCR) and cleaning

A PCR was run in order to amplify the target NADH2 sequence defined by the primers. This method allows for the generation of up to billions of copies of the target fragments from small amounts of DNA (Garibyan & Avashia, 2013). The extracted DNA samples were prepared for PCR using a Qiagen Multiplex PCR kit. The PCR was done with a total volume of 20 µL per sample, comprising 3 µL of the extracted DNA sample, 6.36 µL of H_2O, 0.64 µL of primer mix, and 10 µL of mastermix. To target and amplify the desired NADH2 sequence, a mixture of the universal forward primer ILEM 5'-AAC GAG CAG TTT CAT AGA CT-3' and the reverse primer ASNM 5'-AAC GCT TAG CTG TTA ATT AA-3' was utilized (Naylor et al., 2012). The mixtures containing the samples were then placed into a SimpliAmp thermal cycler, starting with an incubation at 95°C for 15 minutes. This was followed by 35 cycles of 94°C for 30 seconds to denature, 52°C for 1 minute and 30 seconds to anneal, 72°C for 1 minute and 30 seconds to extend, and lastly 72°C for 10 minutes to extend, ending with a drop to 4°C until the samples could be picked up. To evaluate the success of the PCR reactions, the PCR product was analyzed by gel electrophoresis, which indicated the length and quality of the DNA fragments.

Following the PCR, the samples were cleaned using 2 µL of ExoSAP-IT™ PCR Product Reagent (Applied Biosystems, 2017) and 5 µL of PCR product. The mixture was then incubated at 37°C for 15 minutes in order to degrade residual primers and nucleotides, followed by 15 minutes at 80°C so as to inactivate the ExoSAP-IT™ reagent.

2.3.3. Preparation and sequencing

The cleaning reaction was followed by a pre-sequencing reaction using the BigDye XTerminator™ v3.1 Cycle Sequencing Kit (Thermo fisher scientific, Applied Biosystems, 2016). The reaction consisted of using 0.5 µL of primer, 1 µL of DNA, 1 µL of BigDye buffer, 0.5 µL of BigDye, and 2 µL of H_2O. The mixture was then placed into the thermocycler with the following settings: incubation at 96°C for 1 minute, 25 cycles consisting of: 96°C for 10 seconds for denaturation, 50°C for 5 seconds to anneal, and 60°C for 4 minutes to extend, ending with a hold at 4°C until the samples could be picked up.

The 60 chosen samples sent for sequencing were selected to assure representation across maturity stages, sexes, and regions. The samples were also chosen in order to create groups or clusters in different regions that could then be compared. The sequencing was conducted via Sanger sequencing using Applied Biosystems 3500xL Genetic Analyzers at the DNA sequencing lab in the genetics department of the University Hospital of Northern Norway (UNN). The DNA for each individual was sequenced twice, once with the forward primer ILEM and once with the reverse primer ASNM.

2.3.4. Sequence alignment and tree construction

The sequences were aligned using the ClustalW function in the software Molecular Evolutionary Genetics Analysis (MEGA X) version 11 (Tamura et al., 2021). The 5' end and the 3' end of each sequence were trimmed to eliminate the unclear parts. The number of base pairs removed was determined using the clarity of the peaks on the chromatograms, giving a sequence length of 1314 bp for most of the sequences. The forward and reverse sequences were combined and cleaned into one sequence by manually comparing the sequences on MEGA X. In some cases involving ambiguous nucleotides, they were substituted with the most likely nucleotide when all the other sequences agreed on one nucleotide. Furthermore, based on the sequence alignments, some potential nucleotide insertions were found and subsequently removed. Such insertions could be the result of poor DNA quality, PCR amplification errors, or sequencing errors (Al-Shuhaib & Hashim, 2023). It is important to keep in mind these assumptions when reflecting on the accuracy of the results.

To choose the best suitable substitution model, a model selection test based on maximum likelihood was run in MEGA X. The recommended substitution model was then used to create maximum likelihood trees with a bootstrap value of 1000.

2.3.5. Genetic diversity and differences

Additionally, a haplotype network was created using the Integer Neighbour-Joining network model on PopART version 1.7 (Population Analysis with Reticulate Trees) (Leigh & Bryant, 2015). The statistical analysis of the sequences was conducted on Arlequin version 3.5.2.2 (Excoffier & Lischer, 2010). This analysis included an Analysis of Molecular Variance

(AMOVA) test to determine the population genetic structure on different hierarchical levels. The AMOVA was run with 1000 permutations, a computed distance matrix and the distances set to pairwise differences. The five regions were divided into three groups: Group 1 included Norway (BSS, CSS, CSN), Group 2 Greenland and Group 3 the Faroes. Furthermore, the fixation index (θ_{ST}) was calculated in Arlequin to identify population differentiation among the five defined region groups based on pairwise differences (Holsinger & Weir, 2009). The permutation and distance settings for the θ_{ST} were the same as for the AMOVA. To analyze the potential sampling bias from having a smaller sample size in the Faroes and Greenland, ten randomization tests using six samples from each region were conducted in Arlequin. The sample size for randomization was chosen since the Faroes had only six spinytail skate samples due to misidentifications. For each test, RStudio (R Core Team, 2023) was used to select six random samples from each region. Additionally, the molecular diversity within each region was analyzed using the molecular diversity indices test with pairwise differences as a molecular distance method.

2.3.6. Analysis of available CO1 data

In addition to our own NADH2 sequence data, data on the CO1 marker for 80 *Bathyraja spinicauda* individuals were available on the BOLD database from additional regions. These CO1 sequences were compared to one another to determine whether they showed the same patterns as the NADH2 sequences. In this database, there was data from Canada, Greenland, Iceland and Norway. However, not all samples provided a chromatogram; therefore, it was not possible to verify the quality of all sequences. All sequences were compared in MEGA X, and both a phylogenetic tree and a haplotype network were created to identify potential variability.

3. Results

3.1. Morphological analysis

3.1.1. Body measurements

The morphological analysis consisted of an equal number of males and females, with 36 males and 36 females. There was an extensive range of total lengths across both sexes (Figure 8). The largest female reached a length of 1670 mm, surpassing the largest male, which measured 1510 mm. The smallest individual analyzed was a male measuring only 280 mm. Another observation from the data was the prevalence of small individuals over large individuals, a trend that was visible in both sexes.

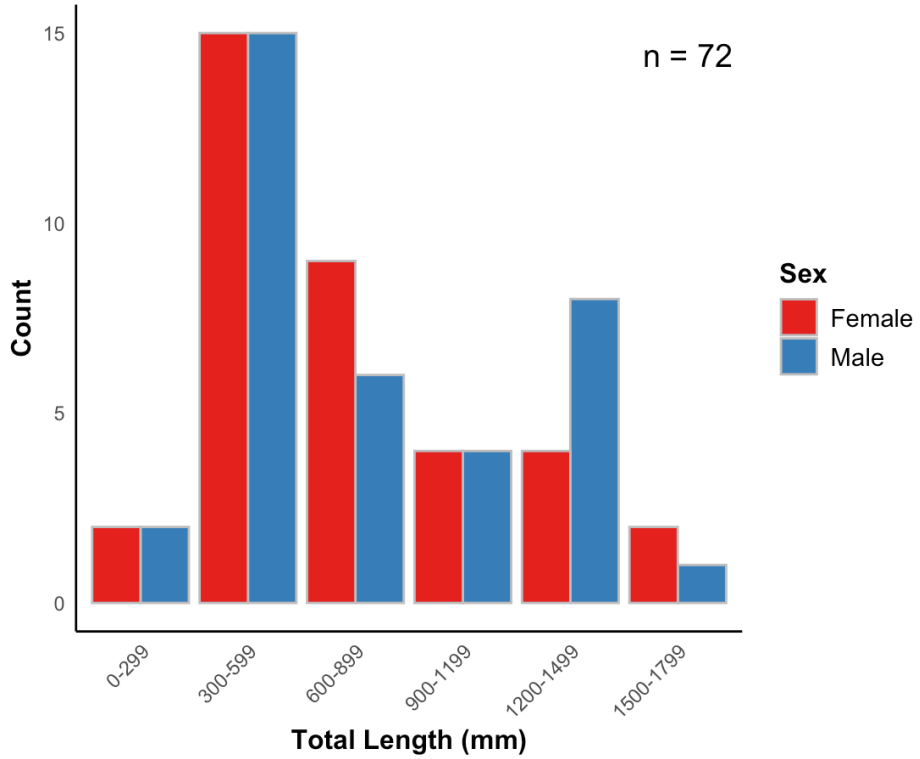

Figure 8: *Size distribution (Total Length) per length class by sex of the 72 individuals analyzed morphologically (n = 36 females, n = 36 males)*

The application of a t-test and a Wilcoxon rank-sum test to the body measurement ratios revealed significant differences in the ratios of D:A, L:A, P:C and P:A (Table 4). This suggests that there is a significant difference in snout as well as mouth length between the

sexes. Females had a slightly longer snout and a narrower mouth than males (Figure 10). For all the other examined ratios (B:A, C:A, E:A, E:C, F:A, G:A, H:A, M:A, M:C, N:A, S:A, T:A), the tests did not detect any significant variations between sexes, suggesting a similarity in those body parts. Furthermore, there were some outliers in the ratios L:A, P:C, and P:A, but no apparent reason was found for these individuals.

Table 4: *Ratios with significant differences between sexes in t test and Wilcoxon rank-sum test (see Table 2 and Figure 6)*

Ratio	**Description**	**Test**	***p* value**	**Females median**	**Males median**
D:A	Snout length to total length	t test	0.0049	0.1801	0.1741
L:A	Preoral length to total length	Wilcoxon rank-sum test	0.0226	0.1784	0.1709
P:C	Mouth width to disk width	Wilcoxon rank-sum test	0.0120	0.1097	0.1141
P:A	Mouth width to total length	Wilcoxon rank-sum test	0.0404	0.0723	0.0763

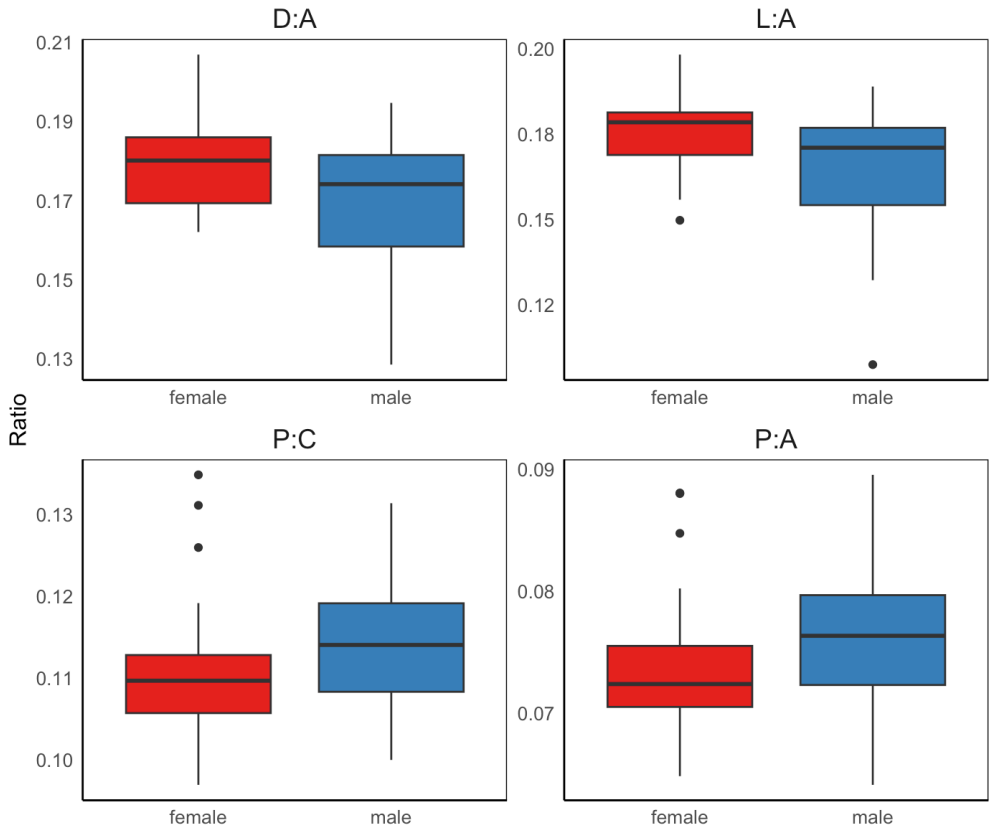

Figure 9: *Boxplot representation of the medians in males and females for the ratios that showed significant differences. Measurements described in Table 2.*

In the analysis of the effect of growth on the different body proportions, the linear regression revealed a total of 12 ratios with significant changes during growth: B:A, C:A, D:A, E:A, F:A, G:A, H:A, L:A, N:A, P:A, S:A, and T:A (Table 5). The findings suggest that disc length (B) and breadth (C), interorbital length (E), length from snout to vent (H), mouth width (P), and preanal length (S) proportionally increase with total length (A) (Figure 10). Conversely, the snout (D), the longitudinal diameter of the eye (F), the length of the eye and spiracle (G), the preoral length (L), the prenasal length (N), and the postanal length (T) proportionally decrease.

Table 5: *Results of the linear regression analysis of the ratios plotted against total length (TL)(n=72). Measurements described in Table 2.*

Ratio	Description	Slope coefficient	Std. error	R^2	*p* value
B:A	Disc length to TL	0.000031	0.000008	0.1718	0.0003
C:A	Disc breadth to TL	0.000016	0.000005	0.1069	0.0050
D:A	Snout length to TL	-0.000009	0.000004	0.0581	0.0412
E:A	Interorbital length to TL	0.000005	0.000001	0.3289	<0.0001
F:A	Longitudinal diameter of eye to TL	-0.000012	0.000001	0.5452	<0.0001
G:A	Length of eye and spiracle to TL	-0.000005	0.000001	0.2274	<0.0001
H:A	Length from snout to vent to TL	0.000064	0.000014	0.2293	<0.0001
L:A	Preoral length to TL	-0.000023	0.000004	0.3073	<0.0001
M:A	Internasal length to TL	0.000004	0.000001	0.0192	0.2459
N:A	Prenasal length to TL	-0.000017	0.000005	0.1368	0.0013
P:A	Mouth width to TL	0.000011	0.000001	0.5055	<0.0001
S:A	Preanal length to TL	0.000039	0.000004	0.5356	<0.0001
T:A	Postanal length to TL	-0.000039	0.000005	0.4928	<0.0001

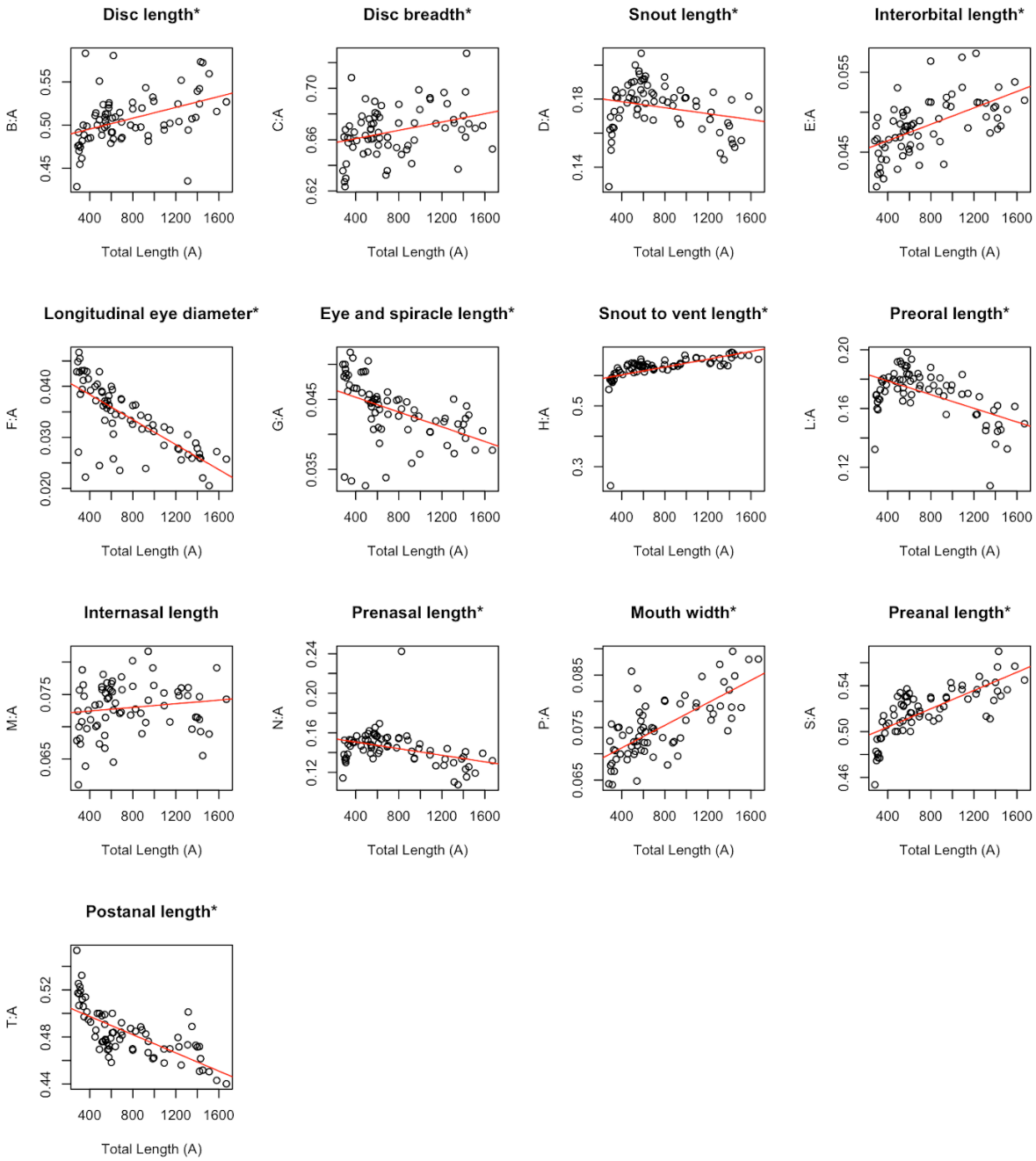

Figure 10: *Morphometric ratios in a linear regression analysis of ratios plotted against total length (*= $p < 0.05$), $n = 72$. Measurements described in Table 2*

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3.1.2. Maturation analysis

The morphometric analysis and the dissections showed a broader range of maturity stages in males compared to females (Figure 11). All females were immature, as there were no females

beyond maturity stage 2. There were 18 females at stage 1 and 8 at stage 2. The males exhibited maturity stages 1 to 3b, with no male at the regressing stage 4a. There were 13 males at stage 1, 5 at stage 2, 2 at stage 3a and 5 at stage 3b. For the remaining 21 individuals from the full morphometric analysis there was no maturation data.

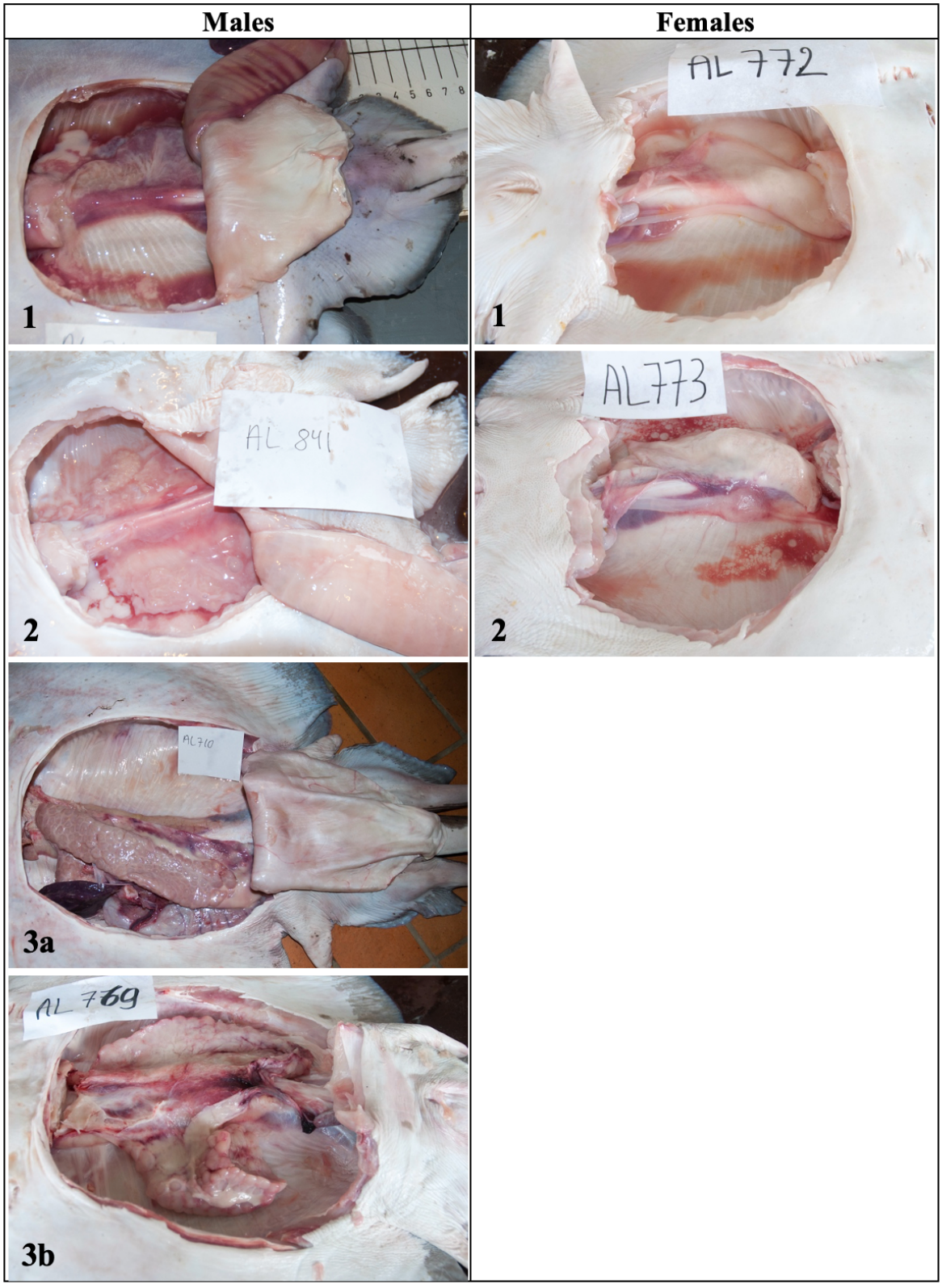


Figure 11: Bathyraja spinicauda *maturity stage comparison for males (stages 1 to 3b) and for females (stages 1 and 2), with males on the left and females on the right*

There were a total of 7 mature male individuals in the data. Since there were no mature females, the size at maturity (L50) was only calculated for male spinytail skates (Figure 12). The median L50 for males was 1311.1 mm, with a confidence interval of 1239.8 mm-1344.4 mm. There were some large females with total lengths of 1420 mm and 1670 mm that were still immature.

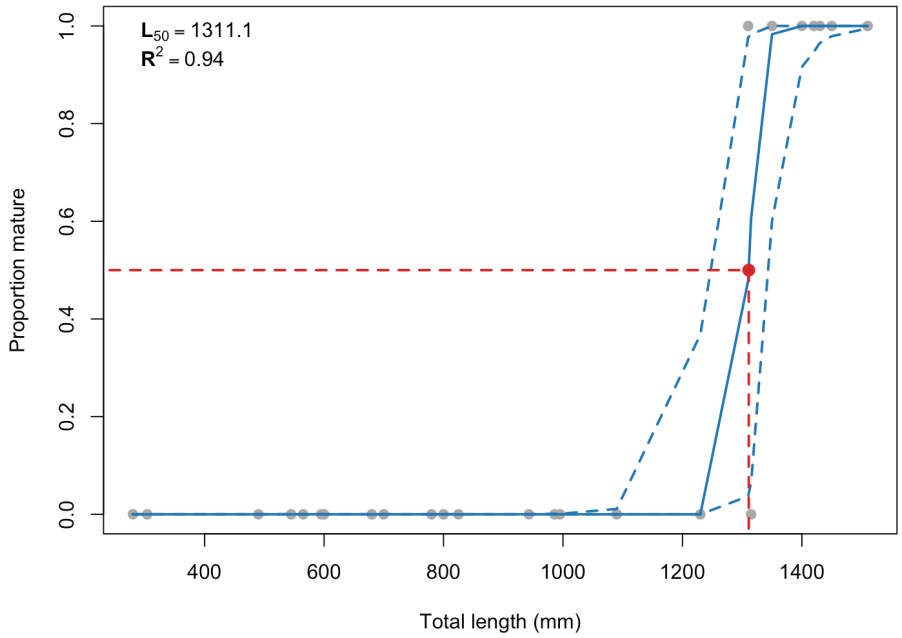


Figure 12: *Size at maturity (L50) for male* Bathyraja spinicauda *using the Bayesian logistic regression method (n = 25)*

3.1.3. Spatial distribution

The Kruskal-Wallis test revealed that there was no significant link (p = 0.1374) between total length and catch depth (Figure 13). The catch depth range was between 90 and 906 m. The individual found at 90 m was an immature male (TL = 280 mm) caught in the BSS in October 2020. Furthermore, the Kruskal-Wallis test showed no significant differences between total length and catch depth within sexes or within regions.

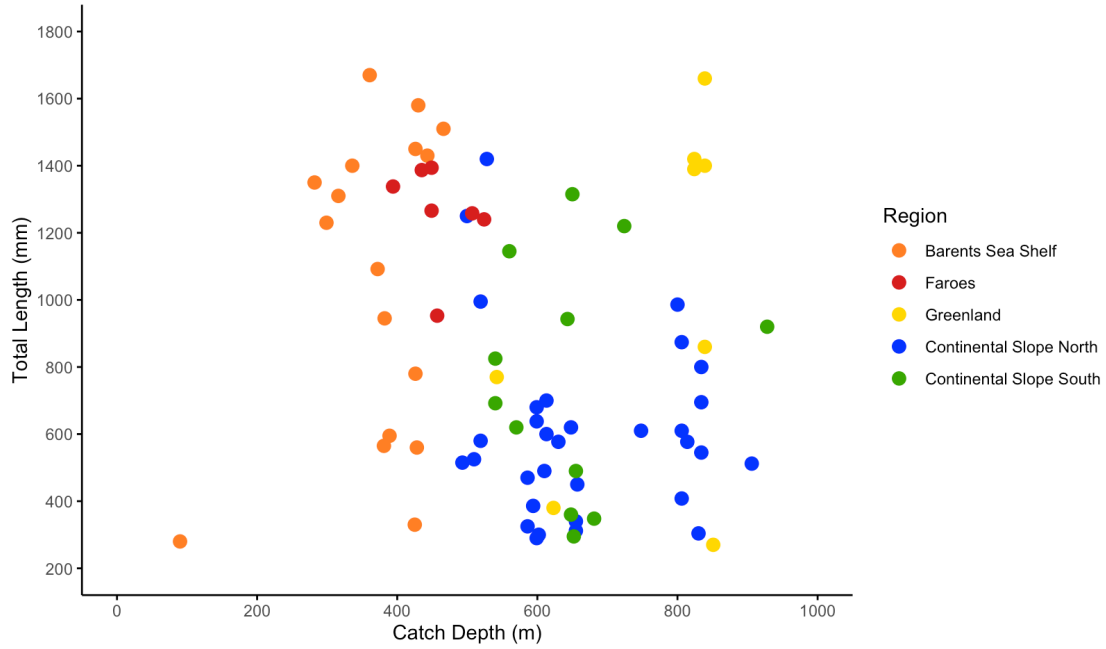


Figure 13: *Relationship between catch depth (m) and total body length (mm) for 87* Bathyraja spinicauda *from the 5 study regions*

The comparison of total length between shelf and slope individuals using a Wilcoxon rank-sum test revealed that shelf individuals were significantly (p = 0.0025) larger than slope individuals (Figure 14). The same result was obtained with randomization using a Wilcoxon rank-sum test (p = 0.0056). There were no significant differences between sexes on the shelf (p = 0.9636) or on the slope (p = 0.8191). The 18 individuals on the Barents Shelf were caught at depths ranging from 90 to 430 m, with an average catch depth of 351 m. The 48 individuals on the slope were caught at a depth range of 493-906 m, with an average catch depth of 670 m. It is also worth noting that all mature individuals were caught on the Barents Shelf.

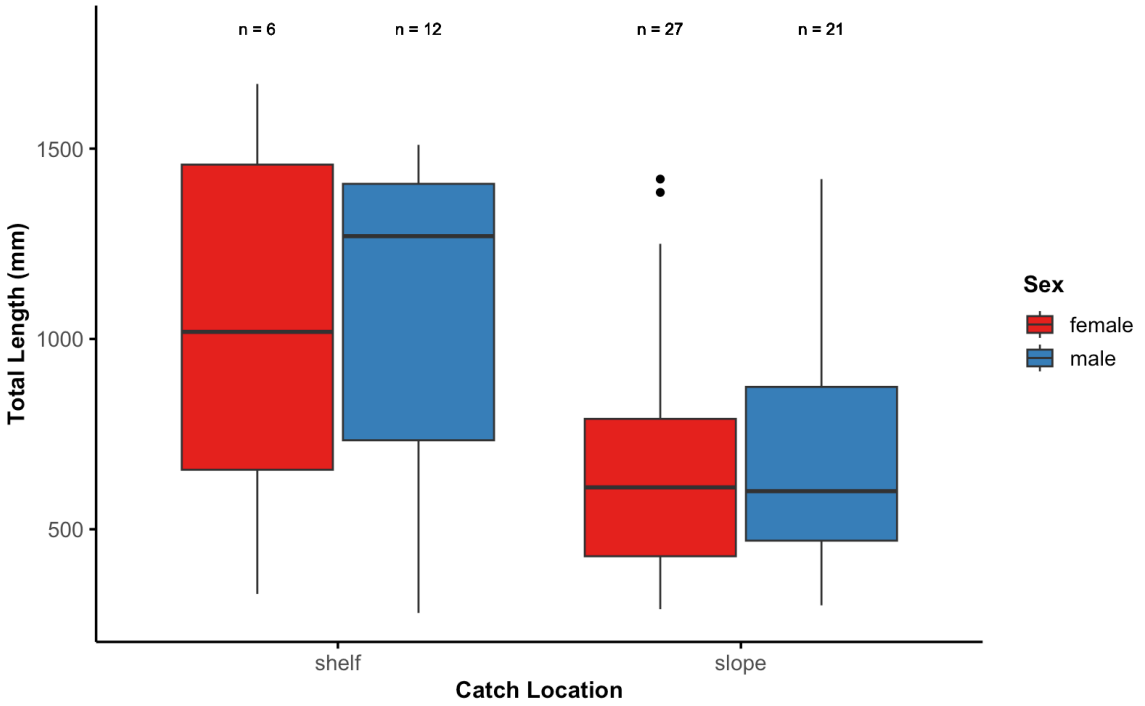


Figure 14: *Mean total length (mm) for shelf vs slope individuals per sex (n = 66).*

3.2. Genetic Analysis

3.2.1. Analysis of own NADH2 sequences

Based on the Akaike Information Criterion (AICc) values from the model selection test, the best-fitting model for the phylogenetic analysis was the Hasegawa-Kishono-Yano (HKY) model (Figure 15). The samples were grouped by haplotype for better visibility (see Appendix D for the full phylogenetic tree). Of the 63 NADH2 sequences, one had to be removed due to low quality. There were also 8 misidentifications, with five sailrays (haplotype H) and 3 Arctic skates (haplotype I) in the studied samples. For the *Bathyraja spinicauda* samples, there were samples from different regions in each clade, therefore there was no correlation between region and pairwise differences across samples. Furthermore, the clades within the species had low bootstrap support (40-69%).

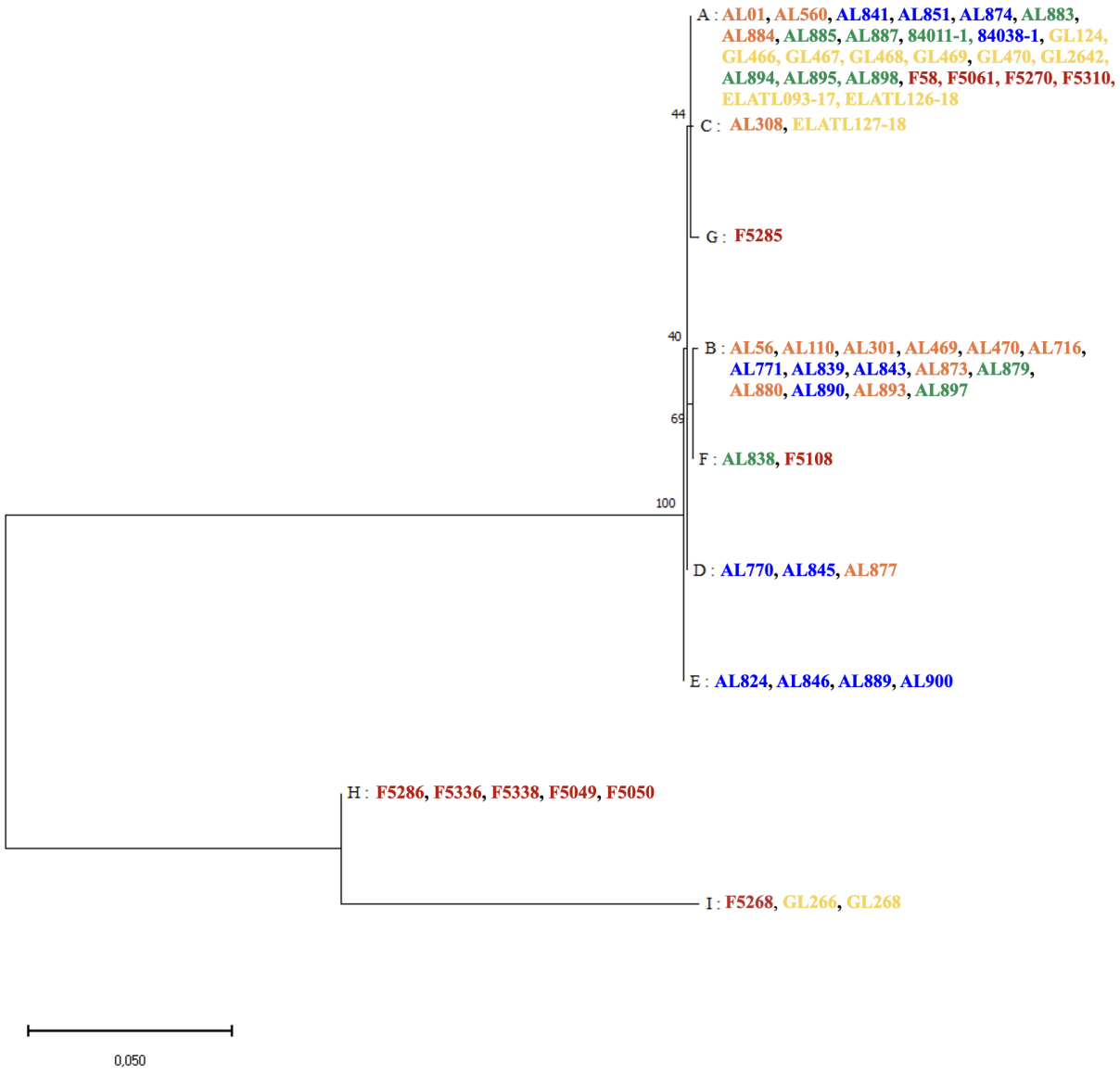


Figure 15: *HKY maximum likelihood tree of 62 NADH2 samples grouped by haplotype with 1000 bootstrap replicates. Sample locations: CSN, CSS and BSS = AL, Greenland = GL and ELATL, and Faroes = F. The distance scale represents the number of pairwise differences and the numbers represent bootstrap values. The samples are colored according to region (see Figure 16)*

The haplotype network analysis revealed low variability with only a few mutations (Figure 16) The misidentifications were excluded for the haplotype network, leaving 54 *Bathyraja spinicauda* samples. In these samples, there were a total of 10 variable sites, leading to a total of 7 different haplotypes. Haplotype A (Cluster 1) was shared across all study regions, and haplotype B (Cluster 2) was shared across three, namely CSN, CSS and BSS. Three haplotypes were shared across two regions, and two were only present in one each. The

mutations did not appear to be related to the spatial distribution of the samples, as identical haplotypes were found in samples separated by large distances.

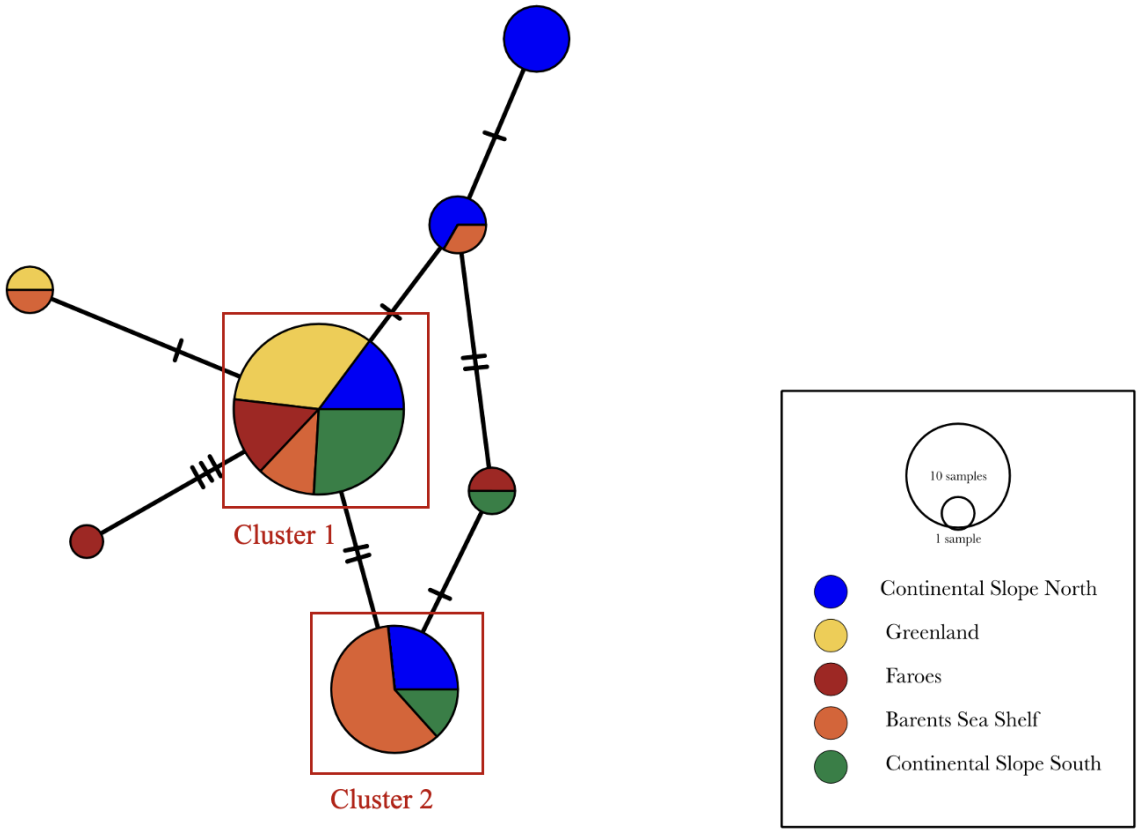


Figure 16: *Unrooted Integer Neighbor Joining haplotype network of the 7 different haplotypes found in the 54* Bathyraja spinicauda *individuals from 5 study regions*

The genetic diversity analysis conducted with Arlequin (Table 6) showed the highest number of haplotypes, that is 4, in the BSS and the CSN. The lowest number of haplotypes was found in Greenland, with 2 haplotypes. The mean haplotype number of the 10 randomizations using 6 randomized samples from each study location showed a lower haplotype number for each region, except for the Faroes. The range of pairwise differences in each region was between 0.2 and 2, while the nucleotide diversity had a range of 0.0001 to 0.0015. The mean number of pairwise differences and the nucleotide diversity within regions were highest in the Faroes, with 2 and 0.0015, respectively.

Table 6: *Genetic diversity analysis. N = number of samples, HN= number of haplotypes*

Region	N	H_N	Mean randomized samples H_N	Mean number of pairwise differences	Nucelotide diversity
CSN	14	4	3.2	1.8461	0.0014
BSS	14	4	3.0	1.7692	0.0013
CSS	10	3	2.2	1.1333	0.0008
Greenland	10	2	1.6	0.2000	0.0001
Faroes	6	3	3.0	2.0000	0.0015

The AMOVA for the NADH2 samples (Table 7) among groups showed the highest percentage of variation occurring within populations and the lowest variation among populations within groups. The percentage of variation among groups was not statistically significant ($p > 0.05$). Conversely, both the variation among populations within groups and the variation within populations were significant ($p < 0.0001$).

Table 7: *AMOVA results among groups (Group 1 = BSS, CSS and CSN; Group 2 = Greenland; Group 3 = Faroes) among populations within groups and within populations. d.f. = degrees of freedom; SS=sum of squares*

Source of variation	**d.f.**	**SS**	**Variance components**	**% of variation**	**F**	**P value**
Among groups	2	28.404	0.7835 Va	11.80	Fct = 0.1180	0.1935
Among populations within groups	2	7.663	-0.1754Vb	-2.64	Fsc = -0.0299	0.0000
Within populations	49	295.433	6.0292 Vc	90.84	Fst = 0.0916	0.0000
Total	53	331.500	6.6373			

For the analysis of the θ_{ST}, there were 10 pairwise comparisons (Table 8). Only 5 of the values obtained were significant. The range of θ_{ST} was between -0.0550 and 0.2942. The highest value was observed between the Continental Slope South (CSS) and the Barents Sea Shelf (BSS). The second highest value was between the BSS and the Faroes.

Table 8: *Population pairwise θ_{ST} for all sample locations. Significance from 1000 permutations (*p<0.05, **p<0.01, ***p<0.001)*

Region	CSN	BSS	CSS	Greenland	Faroes
CSN	0.0000				
BSS	0.2942**	0.0000			
CSS	0.0352	0.2581*	0.0000		
Greenland	0.0462***	0.0751***	0.0045	0.0000	
Faroes	0.0264	0.2837*	-0.0379	-0.0550	0.0000

The results of the randomization (Table 9) showed the same pattern as in Table 8, with lower values. This is consistent with the results of the randomization of H_N in Table 6, since the lower number of samples led to a lower number of haplotypes and lower variability.

Table 9: *Mean population pairwise θ_{ST} for all sample locations based on 10 randomizations of 6 samples from each region*

Region	CSN	BSS	CSS	Greenland	Faroes
CSN	0.0000				
BSS	0.0861	0.0000			
CSS	-0.0469	0.0524	0.0000		
Greenland	0.0366	0.0479	-0.0161	0.0000	
Faroes	-0.0212	0.0919	-0.0666	-0.0919	0.0000

3.2.2. Analysis of CO1 data on BOLD

The best-fitting tree model for the online CO1 sequences was the HKY model. The published sequences had 3 misidentifications (Figure 17). Using BOLD, two of these samples were identified as Arctic skates *Amblyraja hyperborea*, and one as a Pacific white skate *Bathyraja*

spinosissima. Similarly to the phylogenetic analysis of the NADH2 sequences, the phylogenetic tree structure was not related to the geographical distribution of the samples.

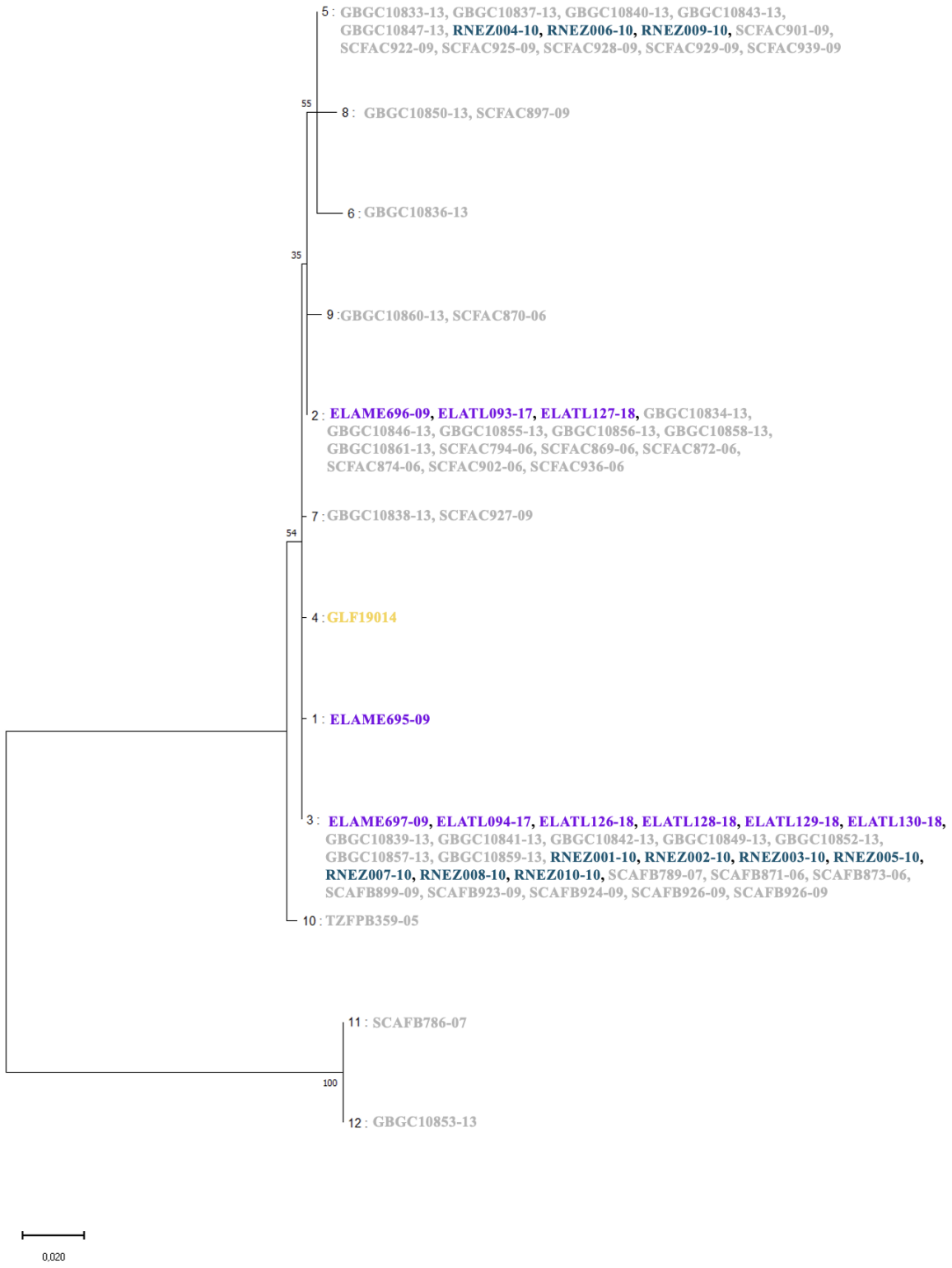


Figure 17: *HKY maximum likelihood tree of 80 CO1* Bathyraja spinicauda *samples from BOLD grouped by haplotype, with Norway = RNEZ, Greenland = GLF, Canada = GBGC, SCFAC and TZFP, Iceland = ELATL and ELAME. The distance scale represents the number of pairwise*

differences and the numbers represent bootstrap values. The samples are colored according to region (see Figure 18)

To analyze the CO1 haplotype network, the misidentifications found in Figure 17, along with 12 *B. spinicauda* sequences that were too short for comparison in PopART, were excluded. A total of 10 different haplotypes were found in the online CO1 data (Figure 18). There was no link found between the haplotype and the geographical region.

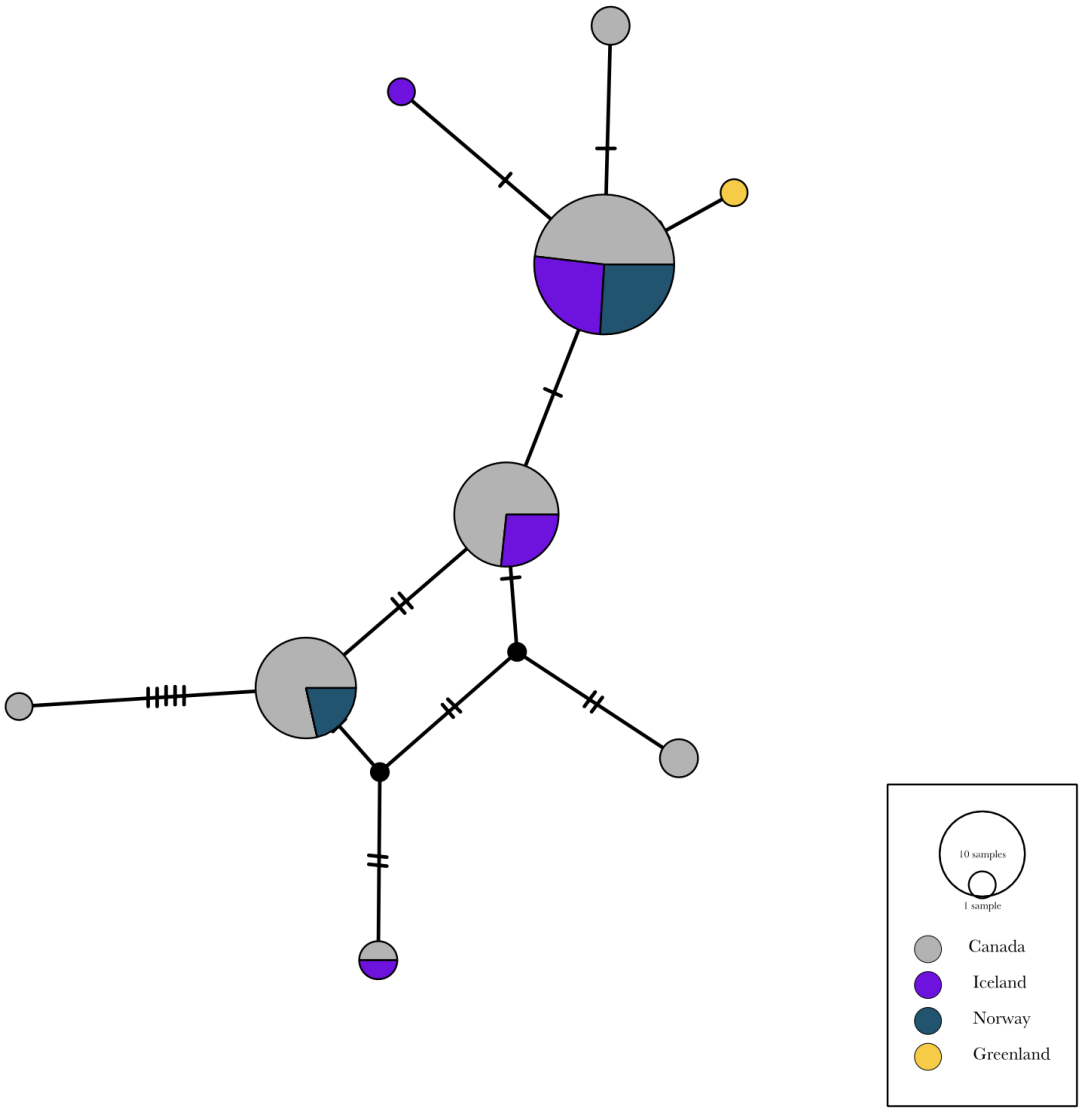


Figure 18: *Integer Neighbor Joining haplotype network of 65* Bathyraja spinicauda *CO1 sequences on BOLD Systems*

4. Discussion

4.1. Maturation and sexual dimorphism

The low number of mature individuals found renders it challenging to come to a reliable conclusion on the differences in body proportions during maturation and between sexes. Despite this complication, the small differences found indicate potential sexual and maturity characteristics that should be further investigated. The variations in morphometric ratios between juveniles and adults, as well as between sexes, may reflect niche-specific or behavioral adaptations.

In the present study, estimating the size at maturity for females was infeasible due to the absence of mature females. Surprisingly, the largest females that were found were larger than the mature males, yet they still appeared to be immature (Figure 19), which could indicate a larger size at sexual maturity. The absence of mature females could be attributed to several factors, such as a high capacity for regeneration. This refers to maturity stage 4b (Table 3), when females that have already spawned at least once begin a new cycle (ICES, 2010). Furthermore, it has been suggested that the median depth for egg nurseries is between 1825 and 1907 meters (Lennon et al., 2021). If this is the case, then mature females could potentially be found in depths where there is no trawling. However, the possibility of errors in maturity stage identification cannot entirely be ruled out, nevertheless, the large size of egg capsules should make the identification clear. Furthermore, for other skate species, such as the little skate *Leucoraja erinacea*, Koob et al. (1986) demonstrated that egg capsules remain in the uterus for an average of only three days before oviposition. The egg deposition process (oviposition) occurs over spawning periods, wherein eggs are laid every few days (Koob et al., 1986). The length of this spawning period is unknown for spinytail skates and could also be affecting the likelihood of finding or correctly identifying mature females. Additionally, the presence of mature males in catches, while still missing males at maturity stage 4a, the regression stage, suggests different reproduction strategies between sexes, with males possibly remaining ready for reproduction for extended periods. Another explanation for the lack of mature females and post-reproductive males could be that there were no surveys

between May and July, which is a time period for which reproduction is at its peak for many skate species (Holden, 1975).

The potential age at maturity can be estimated by comparison with *Bathyraja* species with similar values for size at maturity (Table 10). For example, the white-dotted skate *B. albomaculata,* the Alaska skate *B. parmifera*, the aleutian skate *B. aleutica*, the graytail skate *B. griseocauda* and the whitebrow skate *B. minisposa* present a range of ages at maturity from 7-10 years in the Alaska skate to 23-23.5 years in the whitebrow skate (for references, see Table 10). Based on the maximum total length, it can be estimated that the age of maturity for the spinytail skate is at least 10 years. Additionally, the range of the size at maturity relative to the total length for the five *Bathyraja* species is between 41.9 and 90.9%. The spinytail skates' estimated size at maturity, which is 72% of their maximum total length, falls within this range.

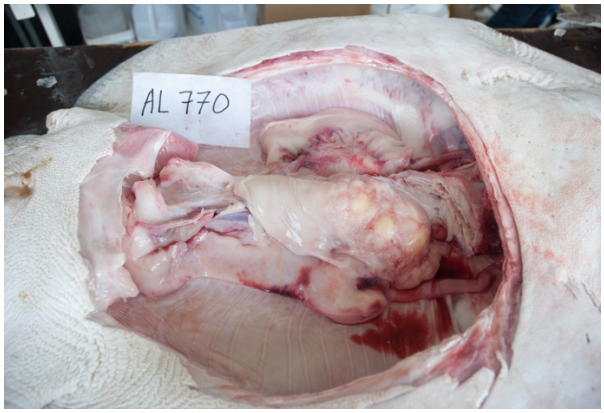


Figure 19: *Dissection of the largest immature* Bathyraja spinicauda *female with a total length of 1670 mm. Photo: A. Lynghammar*

Table 10: *Life history traits of* Bathyraja spinicauda *(* = own data) and other* Bathyraja *species from literature*

Species	Sex	Size at maturity (cm)	Max TL (cm)	Size at maturity relative to TL (%)	Age at maturity (years)	Longevity (years)	Depth range (m)	Source
White-dotted skate (*Bathyraja albomaculata*)	Male	62.8	150	41.9	11	17	55-945	Ruocco et al., 2006; Pollom et al., 2020b
	Female	65.3		43.5	10			
Alaska skate (*Bathyraja parmifera*)	Male	87.9	111.0	79.2	7-9	20	20-1425	Mecklenburg et al., 2002; Ebert et al., 2005
	Female	92.0	109.5	84.0	8-10			
Aleutian skate (*Bathyraja aleutica*)	Male	121.0	133	90.9	8-9	19	15-1602	Ebert et al., 2005; Stevenson et al., 2007
	Female	133.0	154	86.3	9-10			
Graytail skate (*Bathyraja griseocauda*)	Male	94.5	157	60.2	15	28	30-1010	Arkhipkin et al., 2008; Pollom et al., 2020c
	Female	108.2		68.9	17.8			
Whitebrow skate (*Bathyraja minisposa*)	Male	70.1	89.5	78.3	23	37	150-1420	Stevenson et al., 2007; Ainsley et al., 2011
	Female	67.4		75.3	23.5			
Spinytail skate (*Bathyraja spinicauda*)	Male	131.1*	182	72.0	Unknown	Unknown	140-1650	Drevetnyak et al., 2005; Pollom et al., 2020a

The sexual dimorphism in spinytail skates in terms of body proportions can be explained by mating behaviors or differences in niches. For example, the alar thorns on the disc edges in males are used to grip onto the female during copulation. The difference in mouth length (Table 4) could be a result of the difference in feeding apparatus and, consequently, diet (Feduccia & Slaughter, 1974; Orlov & Cotton, 2011); this difference in teeth could also be for 'courtship biting' in order to grip the female during copulation (McEachran, 1977; Pratt & Carrier, 2001). Nevertheless, sexual dimorphism is not only related to behavioral differences between sexes but also to endocrine development. For example, pectoral fin dimorphism is linked to clasper development, which can also contribute to differences in head shape

(Martinez et al., 2019). Despite advancements in understanding reproductive behaviors, knowledge gaps persist in terms of reproductive timing. While the data from the present study indicates that the smallest individuals were caught between August and October, data on freshly laid eggs are missing. As such, we do not know if the spinytail skate spawns year-long or has determined spawning seasons. However, considering their low abundance and the depth distribution, it is likely that there is no set mating and spawning season and that reproduction occurs whenever there is an opportunity. Furthermore, since the length of embryonic development is unknown, knowing the season at which recently hatched individuals are caught is insufficient.

4.2. Link between spatial distribution and morphometrics

The expected correlation between depth and size distribution, wherein larger individuals move to shallower waters to spawn (Krefft, 1956; Baranenkova, 1968), was not observed when comparing total length and depth (Figure 13). This could be due to the predominance of immature individuals among the study samples. Despite this, a significant difference in total length was found between slope and shelf individuals (Figure 14), with all mature individuals in this study found on the Barents shelf. This could still reflect the expected pattern of larger individuals moving to shallower water for spawning. However, the observation of median egg nursery depth for the species by Lennon et al. (2021) contradicts this pattern. Moreover, there was one anomalous individual found at a depth of 90 meters, which is notably shallower than the species' recorded depth range (Last et al., 2016; Moller et al., 2018). While this could indicate a wider depth distribution in the species, the possibility of a data recording error cannot be excluded.

4.3. Genetic population structure

It is difficult to define the value at which two individuals are to be considered members of different populations or different species (Waples & Gaggiotti, 2006). This can in part be attributed to the fact that speciation is a continuous event, wherein individuals in the process of speciation are difficult to identify (Verma et al., 2020). For example, the differences found could be the beginning of a speciation event. Furthermore, intraspecific diversity differs between species, meaning that the threshold for a species to be considered distinct differs

(Ward, 2009). To classify elasmobranch individuals as different species, their p-distance variation in the NADH2 marker should be over 2.12 (Naylor et al., 2012). Similarly, K2P distance measurements have revealed a maximum intra-species variation of 3.14 in the NADH2 markers (Naylor et al., 2012) and a variation of 10.91 in the CO1 marker (Ward, 2009). For a new species to emerge, there needs to be a barrier to gene flow between populations, either currently or previously, and they need to become different enough to prevent interbreeding (Slatkin, 1987). The results (Figure 15 and Appendix D) indicate that there was no new species; therefore, it can be concluded that the previous suspicion was most likely due to a lab error.

The expected result of the NADH2 and CO1 analyses, of high variation across the distribution range, with individuals further apart from one another being more different, indicating isolation by distance (IBD) (Wright, 1943), was not found. This could be an indicator that the spinytail skate is migrating more than previously believed, indicating high connectivity and gene flow. However, the high θ_{ST} (Table 8) indicate the opposite pattern: a high population subdivision and thus little migration (Hedgecock et al., 2007; Bird et al., 2017). Within the analyzed samples, the most visible obstacle to migration and thus gene flow is depth, meaning that it is likely not possible to cross the deep basins of the Norwegian Sea. Furthermore, samples between Greenland and other regions in the east are separated by the Denmark Strait, an important feature when it comes to migration due to its overflow. The underwater waterfall can cause extreme turbulence and therefore act as a barrier to migration (NOAA, 2023). Moreover, swimming capabilities can also cause individuals from a population to remain in the same area (Cowen, 2000). The genetic analysis results could also be an indicator of recent divergence, where changes are too recent to be detected on this marker (Wang et al., 2008). However, for these hypotheses to be accepted, there should be more genetic diversity research using more fine-scaled methods, since there are too many limitations in the markers used in the present study.

4.4. Methodological limitations

Many knowledge gaps for the spinytail skate can be attributed to limitations in research methodologies and most importantly, the access to samples. Numerous limitations can be

found already at the sample collection stage. Firstly, as this is a rather rare species in Norwegian waters, 15 years and 20 research surveys only provided 72 whole specimens that could be used for a full life history trait workup, which resulted in relatively small sample sizes in some of the sample groups according to sex and maturity stage. Additionally, sample collection via bottom trawling is limited since some areas are never explored due to their unsuitability for the bottom trawl net. This means that many potential habitat areas are never explored, and as such, the full range of depth that the species can live in might not be explored. Furthermore, research surveys are conducted at predefined times of the year, depending on the target species which need to be monitored. As none of the research surveys used in this study are 1) designed for skates and 2) conducted in summer, they might miss the reproductive season in the summer and hence the catch of certain age classes. Additionally, since we cannot estimate the population size of the species, there is a possibility that the very method that allows us to discover more about the species could endanger it, either by catching individuals or by habitat destruction through the trawl net (Puig et al., 2012; Lennon et al., 2021).

The morphological analysis was limited by sample size, particularly with regard to mature individuals. Furthermore, the preservation method of samples can also lead to some inaccuracies; for example, it has been found that freezing can lead to shrinkage (Ogle, 2009). Both preservation in ethanol and formalin and freezing were found to have a significant effect. Moreover, there is a risk of inaccuracies or a lack of consistency since not all measurements and maturation estimates were conducted by the same person; this also holds true when comparing results to other studies, as standardization can be difficult (Francis, 2006).

The genetic analysis was limited by the quality of the DNA. This may be the result of various factors, such as poor tissue quality, lab errors, contamination, or poor storage of chemicals. Consequently, for some individuals, the size of the fragments that could be used was shorter (minimum 619 nucleotides), which in turn made comparisons less reliable. The lack of a clear pattern in genetic diversity could also be a result of the marker used, since the information that can be obtained from mitochondrial markers is limited. These markers are often more

efficient at identifying interspecies variability than intraspecies variability (Ward, 2009). Furthermore, DNA barcoding relies on a barcoding "gap" for species identification, which cannot always be achieved as there is often overlap between interspecies and intraspecies variability (Meyer & Paulay, 2005). Additionally, mitochondrial markers only reveal maternally transmitted DNA, making hybrid detection impossible and providing a limited view of the population (Ward et al., 2008; Galtier et al., 2009; Naylor et al., 2012). Moreover, due to the slow rate of mitochondrial substitutions and the slow process of the accumulation of genetic differences, it can be difficult to differentiate between recently diverged species (Martin et al., 1992; Larson et al., 2017). The genetic analysis was also limited by sample size for samples representing the regions of Greenland and the Faroes, with 10 and 6, respectively. This led to a sampling bias, with a higher number of haplotypes found in regions with more samples (Table 6). This sampling bias could also be seen in the θ_{ST} values after randomization (Table 9), wherein the values showed only moderate population differentiation with values below 0.1, while the original values indicated strong population differentiation (Table 8)(Bird et al., 2017). Additionally, the NADH2 analysis did not cover the entire distribution range of the species, particularly with West Greenland and Canada missing.

The issue of misidentifications represents a significant limitation when it comes to genetic analysis, especially in the absence of visual confirmation. Within the samples obtained for this study, there were some notable misidentifications, specifically with the Arctic skate and the sailray. Additionally, there were several misidentifications in the data available online on BOLD and GenBank. This indicates a need for better data verification processes for online repositories. The frequency of errors in sequences available in online depositories, affecting numerous species, has been well documented (Forster, 2003; Pentinsaari et al., 2020). Such inaccuracies can stem from misidentifications, laboratory errors such as contamination, or errors in data entry. Such errors can compromise the reliability of DNA barcoding since it relies on the comparison of new samples with existing sequences.

4.5. Future research and conservation

Identifying reproduction areas, egg nurseries, and juvenile distribution patterns is essential for defining conservation priorities. Establishing the timing or locations of mating and egg

deposition is particularly important, as conservation measures can then be implemented to restrict fishing during these periods or in those locations (Elliott et al., 2020). Additionally, potential nursery grounds can be identified by looking at where the youngest skates were found, assuming that they have limited dispersion capacities (Camhi et al., 1998) or by looking at the presence of egg cases (Hoff, 2008; Lennon et al., 2021). However, the accuracy of the estimations of potential nursery grounds for spinytail skates is limited by the lack of mature females as well as the small number of juveniles found. Additionally, given the variability in reported maximum lengths between the west and east Atlantic, it would be beneficial to conduct a morphometric analysis comparing specimens from different regions (Bigelow & Schroeder, 1954).

Since the species is iteroparous, meaning that there are multiple reproduction events in its lifetime, the removal of mature females from a population can have lasting consequences. This means that it is particularly important to further investigate the maturity of the species by locating and recording mature females. Finding more mature individuals overall will also allow for a better estimate of size at maturity. Furthermore, the age at maturity could be investigated by looking at growth bands on vertebrae and comparing them among different maturity stages (Goldman, 2005). Additionally, determining the time needed after spawning for a female to become reproductively active again could explain the rarity of mature spinytail skate catches. Given the low abundance of the species, the long-term storage of sperm in the female reproductive tract should also be investigated. This phenomenon has been found in other skate species, such as the clearnose skate *Raja eglanteria* (Luer et al., 2007). Considering the previously mentioned limitations in mitochondrial markers and the uncertainty surrounding the results, employing alternative genetic methods such as single-nucleotide polymorphisms (SNPs) with next-generation sequencing may provide more reliable conclusions (Larson et al., 2017).

There are currently no species-specific conservation measures for the spinytail skate; however, regulations concerning target fishing species such as the Greenland halibut *Reinhardtius hippoglossoides* can be beneficial in reducing the bycatch frequency. Additionally, status assessments, such as the assessment that has already been conducted by

the IUCN and an assessment by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), for which the spinytail skate is currently a candidate (Pollom et al., 2020a), are beneficial in determining the vulnerability of the species. However, these detailed status assessments cannot be reliable if there are still no identifications or many misidentifications when it comes to catch data on fishing and research vessels. For this reason, it is important to have identification keys on board and trained personnel; nevertheless, the problem also lies in time constraints and the low commercial importance of the species (Stevens et al., 2000; Liu et al., 2021). These issues could be mitigated by using photographs, preferentially together with skin swabs or tissue samples, to conduct identifications at a later time. The migration patterns of the species could be further investigated using catch and release with tagging, especially on mature individuals.

5. Conclusion

The morphometric analysis revealed differences in body proportions between sexes and throughout growth, which could reflect differences in feeding and dispersion behaviors, such as the known ontogenetic niche shift between juveniles and adults. Additionally, a spatial distribution pattern was found wherein all mature individuals were found on the BSS. Most importantly, the size at maturity for males was determined and can now be used for stock/population assessments. However, the absence of mature females hindered the analysis of female maturity. This highlights the importance of further investigating where and when exactly reproduction occurs for the species and locating mature females. This is dependent on improving species identification during research and fishing surveys, consequently obtaining more reliable catch data.

As for the genetic population analysis, no clear population structure was found. This could either indicate high connectivity and a high dispersal rate or a need for more detailed genetic methods, or a combination of both. It is important to further investigate the population structure of the species for conservation purposes and even to gain a better understanding of the behavior of the species in terms of reproduction and migration. Therefore, the next priority is to use nuclear markers across the genome to get a more comprehensive overview of

the population structure and to either confirm or reject the pattern found by the mitochondrial markers.

6. References

Ainsley, S. M., Ebert, D. A., & Cailliet, G. M. (2011). Age, growth, and maturity of the whitebrow skate, *Bathyraja minispinosa*, from the eastern Bering Sea. *ICES Journal of Marine Science*, *68*(7), 1426-1434. https://doi.org/10.1093/icesjms/fsr072

Al-Shuhaib, M. B. S., & Hashim, H. O. (2023). Mastering DNA chromatogram analysis in Sanger sequencing for reliable clinical analysis. *Journal of Genetic Engineering and Biotechnology*, *21*(1), 115. https://doi.org/10.1186/s43141-023-00587-6

Arkhipkin, A. I., Baumgartner, N., Brickle, P., Laptikhovsky, V. V., Pompert, J. H. W., & Shcherbich, Z. N. (2008). Biology of the skates *Bathyraja brachyurops* and *B. griseocauda* in waters around the Falkland Islands, Southwest Atlantic. *ICES Journal of Marine Science*, *65*(4), 560-570. https://doi.org/10.1093/icesjms/fsn015

Aurelle, D., Tariel, J., Zuberer, F., Haguenauer, A., Ribout, C., Masmoudi, M., Kara, H., Chaoui, L., Garrabou, J., Ledoux, J. B., & Gambi, M. C. (2020). Genetic insights into recolonization processes of Mediterranean octocorals. *Marine Biology*, *167*(6), 73. https://doi.org/10.1007/s00227-020-03684-z

Baker, K. D., Devine, J. A., & Haedrich, R. L. (2009). Deep-sea fishes in Canada's Atlantic: population declines and predicted recovery times. *Environmental Biology of Fishes*, *85*(1), 79-88. https://doi.org/10.1007/s10641-009-9465-8

Baranenkova, A. S., Ponomarenko, V. P., & Serbryakov, V. P. (1962). The spinytail skate (*Bathyraja spinicauda* Jensen) in the Barents Sea. *Voprosy ikhtiologii*, *2*, 18-24.

Bigelow, H. B., & Schroeder, W. C. (1954). *Raja spinicauda* Jensen 1914. *Bulletin of the Museum of Comparative Zoology*, *2*(112), 66-69.

Bird, K. A., An, H., Gazave, E., Gore, M. A., Pires, J. C., Robertson, L. D., & Labate, J. A. (2017). Population Structure and Phylogenetic Relationships in a Diverse Panel of *Brassica rapa* L. *Frontiers in Plant Science*, *8*. https://doi.org/10.3389/fpls.2017.00321

Byrkjedal, I., Christiansen, J., Karamushko, O., Langhelle, G., & Lynghammar, A. (2014). Arctic skate *Amblyraja hyperborea* preys on remarkably large glacial eelpouts *Lycodes frigidus*. *Journal of Fish Biology*, *86*. https://doi.org/10.1111/jfb.12554

Camhi, M., Fowler, S., Musick, J., Bräutigam, A., & Fordham, S. (1998). Sharks and their relatives–ecology and conservation (Vol. 20). *IUCN/SSC Shark Specialist Group.* IUCN, Gland, Switzerland and Cambridge, UK.

Casiraghi, M., Labra, M., Ferri, E., Galimberti, A., & De Mattia, F. (2010). DNA barcoding: a six-question tour to improve users' awareness about the method. *Briefings in Bioinformatics*, *11*(4), 440-453. https://doi.org/10.1093/bib/bbq003

Cowen, R. K., Lwiza, K. M. M., Sponaugle, S., Paris, C. B., & Olson, D. B. (2000). Connectivity of marine populations: open or closed? *Science*, *287*(5454), 857-859. https://doi.org/doi:10.1126/science.287.5454.857

Devine, J. A., Baker, K. D., & Haedrich, R. L. (2006). Deep-sea fishes qualify as endangered. *Nature*, *439*(7072), 29-29. https://doi.org/10.1038/439029a

Di Marco, M., Venter, O., Possingham, H., & Watson, J. (2018). Changes in human footprint drive changes in species extinction risk. *Nature Communications*, *9*. https://doi.org/10.1038/s41467-018-07049-5

Dolgov, A. V. (2005). Feeding and food consumption by the Barents Sea skates. *Journal of Northwest Atlantic Fishery Science*, *37*, 495-503. https://doi.org/10.2960/J.v35.m523

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

Dolgov, A. V., & Prozorkevich, D. V. (2022). Status of skate populations in the Barents Sea in the recent warm period. *Journal of Ichthyology*, *62*(7), 1312-1331. https://doi.org/10.1134/S0032945222060078

Doney, S. C., Ruckelshaus, M., Emmett Duffy, J., Barry, J. P., Chan, F., English, C. A., Galindo, H. M., Grebmeier, J. M., Hollowed, A. B., Knowlton, N., Polovina, J., Rabalais, N. N., Sydeman, W. J., & Talley, L. D. (2012). Climate change impacts on marine ecosystems. *Annual Review of Marine Science*, *4*, 11-37. https://doi.org/https://doi.org/10.1146/annurev-marine-041911-111611

Drevetnyak K.V., D. A. V., Sokolov K.M., Gusev E.V., and Grekov A.A. (2005). Skates in the Barents Sea: stock status and catch by fishing fleet. *2005 ICES Annual Science Conference*

Dulvy, N. K., Fowler, S. L., Musick, J. A., Cavanagh, R. D., Kyne, P. M., Harrison, L. R., Carlson, J. K., Davidson, L. N. K., Fordham, S. V., Francis, M. P., Pollock, C. M., Simpfendorfer, C. A., Burgess, G. H., Carpenter, K. E., Compagno, L. J. V., Ebert, D. A., Gibson, C., Heupel, M. R., Livingstone, S. R., Sanciangco, J.C., Steven, J.D., Valenti, S., White, W. T. (2014). Extinction risk and conservation of the world's sharks and rays. *eLife*, *3*. https://doi.org/10.7554/eLife.00590

Ebert, D. A. (2005). Reproductive biology of skates, *Bathyraja* (Ishiyama), along the eastern Bering Sea continental slope. *Journal of Fish Biology*, *66*(3), 618-649. https://doi.org/https://doi.org/10.1111/j.0022-1112.2005.00628.x

Ebert, D. A., & Bizzarro, J. J. (2007). Standardized diet compositions and trophic levels of skates (Chondrichthyes: Rajiformes: Rajoidei). *Environmental Biology of Fishes*, *80*(2), 221-237. https://doi.org/10.1007/s10641-007-9227-4

Ebert, D., & Stehmann, M. (2013). Sharks, batoids, and chimaeras of the North Atlantic. *FAO Species Catalogue for Fishery Purposes, 7.*

Elliott, S. A. M., Carpentier, A., Feunteun, E., & Trancart, T. (2020). Distribution and life history trait models indicate vulnerability of skates. *Progress in Oceanography*, *181*, 102256. https://doi.org/https://doi.org/10.1016/j.pocean.2019.102256

Excoffier, L., & Lischer, H. E. L. (2010). Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources, 10*(3): 564-567. https://doi.org/10.1111/j.1755-0998.2010.02847.x

Faria, V. V., McDavitt, M. T., Charvet, P., Wiley, T. R., Simpfendorfer, C. A., & Naylor, G. J. P. (2013). Species delineation and global population structure of Critically Endangered sawfishes (Pristidae). *Zoological Journal of the Linnean Society*, *167*(1), 136-164. https://doi.org/https://doi.org/10.1111/j.1096-3642.2012.00872.x

Farrugia, T. J., Goldman, K. J., Tribuzio, C., & Seitz, A. C. (2016). First use of satellite tags to examine movement and habitat use of big skates *Beringraja binoculata* in the Gulf of Alaska. *Marine Ecology Progress Series*, *556*, 209-221. https://www.int-res.com/abstracts/meps/v556/p209-221/

Feduccia, A., & Slaughter, B. H. (1974). Sexual dimorphism in skates (Rajidae) and its possible role in differential niche utilization. *Evolution*, *28*(1), 164-168. https://doi.org/10.2307/2407249

Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R., & Lotze, H. K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters*, *13*(8), 1055-1071. https://doi.org/https://doi.org/10.1111/j.1461-0248.2010.01489.x

Finucci, B., Cheok, J., Ebert, D. A., Herman, K., Kyne, P. M., & Dulvy, N. K. (2021). Ghosts of the deep–Biodiversity, fisheries, and extinction risk of ghost sharks. *Fish and Fisheries*, *22*(2), 391-412.

Finucci, B., Pacoureau, N., Rigby, C., Matsushiba, J., Faure-Beaulieu, N., Sherman, S., Vanderwright, W., Jabado, R., Charvet, P., Mejía-Falla, P., Navia, A., Derrick, D., Kyne, P., Pollom, R., Walls, R., Herman, K., Bineesh, K. K., Cotton, C., Cuevas, J.-M., & Dulvy, N. (2024). Fishing for oil and meat drives irreversible defaunation of deepwater sharks and rays. *Science (New York, N.Y.)*, *383*, 1135-1141. https://doi.org/10.1126/science.ade9121

Forster, P. (2003). To err is human. *Annals of Human Genetics*, *67*(1), 2-4. https://doi.org/https://doi.org/10.1046/j.1469-1809.2003.00002.x

Francis, M. P. (2006). Morphometric minefields—towards a measurement standard for chondrichthyan fishes. *Environmental Biology of Fishes*, *77*(3), 407-421. https://doi.org/10.1007/s10641-006-9109-1

Frankham, R., Ballou, J. D., Ralls, K., Eldridge, M. D. B., Dudash, M. R., Fenster, C. B., Lacy, R. C., Sunnucks, P. (2019). Population fragmentation causes inadequate gene flow and increases extinction risk. *A Practical Guide for Genetic Management of Fragmented Animal and Plant Populations*. Oxford University Press. https://doi.org/10.1093/oso/9780198783411.003.0004

Frisk, M. G., Shipley, O. N., Martinez, C. M., McKown, K. A., Zacharias, J. P., & Dunton, K. J. (2019). First observations of long-distance migration in a large skate species, the winter skate: Implications for population connectivity, ecosystem dynamics, and management. *Marine and Coastal Fisheries*, *11*(2), 202-212. https://doi.org/https://doi.org/10.1002/mcf2.10070

Galtier, N., Nabholz, B., Glémin, S., & Hurst, G. D. D. (2009). Mitochondrial DNA as a marker of molecular diversity: a reappraisal. *Molecular Ecology*, *18*(22), 4541-4550. https://doi.org/https://doi.org/10.1111/j.1365-294X.2009.04380.x

Garibyan, L., & Avashia, N. (2013). Polymerase chain reaction. *J Invest Dermatol*, *133*(3), 1-4. https://doi.org/10.1038/jid.2013.1

Goldman, K. (2005). Age and growth of elasmobranch fishes. *FAO Fisheries Technical Paper*, *474*.

González, C., Román, E., Paz, X., & Ceballos-Roa, E. (2006). Feeding habits and diet overlap of skates (*Amblyraja radiata, A. hyperborea, Bathyraja spinicauda, Malacoraja senta* and *Rajella fyllae*) in the North Atlantic. *NAFO Scientific Council Meeting Doc.*

Forsberg, H, Lynghammar, A., Christiansen, J.S., & Junge, C. (2018). Morphological description of egg capsules of skates (Rajiformes) and potential nursery grounds in the Barents Sea.

Hansen, B., & Østerhus, S. (2000). North Atlantic–Nordic Seas exchanges. *Progress in Oceanography*, *45*(2), 109-208. https://doi.org/https://doi.org/10.1016/S0079-6611(99)00052-X

Hedgecock, D., Barber, P. H., & Edmands, S. (2007). Genetic approaches to measuring connectivity. *Oceanography*, *20*(3), 70-79. http://www.jstor.org/stable/24860097

Hemmingmoore, H., Aronsson, M., Åkesson, M., Persson, J., & Andrén, H. (2020). Evaluating habitat suitability and connectivity for a recolonizing large carnivore. *Biological Conservation*, *242*, 108352. https://doi.org/https://doi.org/10.1016/j.biocon.2019.108352

Henderson, A., Reeve, A., Jabado, R., & Naylor, G. (2016). Taxonomic assessment of sharks, rays and guitarfishes (Chondrichthyes: Elasmobranchii) from south-eastern Arabia, using the NADH dehydrogenase subunit 2 (NADH2) gene. *Zoological Journal of the Linnean Society*, *176*, 399-442. https://doi.org/10.1111/zoj.12309

Hewitt, G. M. (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, *58*(3), 247-276. https://doi.org/10.1111/j.1095-8312.1996.tb01434.x

Hoff, G. R. (2008). A nursery site of the Alaska skate (*Bathyraja parmifera*) in the eastern Bering Sea. *Fishery Bulletin, 106.* https://doi.org/10.1111/jfb.12939

Hoffmann, M., Duckworth, J. W., Holmes, K., Mallon, D. P., Rodrigues, A. S. L., & Stuart, S. N. (2015). The difference conservation makes to extinction risk of the world's

ungulates. *Conservation Biology*, *29*(5), 1303-1313. https://doi.org/https://doi.org/10.1111/cobi.12519

Holden, M. J. (1975). The fecundity of *Raja clavata* in British waters. *ICES Journal of Marine Science*, *36*(2), 110-118. https://doi.org/10.1093/icesjms/36.2.110

Holsinger, K. E., & Weir, B. S. (2009). Genetics in geographically structured populations: defining, estimating and interpreting F(st). *Nature Review Genetics*, *10*(9), 639-650. https://doi.org/10.1038/nrg2611

Hubert, N., & Hanner, R. (2015). DNA barcoding, species delineation, and taxonomy: A historical perspective. *DNA Barcodes*, *3*, 44-58. https://doi.org/10.1515/dna-2015-0006

ICES. (2010). *Report of the workshop on sexual maturity staging of elasmobranches (WKMSEL)* Valetta, Malta.

Jac, R., Höffle, H., Albretsen, J., Jakobsdóttir, K., Staby, A., Søvik, G., & Junge, C. (2022). Of three sharks and one chimaera: varied habitat preferences across a latitudinal range revealed by coastal and offshore surveys. *Journal of Fish Biology*, *100*(3), 660-674.

Kleiven, K. S. (2022). Unexpected feeding behaviour inferred by DNA metabarcoding of Barents Sea skates. *Master's thesis, UiT The Arctic University of Norway.*

Koefoed, E. (1956). *Theragra finnmarchica n.* sp., *Gadus poutassou, Risso, Raia spinicauda, Jensen, Eumicrotremus spinosus* subsp. nov. *eggvinii. Fiskeridirektoratets Skrifter, Serie Havundersøkelser. Report on Norwegian Fishery and Marine-Investigations, 11*, 15-19.

Koob, T. J., Tsang, P., & Callard, I. P. (1986). Plasma Estradiol, Testosterone, and Progesterone Levels during the Ovulatory Cycle of the Skate (*Raja Erinacea*). *Biology of Reproduction*, *35*(2), 267-275. https://doi.org/10.1095/biolreprod35.2.267

Krefft, G. (1956). A contribution to the knowledge of the Greenland Ray Raja Spinicauda Jensen 1914. *Archiv für Fischereiwissenschaf*, *7*, 139-145.

Larson, S., Daly-Engel, T., & Phillips, N. (2017). Review of current conservation genetic analyses of Northeast Pacific sharks. *Advances in Marine Biology 2017*, 77:79-110. https://doi.org/10.1016/bs.amb.2017.06.005

Last, P., White, W., de Carvalho, M., Séret, B., Stehmann, M. and Naylor, G. (2016). *Rays of the World*. CSIRO Publishing, Clayton. https://doi.org/10.1071/9780643109148

Leigh, J. W., & Bryant, D. (2015). Popart: full-feature software for haplotype network construction. *Methods in Ecology and Evolution*, *6*(9), 1110-1116. https://doi.org/https://doi.org/10.1111/2041-210X.12410

Lennon, E., Philips, N. D., Garbett, A., Carlsson, J., Carlsson, J. E. L., Crowley, D., Judge, M., Yeo, I., & Collins, P. C. (2021). Going deeper, darker and further: Observations charting an egg nursery, a range and depth extension for the deep-sea spiny tailed skate *Bathyraja spinicauda*, first records from the Mid Atlantic Ridge. *Deep Sea Research Part I: Oceanographic Research Papers*, *175*, 103584. https://doi.org/https://doi.org/10.1016/j.dsr.2021.103584

Liu, K.-M., Huang, Y.-W., & Hsu, H.-H. (2021). Management implications for skates and rays based on analysis of life history parameters. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.664611

Loh, K. H., Lim, K. C., Then, A. Y., Adam, S., Leung, A. J., Hu, W., Bong, C. W., Wang, A., Sade, A., Musel, J., & Du, J. (2023). Advancing DNA Barcoding to Elucidate Elasmobranch Biodiversity in Malaysian Waters. *Animals (Basel)*, *13*(6). https://doi.org/10.3390/ani13061002

Luther, D., Skelton, J., Fernandez, C., & Walters, J. (2016). Conservation action implementation, funding, and population trends of birds listed on the Endangered Species Act. *Biological Conservation*, *197*, 229-234. https://doi.org/https://doi.org/10.1016/j.biocon.2016.03.019

Knutsen, M., Thangstad, T.H., Søvik, G., & Albert, O.T. (2017). Survey trends of skates in Norwegian waters *Working document for the ICES Elasmobranch Working Group (WGEF)*.

Martin, A. P., Naylor, G. J. P., & Palumbi, S. R. (1992). Rates of mitochondrial DNA evolution in sharks are slow compared with mammals. *Nature*, *357*(6374), 153-155. https://doi.org/10.1038/357153a0

Martinez, C. M., Kao, B. H., Sparks, J. S., & Wainwright, P. C. (2019). Pectoral dimorphism is a pervasive feature of skate diversity and offers insight into their evolution. *Integrative Organismal Biology*, *1*(1). https://doi.org/10.1093/iob/obz012

McEachran, J. D. (1977). Reply to 'Sexual dimorphism in skates (Rajidae)'. *Evolution*, *31*(1), 218-220. https://doi.org/10.2307/2407559

Mecklenburg, C. W., Mecklenburg, T. A., & Thorsteinson, L. K. (2002). *Fishes of Alaska*. American Fisheries Society.

Mecklenburg, C., Lynghammar, A., Johannesen, E., Byrkjedal, I., Christiansen, J., Dolgov, A., Karamushko, O., Mecklenburg, T., Moller, P., Steinke, D., & Wienerroither, R. (2018). Marine fishes of the Arctic region Volume 1. *Conservation of Arctic Flora and Fauna Monitoring Series 28, Norwegian Ministry of Foreign Affairs*, *1*. https://repository.library.noaa.gov/view/noaa/28036 (CAFF Monitoring Series Report 28)

Meyer, C. P., & Paulay, G. (2005). DNA barcoding: error rates based on comprehensive sampling. *PLOS Biology*, *3*(12), e422. https://doi.org/10.1371/journal.pbio.0030422

Moller, P. R., Renaud, C. B., Alfonso, N. R., Dunmall, K., Power, M., Sawatzky, C. D., Berkes, F., Dempson, J. B., Harris, L. N., & Swanson, H. K. (2018). *Marine Fishes of Arctic Canada*. University of Toronto Press. http://www.jstor.org/stable/10.3138/j.ctt1x76h0b

Naylor, G. J. P., Caira, J. N., Jensen, K., Rosana, K. A. M., White, W. T., & Last, P. R. (2012). A DNA sequence–based approach to the identification of shark and ray species and its implications for global elasmobranch diversity and parasitology. *Bulletin of the American Museum of Natural History*, *2012*(367), 1-262, 262. https://doi.org/10.1206/754.1

NOAA. (01/20/23). Where is Earth's Largest Waterfall? https://oceanservice.noaa.gov/facts/largest-waterfall.html

Ogle, D. (2009). The effect of freezing on the length and weight measurements of ruffe (*Gymnocephalus cernuus*). *Fisheries Research - FISH RES*, *99*, 244-247. https://doi.org/10.1016/j.fishres.2009.06.009

Orlov, A. M., & Cotton, C. F. (2011). Sexually dimorphic morphological characters in five North Atlantic deepwater skates (Chondrichthyes: Rajiformes). *Journal of Marine Biology*, *2011*, 842821. https://doi.org/10.1155/2011/842821

Pentinsaari, M., Ratnasingham, S., Miller, S. E., & Hebert, P. D. N. (2020). BOLD and GenBank revisited - Do identification errors arise in the lab or in the sequence libraries? *PLOS One*, *15*(4), e0231814. https://doi.org/10.1371/journal.pone.0231814

Pollom, R., Kulka, D., Derrick, D., Pacoureau, N., & Dulvy, N. (2020a). *Bathyraja spinicauda*-spinytail skate. *The IUCN Red List of Threatened Species 2020*. https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T161366A124472535.en

Pollom, R., Dulvy, N., Acuna, E., Bustamante, C., Cevallos-Garcia, A., Chiaramonte, G., Cuevas, J., Herman, K., Navia, A., Paesch, L., Pompert, J., & Velez-Zuazo, X. (2020b). *Bathyraja albomaculata,* Whitedotted Skate. *The IUCN Red List of Threatened Species*. https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T63102A124458655.en

Pollom, R., Dulvy, N., Acuna, E., Bustamante, C., Chiaramonte, G., Cuevas, J., Herman, K., Paesch, L., Pompert, J., & Velez-Zuazo, X. (2020c). *Bathyraja griseocauda,* Graytail Skate. *The IUCN Red List of Threatened Species*. https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T63113A124459226.en

Pratt, H. L., & Carrier, J. C. (2001). A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma Cirratum*. *Environmental Biology of Fishes*, *60*(1), 157-188. https://doi.org/10.1023/A:1007656126281

Puig, P., Canals, M., Company, J. B., Martín, J., Amblas, D., Lastras, G., Palanques, A., & Calafat, A. M. (2012). Ploughing the deep sea floor. *Nature*, *489* (7415), 286-289. https://doi.org/10.1038/nature11410

Reynolds, J. D., Dulvy, N. K., Goodwin, N. B., & Hutchings, J. A. (2005). Biology of extinction risk in marine fishes. *Proc Biol Sci*, *272*(1579), 2337-2344. https://doi.org/10.1098/rspb.2005.3281

Riginos, C., & Liggins, L. (2013). Seascape Genetics: Populations, individuals, and genes marooned and adrift. *Geography Compass*, *7*, 197–216. https://doi.org/10.1111/gec3.12032

Ruocco, N. L., Lucifora, L. O., Díaz de Astarloa, J. M., & Wöhler, O. (2006). Reproductive biology and abundance of the white-dotted skate, *Bathyraja albomaculata*, in the Southwest Atlantic. *ICES Journal of Marine Science*, *63*(1), 105-116. https://doi.org/10.1016/j.icesjms.2005.08.007

Savolainen, O., Lascoux, M., & Merilä, J. (2013). Ecological genomics of local adaptation. *Nature Reviews Genetics*, *14*(11), 807-820. https://doi.org/10.1038/nrg3522

Shiffman, D. S., Ajemian, M. J., Carrier, J. C., Daly-Engel, T. S., Davis, M. M., Dulvy, N. K., Grubbs, R. D., Hinojosa, N. A., Imhoff, J., Kolmann, M. A., Nash, C. S., Paig-Tran, E.

W. M., Peele, E. E., Skubel, R. A., Wetherbee, B. M., Whitenack, L. B., & Wyffels, J. T. (2020). Trends in chondrichthyan research: An analysis of three decades of conference abstracts. *Copeia*, *108*(1), 122-131, 110. https://doi.org/10.1643/OT-19-179R

Simpfendorfer, C. A., & Kyne, P. M. (2009). Limited potential to recover from overfishing raises concerns for deep-sea sharks, rays and chimaeras. *Environmental Conservation*, *36*(2), 97-103. https://doi.org/10.1017/S0376892909990191

Slatkin, M. (1987). Gene flow and the geographic structure of natural populations. *Science*, *236*(4803), 787-792. http://www.jstor.org.mime.uit.no/stable/1699930

Stevens, J. D., Bonfil, R., Dulvy, N. K., & Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science*, *57*(3), 476-494. https://doi.org/10.1006/jmsc.2000.0724

Stevenson, D. E., Orr, J. W., Hoff, G. R., & McEachran, J. D. (2007). *Field Guide to Sharks, Skates, and Ratfish of Alaska*.

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.

Tamura, K., Stecher, G., & Kumar, S. (2021). MEGA11: Molecular Evolutionary Genetics Analysis Version 11. *Molecular biology and evolution*, *38*. https://doi.org/10.1093/molbev/msab120

R Core Team. (2023). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing https://www.R-project.org/

Ratnasingham, S., & Hebert, P. D. (2007). BOLD: The Barcode of Life Data System (http://www.barcodinglife.org). *Mol Ecol Notes*, *7*(3), 355-364. https://doi.org/10.1111/j.1471-8286.2007.01678.x

Templeman, W. (1984). Migrations of thorny skate, *Raja radiata*, tagged in Newfoundland. *Journal of Northwest Atlantic Fishery Science*, *5*, 55-63. https://doi.org/10.2960/j.v5.a6

Veríssimo, A., McDowell, J. R., & Graves, J. E. (2010). Global population structure of the spiny dogfish *Squalus acanthias*, a temperate shark with an antitropical distribution.

Molecular Ecology, *19*(8), 1651-1662. https://doi.org/https://doi.org/10.1111/j.1365-294X.2010.04598.x

Veríssimo, A., McDowell, J. R., & Graves, J. E. (2012). Genetic population structure and connectivity in a commercially exploited and wide-ranging deepwater shark, the leafscale gulper (*Centrophorus squamosus*). *Marine and Freshwater Research*, *63*(6), 505-512.

Verma, K. K., Jolivet, P. H., & Saxena, R. (2013). Species and speciation. *Biological Forum – An International Journal, 5*(1): 42-49

Villasante, S., Morato, T., Rodriguez-Gonzalez, D., Antelo, M., Österblom, H., Watling, L., Nouvian, C., Gianni, M., & Macho, G. (2012). Sustainability of deep-sea fish species under the European Union Common Fisheries Policy. *Ocean & Coastal Management*, *70*, 31-37. https://doi.org/https://doi.org/10.1016/j.ocecoaman.2012.07.033

Wang, J. Y., Frasier, T. R., Yang, S. C., & White, B. N. (2008). Detecting recent speciation events: the case of the finless porpoise (genus Neophocaena). *Heredity*, *101*(2), 145-155. https://doi.org/10.1038/hdy.2008.40

Waples, R. S., & Gaggiotti, O. (2006). INVITED REVIEW: What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology*, *15*(6), 1419-1439. https://doi.org/https://doi.org/10.1111/j.1365-294X.2006.02890.x

Ward, R., Holmes, B., White, W., & Last, P. (2008). DNA barcoding Australasian chondrichthyans: Results and potential uses in conservation. *Marine and Freshwater Research*, *59*, 57-71. https://doi.org/10.1071/MF07148

Ward, R. D. (2009). DNA barcode divergence among species and genera of birds and fishes. *Molecular Ecology Resources*, *9*(4), 1077-1085. https://doi.org/https://doi.org/10.1111/j.1755-0998.2009.02541.x

Wearmouth, V. J., & Sims, D. W. (2009). Movement and behaviour patterns of the critically endangered common skate *Dipturus batis* revealed by electronic tagging. *Journal of Experimental Marine Biology and Ecology*, *380*(1), 77-87. https://doi.org/https://doi.org/10.1016/j.jembe.2009.07.035

Weigmann, S. (2016). Annotated checklist of the living sharks, batoids and chimaeras (Chondrichthyes) of the world, with a focus on biogeographical diversity. *Journal of Fish Biology*, *88*(3), 837–1037.

Wright, S. (1943). Isolation by distance. *Genetics*, *28*(2), 114-138. https://doi.org/10.1093/genetics/28.2.114

Appendix

Appendix A: Survey information

Survey	Aim	Area	Number of samples	Years	Institution
Tagging of greenland halibut survey	Monitor *Reinhardtius hippoglossoides*	Eggaslope	6	2008	Institute of Marine Research (IMR)
Egga Nord	Monitor species: *Sebastes mentella, Reinhardtius hippoglossoides* and *Sebastes norvegicus*	Eggaslope Bjørnøyrenna	29	2009 2011 2019 2021 2023	
Joint Norwegian/Russian Ecosystem survey	Monitor abiotic and biotic ecosystem factors	Barents sea	5	2010 2023	
Winter survey	Monitor abiotic and biotic ecosystem factors	Barents sea	10	2011 2012 2020	
Shrimp survey	Monitor *Pandalus borealis*	Norwegian Deep and Skagerrak	2	2020	
Trawl testing	Development of trawl fishery technology	Barents sea	6	2010 2012 2021	Norwegian College of Fisheries Science UiT
Greenland	Monitor *Reinhardtius hippoglossoides*	East Greenland	9	2023	Greenland Institute of Natural Resources
Deepwater survey	Monitor *Reinhardtius hippoglossoides*	Faroe Islands	13	2023	Faroe Marine Research institute

Appendix B: DNA extraction protocol

DNA extraction using the DNeasy® Blood & Tissue Kit protocol

1. Weigh approximately 20 mg of tissue, then mince it into small pieces, and transfer into a 1.5 mL centrifuge tube
2. Add 180 µL lysis buffer ATL and 20 µL proteinase K, and vortex for 15s
3. Incubate 6-12 hours at 56 °C until the tissue is fully lysed. Vortex occasionally during the incubation and before proceeding to step 4
4. Add 200 µL buffer AL and 200 µL of 96-100% ethanol. Vortex before transfering the mixture to a DNeasy Mini spin column placed in a 2 mL collection tube
5. Centrifuge for 1 minute at 6000 x *g* and transfer spin column to a new collection tube. Discard the old collection tube and its content.
6. Add 500 µL washer buffer AW1 and centrifuge for 1 minute at 6000 x *g*
7. Transfer to a new collection tube and add 500 µL washer buffer AW2
8. Centrifuge for 3 minutes at 20 000 x *g*
9. Transfer to 1,5 mL tube and add 200 µL elution AE Buffer. Incubate at room temperature (15-25°C) for 1 minute
10. Centrifuge for 1 minute at 6000 x *g*

Appendix C: Individual metadata

List of tissue samples/whole individuals used for the morphometric and genetic analysis. Information on the location, sex and total length (TL) of each individual.

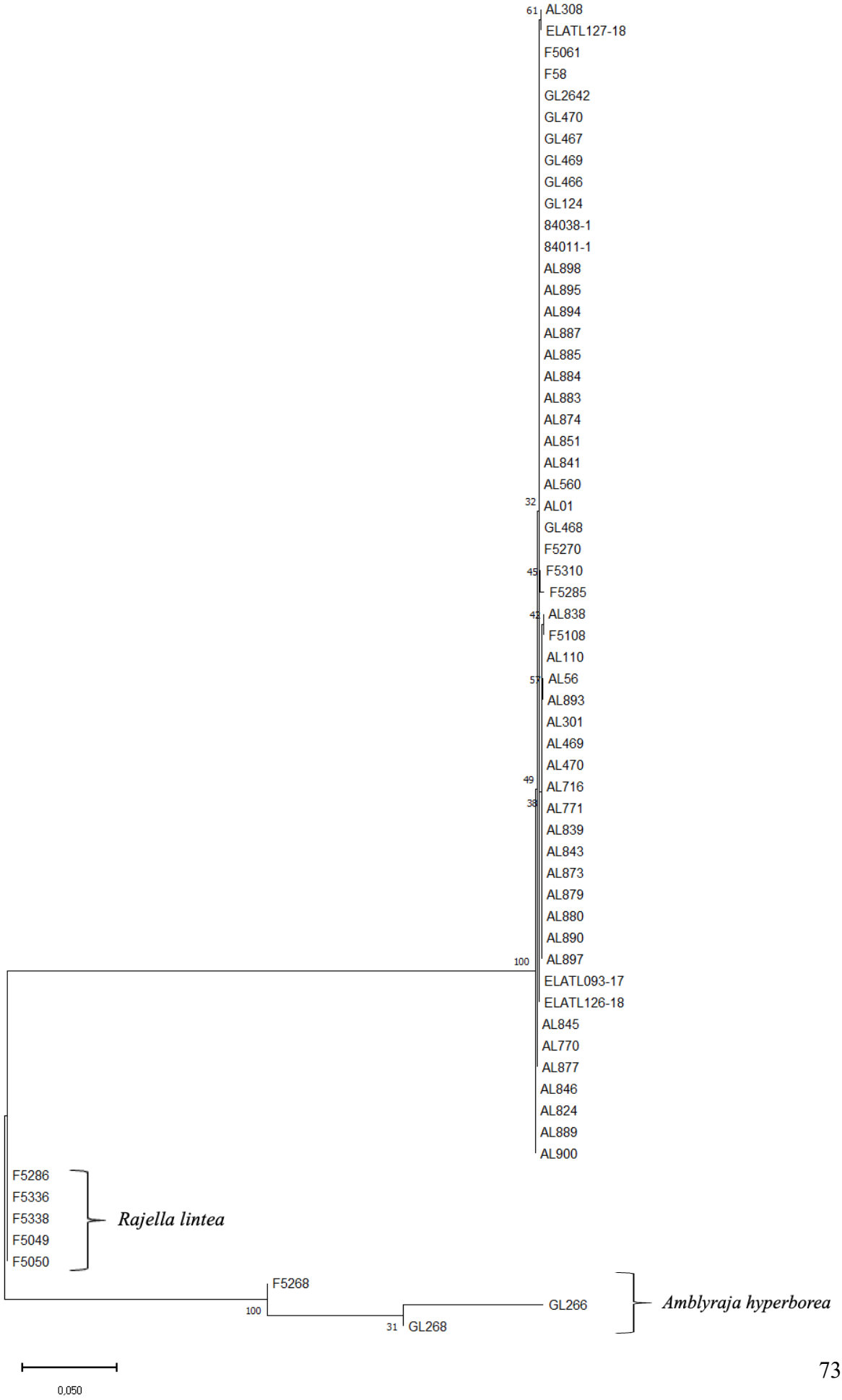
ID	Latitude	Longitude	Region	Depth	Date	Sex	TL (mm)
82138	76.57	13.83	CSN	586	08/11/2009	male	470
82157	77.55	10.88	CSN	610	08/13/2009	female	490
82158	77.57	10.75	CSN	814	08/13/2009	male	577
2008-ARV-020 (IMR6)	unknown	unknown	NA	unknown	unknown	male	308
82118_1	75.55	13.9	CSN	806	08/10/2009	female	610
82128_1	76.17	14.25	CSN	655	08/11/2009	male	312
82128_2	76.17	14.25	CSN	655	08/11/2009	female	340
82148_1	77.17	11.32	CSN	806	08/12/2009	male	874
82148_2	77.17	11.32	CSN	806	08/12/2009	female	408
84011-1	70.50	17.13	CSS	680	11/23/2011	female	550
84038-1	74.60	15.97	CSN	671	11/29/2011	female	420
AL1	71.53	26.23	BSS	291	02/28/2011	female	1000
AL110	72.43	32.30	BSS	280	08/30/2010	female	736
AL301	71.27	27.53	BSS	284	26/11/2010	male	813
AL308	71.26	27.57	BSS	284	26/11/2010	male	860
AL469	70.83	30.37	BSS	350	03/2012	male	1460
AL470	70.83	30.37	BSS	350	03/03/2012	female	920
AL474	unknown	unknown	NA	unknown	unknown	female	1125
AL544	73.47	30.32	BSS	377	11/02/2012	male	1440
AL56	73.30	20.23	BSS	470	09/05/2010	female	1100
AL560	72.86	25.05	BSS	394	02/2011	female	650
AL710	unknown	unknown	NA	unknown	unknown	male	1420
AL711						female	1385
AL712	70.56	30.79	BSS	90	10/10/2020	male	280
AL715	71.67	23.04	BSS	381	18/08/2020	male	565
AL716	72.72	20.67	BSS	426	23/08/2020	male	780
AL717	71.57	21.05	BSS	316	20/08/2020	male	1310
AL768	71.99	29.31	BSS	282	14/02/2020	male	1350
AL769	71.87	20.36	BSS	335	25/02/2020	male	1400
AL770	73.95	16.23	BSS	360	26/01/2020	female	1670
AL771	71.80	15.88	CSN	527	23/01/2020	female	1420
AL772	unknown	unknown	NA	unknown	unknown	female	885
AL773	73.53	15.39	CSN	499	25/01/2020	female	1250
AL824	74.53	16.22	CSN	509	26/01/2020	female	525
AL838	71.81	15.57	CSS	724	06/09/2019	female	1220
AL839	76.23	14.11	CSN	800	11/09/2019	male	986

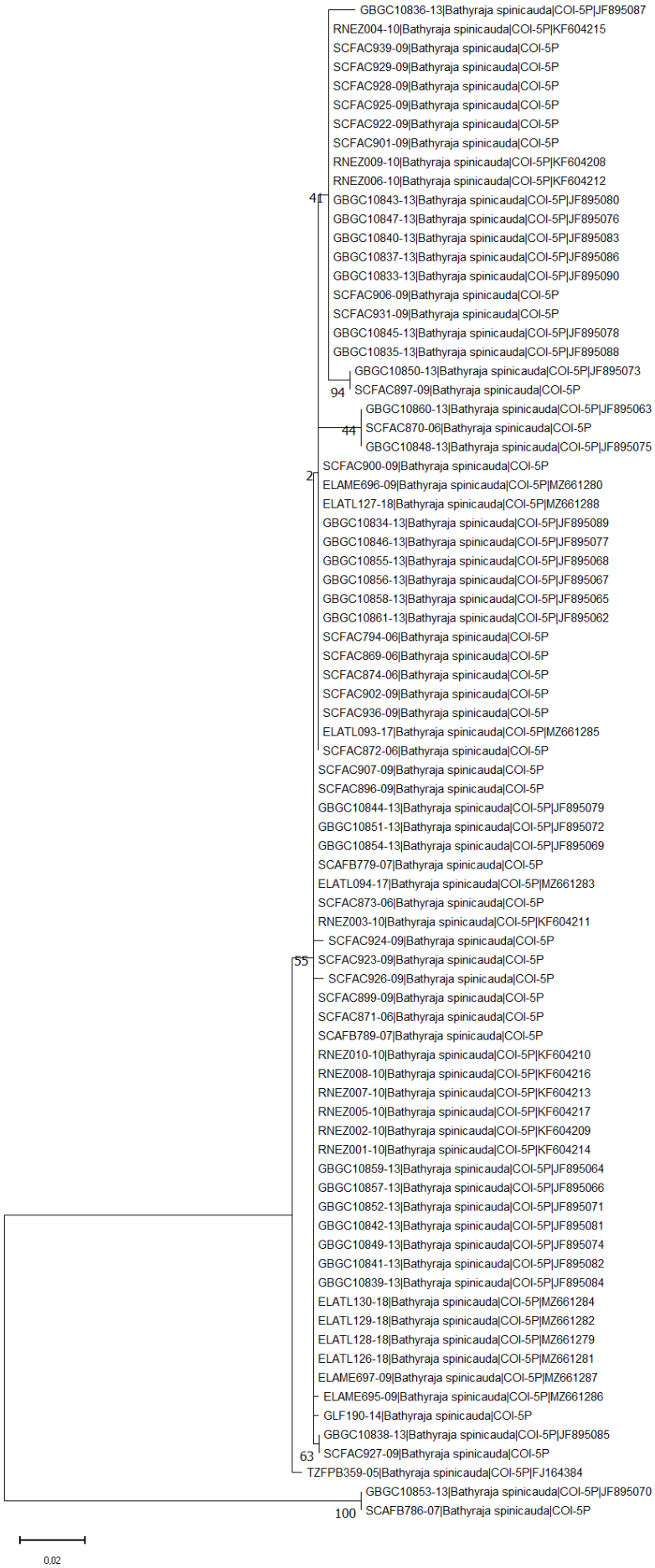
AL841	74.41	16.27	CSN	519	09/09/2019	male	995
AL843	74.58	16.09	CSN	586	09/09/2019	female	325
AL844	72.23	15.81	CSS	681	06/09/2019	female	348
AL845	75.56	13.87	CSN	830	10/09/2019	male	304
AL846	72.94	14.31	CSN	906	07/09/2019	female	512
AL847	74.25	16.13	CSN	748	09/09/2019	female	610
AL849	74.90	15.40	CSN	834	10/09/2019	female	695
AL850	74.90	15.40	CSN	834	10/09/2019	male	545
AL851	74.90	15.40	CSN	834	10/09/2019	male	800
AL852	74.41	16.26	CSN	519	09/09/2019	female	580
AL873	71.50	26.60	BSS	299	13/01/2021	male	1230
AL874	77.27	11.40	CSN	493	14/09/2020	female	515
AL875	72.75	22.56	BSS	389	08/03/2020	male	595
AL876	64.68	5.56	CSS	570	27/03/2020	female	620
AL877	73.54	26.44	BSS	428	23/08/2022	female	560
AL879	71.87	15.79	CSS	560	10/15/2021	female	1145
AL880	73.55	28.44	BSS	382	26/08/2022	female	945
AL881	72.95	26.54	BSS	372	23/08/2022	female	1092
AL882	73.35	23.44	BSS	413	2021	male	1090
AL883	68.81	12.72	CSS	650	10/9/2021	male	1315
AL884	72.95	21.94	BSS	430	17/04/2022	female	1580
AL885	71.14	16.83	CSS	643	13/04/2022	male	943
AL886	66.95	8.18	CSS	540	03/04/2022	male	825
AL887	66.95	8.18	CSS	540	03/04/2022	female	692
AL888	72.70	20.55	BSS	425	28/08/2021	female	330
AL889	74.84	15.57	CSN	613	09/07/2021	male	600
AL890	74.84	15.57	CSN	613	09/07/2021	male	700
BKT80030_4	79.72	8.13	CSN	630	09/08/2008	male	577
BKT80034	79.82	8.07	CSN	602	09/09/2008	male	300
BKT80037_8	79.90	7.85	CSN	594	09/09/2008	male	386
BKT80039_4	79.92	7.77	CSN	599	09/09/2008	female	638
BKT80039_5	79.92	7.77	CSN	599	09/09/2008	female	290
BKT80056_1	79.80	7.92	CSN	657	09/11/2008	female	450
891	73.11	18.24	BSS	443	29/08/2023	male	1430
892	73.03	16.15	BSS	466	29/08/2023	male	1510
893	72.44	20.38	BSS	426	28/08/2023	male	1450
894	70.89	17.11	CSS	652	24/10/2023	female	295
895	71.33	16.46	CSS	928	26/10/2023	female	920
896	71.64	16.19	CSS	648	26/10/2023	female	360
897	71.64	16.19	CSN	648	26/10/2023	female	620
898	71.82	15.67	CSS	655	28/10/2023	male	490
900	74.59	16.09	CSN	599	31/10/2023	male	680
GR124	67.16	-26.52	Greenland	542	21/09/2023	female	770

GR266	66.15	-30.47	Greenland	490	22/09/2023	male	510
GR268	66.15	-30.47	Greenland	490	22/09/2023	male	710
GR466	65.36	-30.87	Greenland	824	23/09/2023	female	1390
GR467	65.36	-30.87	Greenland	824	23/09/2023	male	1420
GR468	65.39	-31.31	Greenland	839	23/09/2023	female	1660
GR469	65.39	-31.31	Greenland	839	23/09/2023	female	860
GR470	65.39	-31.31	Greenland	839	23/09/2023	female	1400
GR2642	64.41	-37.62	Greenland	851	25/09/2023	female	270
F5285	62.04	-3.53	Faroes	457	03/06/2023	female	953
F5286	62.04	-3.53	Faroes	457	03/06/2023	female	955
F5270	61.47	-4.31	Faroes	449	03/06/2023	female	1266
F5274	61.47	-4.31	Faroes	449	03/06/2023	female	1394
F5108	61.00	-5.19	Faroes	435	04/06/2023	male	1387
F5310	60.43	-5.58	Faroes	524	04/06/2023	male	1240
F5336	60.44	-7.01	Faroes	437	05/06/2023	male	1229
F5338	60.44	-7.01	Faroes	437	05/06/2023	male	1197
F5049	61.02	-7.11	Faroes	500	05/06/2023	male	1141
F5050	61.02	-7.11	Faroes	500	05/06/2023	female	1247
F5268	61.02	-5.17	Faroes	437	06/06/2023	male	1266
F58	60.20	-8.23	Faroes	507	06/10/2023	male	1258
F5061	60.42	6.04	Faroes	394	13/08/2023	NA	1338

Appendix D: Phylogenetic tree

Full phylogenetic trees obtained for the NADH2 and CO1 samples (first and second tree, respectively), using the HKY maximum likelihood model.


61
AL308
ELATL127-18
F5061
F58
GL2642
GL470
GL467
GL469
GL466
GL124
84038-1
84011-1
AL898
AL895
AL894
AL887
AL885
AL884
AL883
AL874
AL851
AL841
AL560
32
AL01
GL468
F5270
45
F5310
F5285
42
AL838
F5108
AL110
57
AL56
AL893
AL301
AL469
AL470
49
AL716
38
AL771
AL839
AL843
AL873
AL879
AL880
AL890
100
AL897
ELATL093-17
ELATL126-18
AL845
AL770
AL877
AL846
AL824
AL889
AL900
F5286
F5336
F5338
F5049
F5050
Rajella lintea
F5268
100
GL266
Amblyraja hyperborea
31
GL268
0,050


GBGC10836-13|Bathyraja spinicauda|COI-5P|JF895087
RNEZ004-10|Bathyraja spinicauda|COI-5P|KF604215
SCFAC939-09|Bathyraja spinicauda|COI-5P
SCFAC929-09|Bathyraja spinicauda|COI-5P
SCFAC928-09|Bathyraja spinicauda|COI-5P
SCFAC925-09|Bathyraja spinicauda|COI-5P
SCFAC922-09|Bathyraja spinicauda|COI-5P
SCFAC901-09|Bathyraja spinicauda|COI-5P
RNEZ009-10|Bathyraja spinicauda|COI-5P|KF604208
RNEZ006-10|Bathyraja spinicauda|COI-5P|KF604212
41
GBGC10843-13|Bathyraja spinicauda|COI-5P|JF895080
GBGC10847-13|Bathyraja spinicauda|COI-5P|JF895076
GBGC10840-13|Bathyraja spinicauda|COI-5P|JF895083
GBGC10837-13|Bathyraja spinicauda|COI-5P|JF895086
GBGC10833-13|Bathyraja spinicauda|COI-5P|JF895090
SCFAC906-09|Bathyraja spinicauda|COI-5P
SCFAC931-09|Bathyraja spinicauda|COI-5P
GBGC10845-13|Bathyraja spinicauda|COI-5P|JF895078
GBGC10835-13|Bathyraja spinicauda|COI-5P|JF895088
GBGC10850-13|Bathyraja spinicauda|COI-5P|JF895073
94
SCFAC897-09|Bathyraja spinicauda|COI-5P
GBGC10860-13|Bathyraja spinicauda|COI-5P|JF895063
44
SCFAC870-06|Bathyraja spinicauda|COI-5P
GBGC10848-13|Bathyraja spinicauda|COI-5P|JF895075
SCFAC900-09|Bathyraja spinicauda|COI-5P
2
ELAME696-09|Bathyraja spinicauda|COI-5P|MZ661280
ELATL127-18|Bathyraja spinicauda|COI-5P|MZ661288
GBGC10834-13|Bathyraja spinicauda|COI-5P|JF895089
GBGC10846-13|Bathyraja spinicauda|COI-5P|JF895077
GBGC10855-13|Bathyraja spinicauda|COI-5P|JF895068
GBGC10856-13|Bathyraja spinicauda|COI-5P|JF895067
GBGC10858-13|Bathyraja spinicauda|COI-5P|JF895065
GBGC10861-13|Bathyraja spinicauda|COI-5P|JF895062
SCFAC794-06|Bathyraja spinicauda|COI-5P
SCFAC869-06|Bathyraja spinicauda|COI-5P
SCFAC874-06|Bathyraja spinicauda|COI-5P
SCFAC902-09|Bathyraja spinicauda|COI-5P
SCFAC936-09|Bathyraja spinicauda|COI-5P
ELATL093-17|Bathyraja spinicauda|COI-5P|MZ661285
SCFAC872-06|Bathyraja spinicauda|COI-5P
SCFAC907-09|Bathyraja spinicauda|COI-5P
SCFAC896-09|Bathyraja spinicauda|COI-5P
GBGC10844-13|Bathyraja spinicauda|COI-5P|JF895079
GBGC10851-13|Bathyraja spinicauda|COI-5P|JF895072
GBGC10854-13|Bathyraja spinicauda|COI-5P|JF895069
SCAFB779-07|Bathyraja spinicauda|COI-5P
ELATL094-17|Bathyraja spinicauda|COI-5P|MZ661283
SCFAC873-06|Bathyraja spinicauda|COI-5P
RNEZ003-10|Bathyraja spinicauda|COI-5P|KF604211
SCFAC924-09|Bathyraja spinicauda|COI-5P
55
SCFAC923-09|Bathyraja spinicauda|COI-5P
SCFAC926-09|Bathyraja spinicauda|COI-5P
SCFAC899-09|Bathyraja spinicauda|COI-5P
SCFAC871-06|Bathyraja spinicauda|COI-5P
SCAFB789-07|Bathyraja spinicauda|COI-5P
RNEZ010-10|Bathyraja spinicauda|COI-5P|KF604210
RNEZ008-10|Bathyraja spinicauda|COI-5P|KF604216
RNEZ007-10|Bathyraja spinicauda|COI-5P|KF604213
RNEZ005-10|Bathyraja spinicauda|COI-5P|KF604217
RNEZ002-10|Bathyraja spinicauda|COI-5P|KF604209
RNEZ001-10|Bathyraja spinicauda|COI-5P|KF604214
GBGC10859-13|Bathyraja spinicauda|COI-5P|JF895064
GBGC10857-13|Bathyraja spinicauda|COI-5P|JF895066
GBGC10852-13|Bathyraja spinicauda|COI-5P|JF895071
GBGC10842-13|Bathyraja spinicauda|COI-5P|JF895081
GBGC10849-13|Bathyraja spinicauda|COI-5P|JF895074
GBGC10841-13|Bathyraja spinicauda|COI-5P|JF895082
GBGC10839-13|Bathyraja spinicauda|COI-5P|JF895084
ELATL130-18|Bathyraja spinicauda|COI-5P|MZ661284
ELATL129-18|Bathyraja spinicauda|COI-5P|MZ661282
ELATL128-18|Bathyraja spinicauda|COI-5P|MZ661279
ELATL126-18|Bathyraja spinicauda|COI-5P|MZ661281
ELAME697-09|Bathyraja spinicauda|COI-5P|MZ661287
ELAME695-09|Bathyraja spinicauda|COI-5P|MZ661286
GLF190-14|Bathyraja spinicauda|COI-5P
GBGC10838-13|Bathyraja spinicauda|COI-5P|JF895085
63
SCFAC927-09|Bathyraja spinicauda|COI-5P
TZFPB359-05|Bathyraja spinicauda|COI-5P|FJ164384
GBGC10853-13|Bathyraja spinicauda|COI-5P|JF895070
100
SCAFB786-07|Bathyraja spinicauda|COI-5P
0,02