diversity

Article

Sibling Species *Amblyraja hyperborea* and *A. jenseni* in Slope Waters of Eastern Canada: An Ecomorphological Description

David W. Kulka [1,*,†], Carolyn M. Miri [2], Sheila Atchison [3] and Mark R. Simpson [2]

[1] Department of Fisheries and Oceans Canada, Canada
[2] Department of Fisheries and Oceans Canada, Northwest Atlantic Fisheries Centre, P.O. Box 5667, St. John's, NL A1C 5X1, Canada; carolyn.miri@dfo-mpo.gc.ca (C.M.M.)
[3] Department of Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada; sheila.atchison@dfo-mpo.gc.ca
* Correspondence: davekulka@gmail.com
† Retired.

Abstract: Deepwater survey data and specimens collected from the Grand Banks to Baffin Bay in the Northwest Atlantic were used to examine the distribution, morphometrics, meristics and maturity of two siblings, *Amblyraja hyperborea* and *A. jenseni*. Our study confirmed that the two species occupy different locations, their distributions separated by Davis Strait, a biogeographic break separating Atlantic from Arctic waters. *A. hyperborea* with a smaller maximum size and size at maturity inhabited colder Arctic slope waters in Baffin Bay while larger *A. jenseni* were located in warmer Atlantic slope waters. Despite their distributional separation and thus reproductive isolation, spine counts and body morphology were almost indistinguishable between species. Only upper jaw teeth row count and difference in the size of spines on the mid-rear wings differentiated the two species. Also, for both species, the proportion of dorsal fins joined, disc shape and relative tail length changed with total length. Secondary reproductive anatomy, clasper length and vas deferens weight, shell gland and uterus weight underwent initial acceleration in growth when the gonads transitioned to stage 2 (adolescent, maturing). Also, YOY *A. hyperborea* were found to distribute at shallower depths than larger stages, constituting a nursery, which was not observed for *A. jenseni*.

Keywords: deepwater skates; spatial ecology; distribution; habitat; taxonomy; nursery grounds

Citation: Kulka, D.W.; Miri, C.M.; Atchison, S.; Simpson, M.R. Sibling Species *Amblyraja hyperborea* and *A. jenseni* in Slope Waters of Eastern Canada: An Ecomorphological Description. *Diversity* **2024**, *16*, 479. https://doi.org/10.3390/d16080479

Academic Editor: Simon Weigmann

Received: 8 July 2024
Revised: 25 July 2024
Accepted: 26 July 2024
Published: 7 August 2024

1. Introduction

There are currently 10 recognized species of skate within the genus Amblyraja (Rajiformes: Rajidae), three that occur in the North Atlantic: *A. radiata*, Thorny Skate (Donovan, 1808) [1]; *A. jenseni*, Jensen's or Shorttail Skate (Bigelow and Schroeder, 1950) [2] and *A. hyperborea*, Arctic or Boreal Skate (Collett, 1879) [3], the first two endemic. These three species possess similar physical characteristics including spine counts and body shape but the morphological similarities are greatest between *A. hyperborea* and *A. jenseni* [4], and this has led to confusion in descriptions of classification and distribution of these latter two species. Various studies, particularly species guides, usually lacking in details on how *A. hyperborea* and *A. jenseni* were identified, provide conflicting descriptions of distribution. Some authors described their distributions as overlapping over much of the North Atlantic [5–7] while others [4,8] specified that they are separate.

A. jenseni but not *A. hyperborea* were observed in survey catches along the Atlantic slope from the Grand Banks to the Labrador Shelf (see Figure 1) while records of *A. hyperborea* were recorded further north in Baffin Bay [8,9]. *A. hyperborea* were observed to be common along the eastern slope of Baffin Basin between Greenland and Canada but *A. jenseni* were not recorded there [9–11].

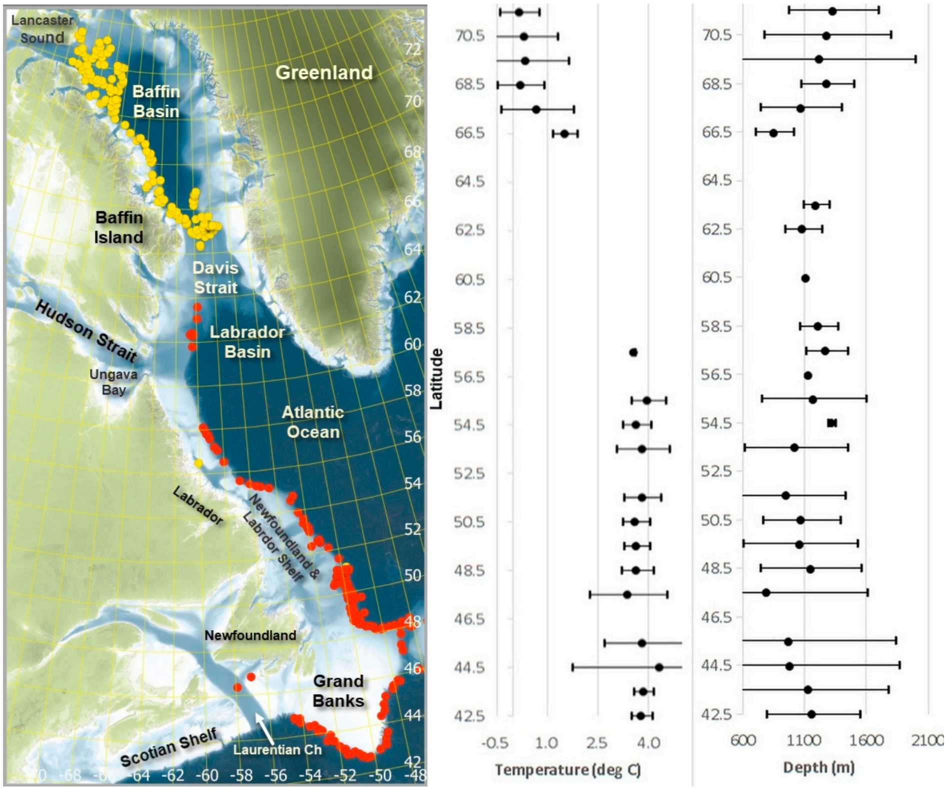


Figure 1. (**Left**) panel—Map of study area. Red dots show where specimens identified as *A. jenseni* were taken, yellow dots for *A. hyperborea*. (**Right**) panel—Average bottom temperature and depth by each degree of latitude. Bars illustrate ranges of temperature and depth.

Previously, the most comprehensive examination of morphometrics and meristics for *A. jenseni*, 22 specimens examined from various parts of the North Atlantic, included 9 specimens from our study area [12]. For *A. hyperborea*, morphological descriptions were even more scarce, limited to identification manuals based on a few museum specimens, i.e., [4–6]. Given these inconsistencies and gaps in knowledge, we examined the morphology of the two species using a relatively large number of specimens collected from a wide area in the Northwest Atlantic and Arctic waters of Canada. The study focuses on similarities/differences in spine and upper jaw teeth row counts as well as common measures of body parts.

In addition, we looked at habitat preferences of both species, not previously examined except in a small part of their range in Cumberland Sound for *A. hyperborea* [13]. Based on specimens identified in the lab plus data from Canadian research surveys covering most of the Northwest Atlantic and eastern Arctic and encompassing much of the known bathymetric distribution of the two species, 300–2500 m [4,14], we describe the distribution including bathymetric and thermal preferences of *A. hyperborea* and *A. jenseni*.

We also investigate reproductive attributes of the two species. A previous study [11] examined maturity of *A. hyperborea* but that work was conducted outside of our study area in Icelandic waters and the Barents Sea. No such biological information exists in the Northwest Atlantic for *A. hyperborea*, or globally for *A. jenseni*. This paper is one of two that examines the genus *Amblyraja* in the northwest Atlantic off Canada.

2. Materials and Methods

Our study area is bounded by Lat 42° and 75.5°, a distance of 5500 km along the continental slope and from Lon −45° to −80°, and encompasses most of the Canadian Atlantic, Grand Bank to Labrador Shelf plus eastern Arctic waters including Davis and Hudson Straits, Ungava Bay and the western side of Baffin Basin (Figure 1).

2.1. Specimens Collected

Specimens of *A. jenseni* (n = 301) and *A. hyperborea* (n = 1823) were collected, frozen at sea and returned to the lab over an 11-year period by Fisheries and Oceans Canada (DFO) staff on survey vessels and by fisheries observers on commercial fishing vessels. Samples were collected from depths between 102 and 1474 m and temperatures between −0.14 and 7.8 °C in the study area (Table 1).

Table 1. Number of specimens collected from Fisheries and Oceans Canada surveys and commercial fishing vessels. UNK refers to unknown year.

	A. hyperborea				***A. jenseni***			**Depth Collected (m)**		**Temperature Collected Deg C**	
Year	**Unsexed**	**F**	**M**	**Total**	**F**	**M**	**Total**	**Min**	**Max**	**Min**	**Max**
2002					6	7	13	975	1395	3.3	3.5
2003						4	4	228	1401	4.1	7.8
2004					10	12	22	457	1412	3.3	4.2
2005					6	6	12	226	1445	2.6	4.1
2006		6	29	35	48	62	110	511	1443	−0.1	4.4
2007	1	27	233	261	18	32	50	102	1424	3.4	6.9
2008	2	106	867	975	3	13	16	143	1439	3.5	5
2009			1	1	14	29	43	587	1409	3.5	5
2010		8	86	94	9	12	21	852	1442	3.6	4.3
2011		3	26	29	1	5	6	859	1067	3.7	3.8
2012	1	237	186	424	2		2	442	1474	−0.14	1.64
UNK			4	4	1	1	2	1149	1149		
Total	4	387	1432	1823	118	183	301	102	1474	−0.14	7.8

Note: Grey column constitutes the total of male and female specimens.

In the lab, specimens were defrosted and speciated, primarily by upper jaw teeth row counts [4,6] and examined/dissected using prescribed methods (Table 2). The following are the body parts examined.

Morphometrics (lengths in cm, weights in kg)

- Total length (TL): from tip of the snout (rostrum) to tip of the tail.
- Round weight: total weight of whole, undissected skate.
- Disc length: from tip of the snout to beginning of tail (axils of pelvic fins).
- Disc width: from tip of the left pectoral fin to tip of right pectoral fin.
- Tail length: Disc length subtracted from total length.

Note—Generally measured from the center of the cloaca, our measurement of tail length was from the end of the disc (axils of pelvic fins) to tip of the tail.

- Dorsal fins joined: whether two dorsal fins are joined or separate at their base.

Meristics

- Spines between dorsal fins: spines located between the first and second dorsal fin.
- Midline spines on body: median row of spines/thorns from nuchal region to the leading edge of the first dorsal fin base.
- Midline spines on tail: median row of spines/thorns on tail from axils of pelvic fins to leading edge of the 1st dorsal fin base contiguous with the midline row of disc spines.
- Spines, eyes: spines located on orbital ring of each eye, averaged.
- Spines, spiracles: spines near inner edge of each spiracle, averaged.
- Spines, shoulders: spines on each shoulder behind the spiracles, averaged.
- Teeth Rows: rows of teeth on the upper jaw.

Statistical analyses were used to differentiate counts and relative measures listed below ($\alpha = 0.05$) between species and sex. To examine changes in morphometrics and meristics as a function of TL between species and sexes (i.e., four groups), analysis of covariance (ANCOVA) was employed on the following parameters:

- Disc length by disc width.
- Disc width/Disc length by TL.
- Tail length/TL by TL.
- Round Weight by TL (ln-transformation of raw data).
- Midline spines (body plus tail).
- Proportion of total midline spines located on the tail.
- Teeth rows in the upper jaw.

Table 2. Morphometric measurements, meristics and reproductive attributes examined in this study.

	A. hyperborea			*A. jenseni*			Total
Attribute	**Female**	**Male**	**F&M**	**Female**	**Male**	**F&M**	
Morphometrics							
Total length (cm)	387	1416	1803	117	183	300	2104
Round weight (kg)	385	1409	1794	118	181	299	2096
Disc length (cm)	258	537	795	115	162	277	1072
Disc width (cm)	258	537	795	115	162	277	1072
Tail Length (cm)	257	537	794	114	162	276	1070
Dorsal fins joined	389	1435	1824	118	183	301	2129
Meristics							
Spines between dorsal fins	170	288	458	66	90	156	630
Midline spines/thorns	386	1402	1788	118	179	297	2096
Midline tail spines/thorns	384	670	1054	116	167	283	1347
Midline body spines/thorns	385	675	1060	117	168	285	1346
Spines, eye	256	537	793	115	162	277	1076
Spines, spiracle	256	538	794	115	162	277	1076
Spines, shoulder	256	538	794	115	162	277	1076
Teeth rows (upper jaw)	248	526	774	108	153	261	1035
Reproductive attributes							
Maturity stage	384	1427	1811	118	181	299	2113
Gonad weight (g)	7	26	33	56	72	128	161
Right Clasper length (mm)		536	536		159	159	694
Alar spine rows		509	509		70	70	579
Ovaries/Testes weight (g)	245	536	781	60	98	158	939
Shell gland width (mm)	238		238	46		46	284
Shell gland weight (g)	239		239	49		49	288
Uterus/Vas deferens weight (g)	245	536	781	59	98	157	938
Number of Purses in utero	8		8	7		7	15
Percent Purses formed	8		8	7		7	15
Purse width (mm)	7		7	4		4	11
Purses length without horns, mm	8		8	6		6	14
Purses total length including horns, mm	6		6	6		6	12

Note: F&M (columns highlighted in grey) refers to the total of male and female specimens. Refer to [4] for illustrations of external body parts.

Reproductive attributes (lengths are linear in mm, weight in g)

Maturity was classified with 4 stages for males, 6 for females according to [15], and a modification of Stehmann's 1987 scale. We further modified/clarified the maturity classification (clarifications bolded) as follows:

- Stage 1 and 2—see [15] for a full description.
- Stage 3 (mature male)—Sperm ducts covering 50% **to 74%** of kidneys.
- Stage 4 (mature/running male)—Sperm ducts covering $\geq$ 75% of kidneys.
- Stage 4 (mature female)—If present, egg cases partially extruded **(i.e., cases 10% to 90% formed)** from shell glands.
- Stage 5 (mature/laying female)—Oviducts developed; walls thick and venous, or stretched **by egg cases that have been fully extruded from the shell glands**.
- Stage 6 (mature/resting female)—No eggs in Fallopian tubes, **shell glands** or oviducts. Oviducts developed; walls thick, venous and stretched **after a period of laying egg cases**.

The following sexual characteristics were examined:

- Gonad weight: weight of both testes or ovaries.

- Clasper length: from innermost axil of the right clasper to its tip.
- Alar spine rows: spines that form rows on the upper surface of each pectoral fin near its tip (maturing and mature males), averaged. Count is number of halves plus complete rows, not number of spines.
- Testis weight: average weight of left and right testis.
- Vas deferens weight: average weight of left and right vas deferens.
- Ovary weight: average weight of left and right ovary.
- Shell gland width: average maximum width of the left and right shell (oviducal) gland.
- Shell gland weight: average weight of left and right shell gland.
- Uterus weight: average weight of left and right uterus.
- Number of purses in utero: number of egg cases/purses inside each female.
- Percent purses formed: percent development of two egg cases/purses extruding/extruded separately from shell glands. Example: 50% for 2 purses half-extruding from two shell glands, i.e., each fertilized egg is only half-covered by developing hard-shelled case.
- Purse width: averaged maximum width of the left and right purse.
- Purse length without horns: averaged total length of the left and right purse, excluding the horns.
- Purse length including horns: averaged linear total length of the left and right purse, including horns.

2.2. Surveys and Mapping

Within our study area (Figure 1), DFO, Newfoundland and Labrador Region conducts annual demersal multispecies stratified random surveys on the Grand Banks north to the Labrador Shelf [16]. A Campelen 1800 shrimp trawl with a 40 mm sized mesh was employed, a gear that effectively captures a wide range of sizes of fish. The random stratified survey method assigns a consistent number of sets within depth/area strata annually and covers a depth range from 32 to 1504 m. An average of 1175 sets were done per year, 26,634 sets in total, survey years spanning 1995 to 2017. The number of sets at depths exceeding 250 m, encompassing the range of *A. jenseni* was 11,232 sets with 422 *A. jenseni* recorded.

In addition, DFO, Arctic Region undertakes two annual demersal multispecies stratified random surveys in Baffin Bay, Davis Strait, and Ungava Bay, including a single survey in Hudson Strait (Figure 1). One survey uses an Alfredo III trawl with mesh size of 140 mm and a 30 mm mesh-liner in the codend and covers a depth range from 400 m to 1500 m. The other survey employs both a standard and a modified Campelen 1800 shrimp trawl with 12.7 mm codend mesh [17,18]. From 1999 to 2021, an average of 339 sets were conducted per year, 7109 sets in total. Spatial coverage substantially overlaps the known distribution of both species with 1827 *A. hyperborea* and 302 *A. jenseni* captured.

The basemap used for GIS analyses incorporated GEBCO layers of bathymetry (https://www.gebco.net/about_us/faq/) accessed on 12 June 2020 and spatial analyses were done in QGIS v3.16 (http://qgis.osgeo.org) accessed on 27 December 2020. Survey set locations and numbers of fish captured per standard tow were used to examine the distribution of the two species. The Heatmap function in QGIS 3.16 was used to transform point data (i.e., standardized number per tow for each survey set) to classified density surfaces, to derive areas of similar density, by placing a circle around each point and averaging the values of all points that fall within the circle, then overlaying the circles. A scanning radius of 0.15 degrees of latitude (about 16 km) was used to ensure that the surface of the resulting heat map was continuous (i.e., no gaps over the surface of the surveyed area) but that the interpolation did not extend too far beyond the surveyed area and was able to distinguish areas of different levels of density of fish while maximizing the spatial detail. Bottom depth and temperature recorded with each set were used to examine habitat associations.

3. Results

Sampling opportunities covered most of the shelf and slope but 99.5% of specimens were encountered from bottom depths exceeding 450 m. All but 7 of the 1823 specimens identified as *A. hyperborea* by teeth row count were collected north of Lat 66° in the Baffin Basin and all but 2 of the 301 specimens identified as *A. jenseni* came from the Atlantic Basin slope south of Lat 64° (Figure 1).

The average and range of depths at which *A. jenseni* specimens were captured was 1087 m (217–1448 m), very similar for *A. hyperborea*, 1101 m (355–1474 m) (Figure 1, right panel). However, there was little overlap in bottom temperatures between species (Figure 1, left panel). At Lat > 66° in Arctic waters where *A. hyperborea* were captured, the temperature mean and range were 0.4 °C (−0.1 to 4.9 °C). South of Lat 64° from the Atlantic slope, temperatures were warmer, 3.8 °C (2.6–6.9 °C).

3.1. Meristics

Spine counts were highly overlapping between species (Figure 2). The number of spines in the cluster near the spiracles for both species ranged between 0 and 3 spines per side, 1–7 spines near the eye, 0–5 spines on the shoulder, 0–2 spines between dorsal fins and 19–40 along the midline of the disc and tail. Counts on the left side versus the right side were highly overlapping, not significantly different at 95% CI.

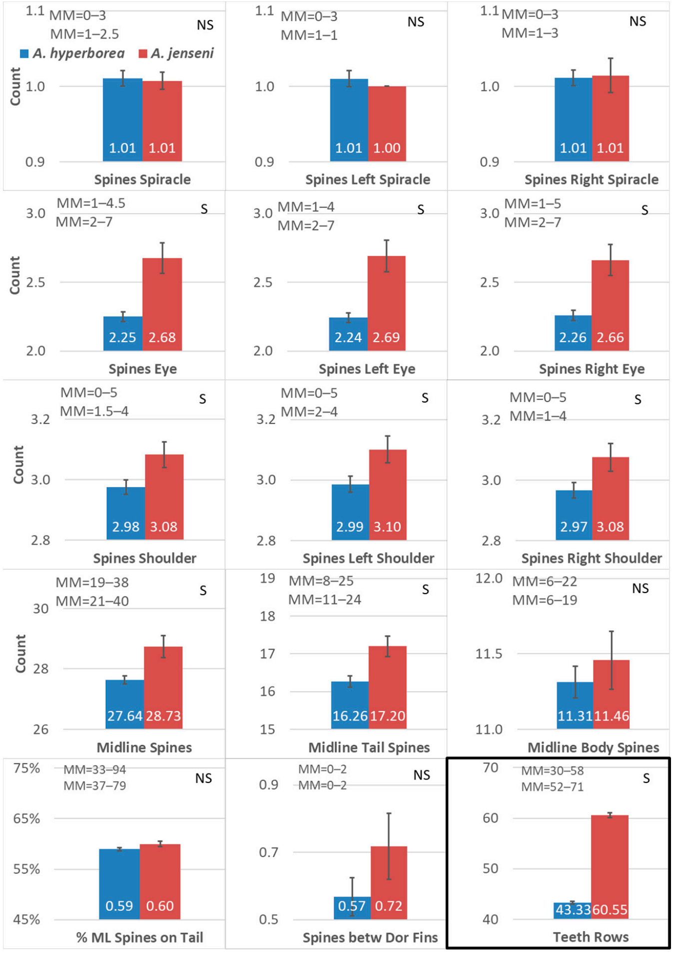


Figure 2. Spine and upper jaw teeth row counts for *A. hyperborea* and *A. jenseni*. Number at the bottom of each bar is the mean value. MM in the upper left of each graph are minimum and maximum values observed for each species. Upper value refers to, *A. hyperborea*. The error bars are 95% confidence intervals and NS refers to not significantly different counts between species; S, significantly different.

Counts of midline body spines, spines near the spiracles, spines between the dorsal fins and percent of mid-line spines located on the tail were not significantly different between species while counts of midline spines (tail and body combined), midline tail spines, spines above the left and right eyes and shoulder spines were significantly different between species ($p < 0.05$, Figure 2) but with a high degree of overlap in range of counts between species.

The proportion of total midline spines on the tail was not significantly different between species (ANCOVA, F = 0.29, df = 3, n = 1335, *p* = 0.83) and by sex; *A. hyperborea*—0.59 (males and females—0.59) and *A. jenseni*—0.61 (males—0.61, females—0.60). Also, the proportion of total midline spines on the tail did not vary significantly with the size of fish (ANCOVA, F = 0.0107, df = 1, n = 1335, *p* = 0.9176).

However, multiple spines on a patch located on the mid-rear portion of each wing were noticeably larger for larger *A. hyperborea* compared to large *A. jenseni* (Figure 3). The patches were absent in fish < 18 cm TL fish (YOY) but appeared in small juveniles as very fine spines in both species. For *A. hyperborea*, the spines in each patch increased in size with increasing TL but for *A. jenseni*, the spines remained small even on the largest specimens. There was no difference between sexes.

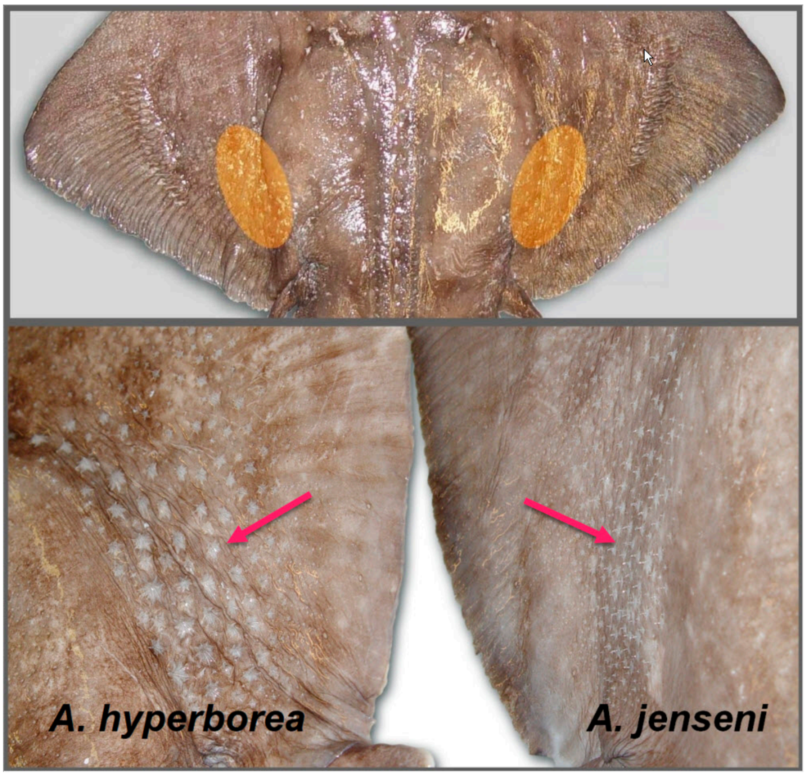


Figure 3. Patch of spines on mid-rear portion of the wings in larger specimens: (**Upper**) figure—yellow ovals show the location of the wing spine patches. (**Lower**) figure—red arrows point to close-ups of one patch for each species.

Of all the meristics examined, only upper jaw teeth row counts exhibited sufficient separation in the range of counts to facilitate differentiation of the two species in all sizes of fish (Figure 4). Overlap in counts between species was minimal; 4 of 770 *A. hyperborea* specimens examined had a teeth row count > 52 while 2 of 301 *A. jenseni* sampled were 52–53. Geographically, 99.1% of specimens with a teeth row count $\leq$ 52 were located north of Lat 66° while 96.2% of specimens with a teeth row count > 52 were located south of Lat 64° (Figure 1). The difference in teeth row counts did not change significantly with the size of fish for either species/sex, i.e., slope not significantly different from zero (ANCOVA, F = 1.4701, df = 3, n = 1025, *p* = 0.22).

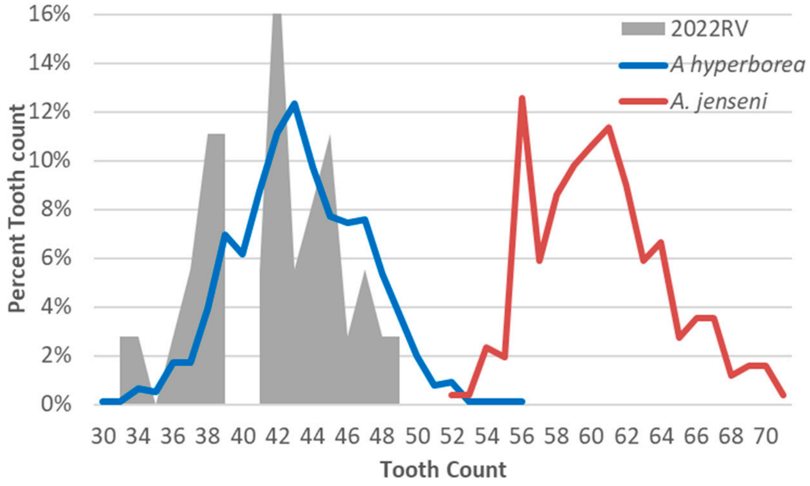


Figure 4. Length frequency of upper jaw teeth row count by species. Blue and red lines are frequencies from collected samples (n = 216 for *A. hyperborea*, 774 for *A. jenseni*). Grey area represents 36 specimens from the 2022 Arctic survey.

3.2. Morphometrics

The smallest TL observed for *A. hyperborea* was 10 cm and 14 cm for *A. jenseni*, likely corresponding to the size at hatching. A different maximum size was observed, 90 cm TL for *A. hyperborea* versus 110 cm for *A. jenseni* (Figure 5). The proportion of *A. hyperborea* captured peaked at 46–65 cm. For *A. jenseni*, the peak occurred at 41–55 cm for males and 46–65 cm for females.

Length/weight relationships were as follows:

A. hyperborea—female, $y = 9 \times 10^{-6} x^{3.0003}$, $r^2 = 0.9594$; male $y = 2 \times 10^{-5} x^{2.8379}$, $r^2 = 0.9367$.
A. jenseni—female, $y = 3 \times 10^{-6} x^{3.2442}$, $r^2 = 0.9531$; male $y = 3 \times 10^{-6} x^{3.2239}$, $r^2 = 0.9539$.

The relationship between TL (cm) and total weight (kg) was significantly different between sexes for *A. hyperborea* (ANCOVA, F = 10.0374, df = 3, n = 315, $p < 0.001$), but not for *A. jenseni* (ANCOVA, F = 0.08, df = 1, n = 294, $p = 0.77$). The relationship was also tested between species (sexes combined) and was significantly dependent on species (ANCOVA, F = 5.8367, df = 1, n = 2085, $p = 0.016$). However, practically speaking, length/weight relationships for the two species were quite similar and nearly identical at TL < 65 cm.

Like all Rajidae, *A. hyperborea* and *A. jenseni* have two dorsal fins on the tail that are sometimes joined (i.e., no gap between their bases). The proportion of dorsal fins joined increased as the fish increased in size (Figure 6). The relationship between TL (cm) and the proportion of joined dorsal fins was significantly different for *A. hyperborea* (ANCOVA, F = 77.65, df = 1, n = 1804, $p < 0.0001$) and *A. jenseni* (ANCOVA, F = 13.88, df = 1, n = 300, $p = 0.0002$). No dorsal fins were joined for the smallest *A. hyperborea* increasing to 45% on average, for the largest fish. For *A. jenseni*, 10% were joined for the fish < 20 cm and 52% for the largest specimens (Figure 6).

Although there were significant differences between species for various body proportions, these differences were very small (Figure 7). The 95% CIs were close to overlapping, indicating that the two species have similar body proportions; body shape is not visually distinguishable between the two species. The large sample sizes detect significant but trivial differences not useful for differentiating species.

However, disc length/disc width diminishes with increasing TL; for *A. hyperborea* from 1.32 for 14 cm fish to 1.12 for 86 cm fish and for *A. jenseni*, from 1.26 at 16 cm to 1.11 at 110 cm. Thus, the disc becomes about 10% wider in the largest fish as compared to the smallest fish. The relationship was significant (ANCOVA F = 8.5352, df = 3, n = 1054, $p = 1.3293 \times 10^{-5}$).

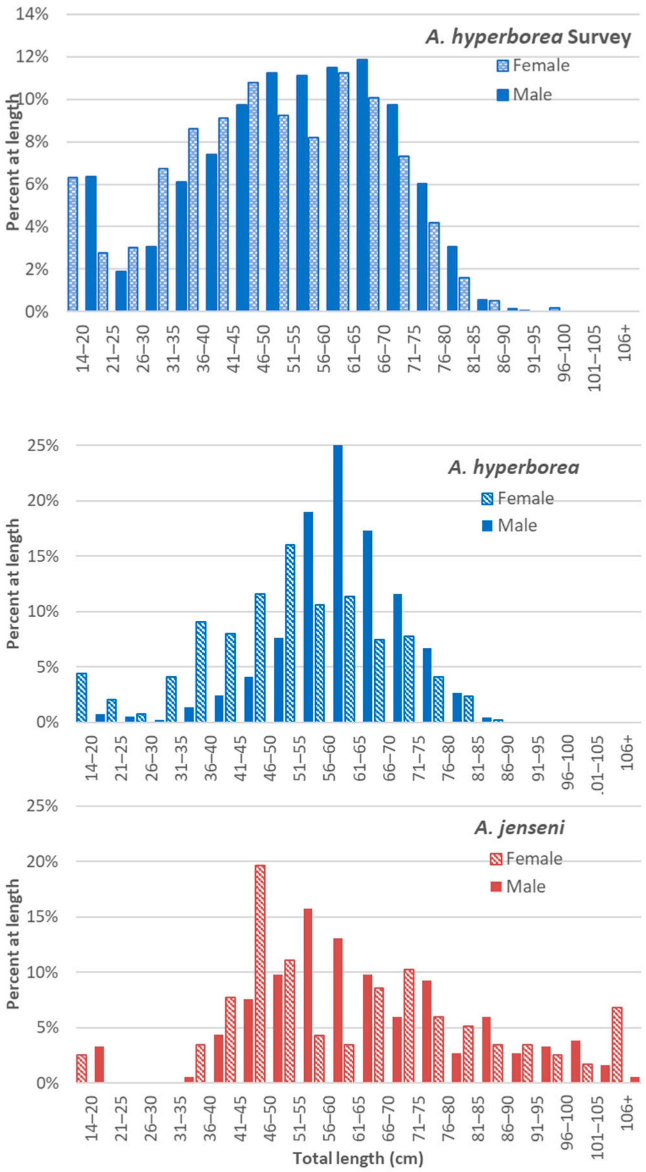


Figure 5. (**Upper graph**)—Length frequency of *A. hyperborea* measured at sea during Arctic surveys. (**Lower two graphs**)—Length frequency from lab specimens of *A. hyperborea* and *A. jenseni* specimens, speciated by teeth row count. *A. jenseni* were not measured during the surveys.

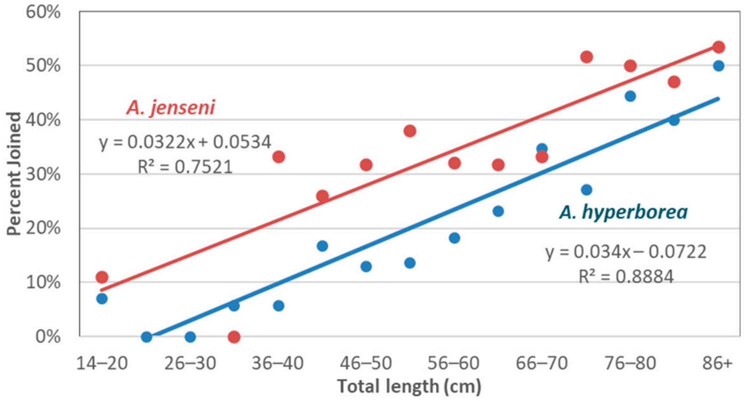


Figure 6. Proportion of dorsal fins joined with respect to total length (cm).

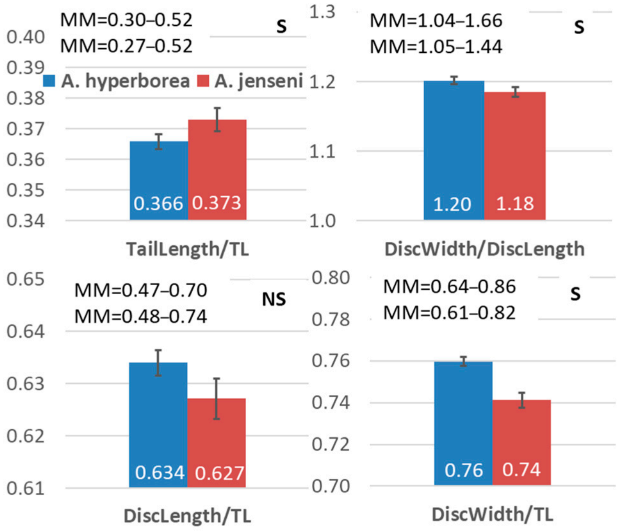


Figure 7. Disc length and width and tail length in relation to total length and disc width in relation to disc length. Error bars are 95% CIs. MM in the upper left of each graph are minimum and maximum values observed for each species, upper value refers to, *A. hyperborea*. Upper right letters signify significant (S) or not significant (NS).

Also, tail length/TL diminishes from 0.39 for 16 cm to 0.35 for 85 cm *A. hyperborea* and from 0.41 for 14 cm to 0.34 for 110 cm *A. jenseni*. There is no significant difference between species combined (ANCOVA F = 0.0052, df= 1, 1061, p = 0.9423); however, there is a trivial but significant difference between sexes (ANCOVA, F = 3.0564, df = 3, n = 1057, p = 0.02756).

3.3. Distribution

Survey records show that *A. hyperborea* and *A. jenseni* together form a nearly continuous distribution in slope waters from northern Baffin Bay south to the Grand Banks (Figure 8). Only 0.07% of survey sets conducted in depths < 300 m contained either species, whereas at depths exceeding 300 m, 19.5% of sets contained *A. hyperborea* along the Baffin Basin slope and Hudson Strait/Ungava Bay and 4.5% of sets contained *A. jenseni* along the Atlantic slope (see Figure 1 for locations). Thus, *A. hyperborea* is common, less so for *A. jenseni*, in slope waters off Canada. In Davis Strait, in an area separating Box B from Box D (Figure 8, arrow and inset), there is a distinct gap between Lat 64 and 66° where only 3 fish from 1244 sets (0.24%) were encountered. No fish were observed between Lat 64.2° and 65.8° in 1043 sets, a 200 km distance. The average depth in Davis Strait was 408 m, with much of the area shallower than the typical depth range of either species.

The study area was divided into seven areas that represent physically/ecologically different regions: the Grand Banks (Area G), the northeast Newfoundland and Labrador Shelf (D–F), relatively shallow Hudson Strait (C), Baffin Basin (B) and shallower surrounds to the north (A). The survey encounter rate and density of *A. hyperborea* in A–C (17.1% of sets contained skate, 1.65 skates per standard tow) is substantially higher than in D–G (4.5%, 0.074) (Table 3). The highest abundance of *A. hyperborea* was encountered in A and B and for *A. jenseni* in F, southern Newfoundland and Labrador Shelf. While different survey gears are used in A–C versus D–G, the large differences observed in the percent of sets with skates and mean number per tow suggest that *A. hyperborea* are more abundant than *A. jenseni* at the depths sampled.

The depth range where skates were encountered was similar among all areas (Table 3). However, thermal conditions, although similar across A–C in Arctic waters (avg. 0.7 °C, range −1.1 to 4.0 °C) are considerably cooler than in D–G, the Atlantic Basin (avg. 3.7 °C, range 3.0 to 6.2 °C).

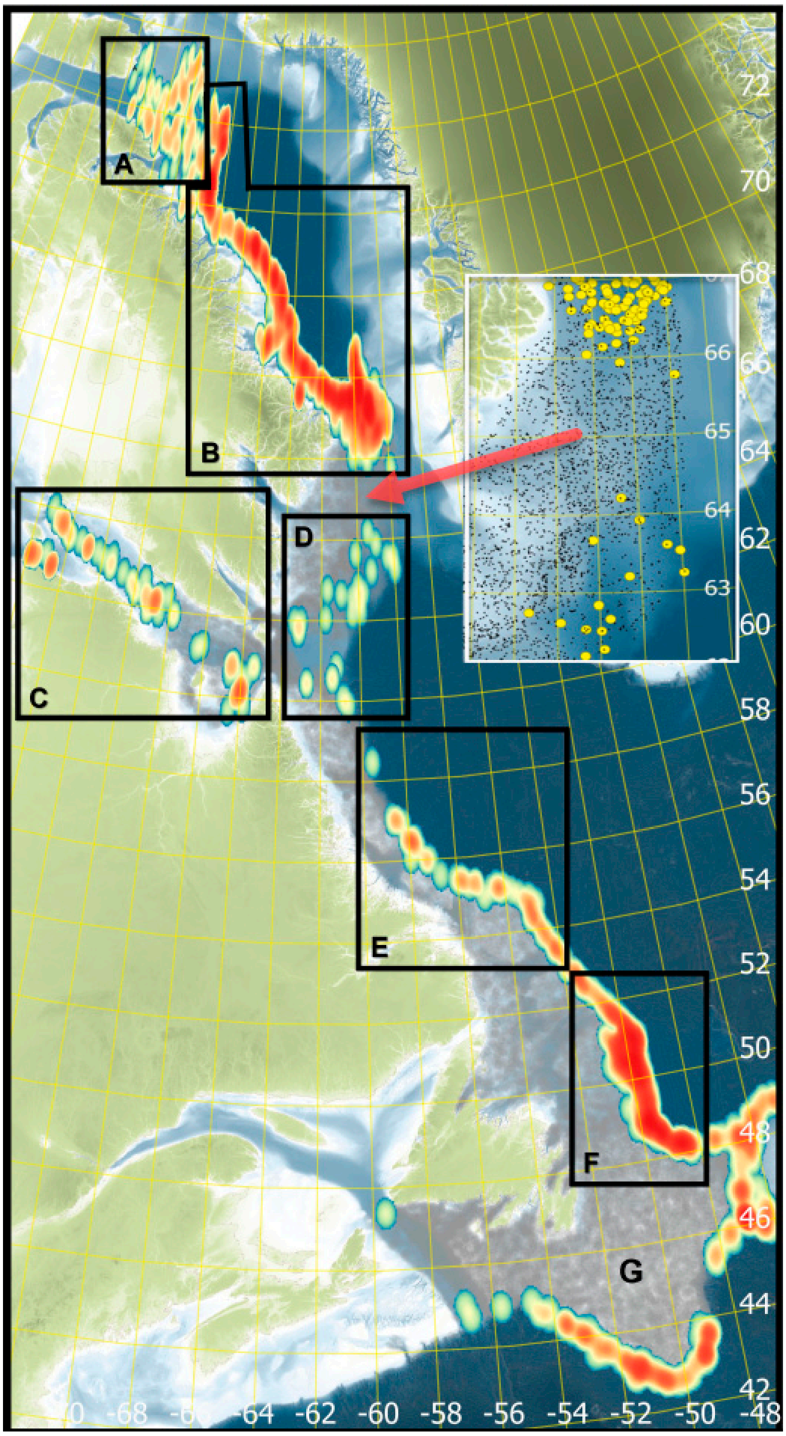


Figure 8. Heat map derived from DFO survey catch rates of *A. hyperborea* and *A. jenseni*. Red depicts the highest catch rates through green, the lowest. Grey areas show where survey sets were undertaken but no skates were caught. Catch and environmental characteristics for seven areas A–G are summarized in Table 3. Insert shows the gaps where neither species was captured.

Table 3. Percent of occurrence (% of sets with skates), catch rates (mean number per tow), temperature and depth statistics for the seven areas within the study area, as illustrated in Figure 8.

Area	% with Skate	Mean #/Tow	Temperature Deg C			Depth (m)			Species
			Mean	**Min**	**Max**	**Mean**	**Min**	**Max**	
A	55.9%	1.308	0.9	0.0	1.6	774	429	1118	*A. hyperborea*
B	44.0%	2.436	0.7	−0.2	4.0	1065	347	1497	*A. hyperborea*
C	5.3%	0.237	−0.3	−1.1	2.8	402	308	683	*A. hyperborea*
A–C	17.1%	1.650	0.7	−1.1	4.0	996	308	1497	*A. hyperborea*
D	1.0%	0.010	3.7	2.5	4.3	853	311	1486	*A. jenseni*
E	3.4%	0.041	3.7	3.0	4.4	1136	375	1473	*A. jenseni*
F	7.2%	0.126	3.7	3.0	4.7	1088	308	1444	*A. jenseni*
G	2.7%	0.045	3.7	3.0	6.2	1093	415	1446	*A. jenseni*
D–G	4.5%	0.074	3.7	3	6.2	1096	308	1473	*A. jenseni*

The average depth of capture weighted for number per tow was nearly identical, 1153 m for *A. hyperborea* and 1116 m for *A. jenseni*. Only 10% *of A. hyperborea* and 4% of *A. jenseni* were captured at <600 m, although 91% of survey effort occurred at <600 m. Although the range of depths occupied by the two species was similar, *A. hyperborea* was relatively less densely distributed at depths of 600 to 1200 m than *A. jenseni*, suggesting that *A. hyperborea* distributes deeper than *A. jenseni* (Figure 9). Also, the two species reached maximum density at the greatest depths sampled, indicating that both species would occur in significant numbers beyond the surveyed depths.

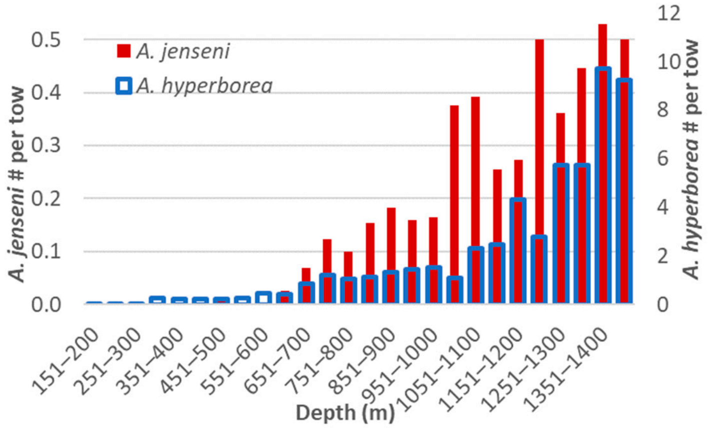


Figure 9. Fish density at depth expressed as survey numbers per tow.

Unlike depth, temperature ranges in which *A. hyperborea* (−1.1 to 4.0 °C) and *A. jenseni* (2.6–6.2 °C) distribute are nearly exclusive (Figure 10). Peak density occurred in −0.4 to 0 °C for *A. hyperborea* in Baffin Basin and surrounds and only 9 out of 3468 (0.26%) were caught in temperatures exceeding 2.1 °C. In contrast, in warmer Atlantic slope waters, density *of A. jenseni* peaked in 3.6–4.0 °C. The average temperature at point of capture weighted by number per tow was 0.3 °C for *A. hyperborea* and 3.6 °C for *A. jenseni.*

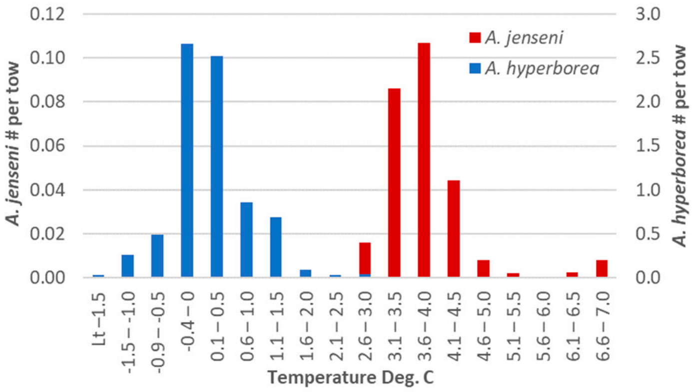
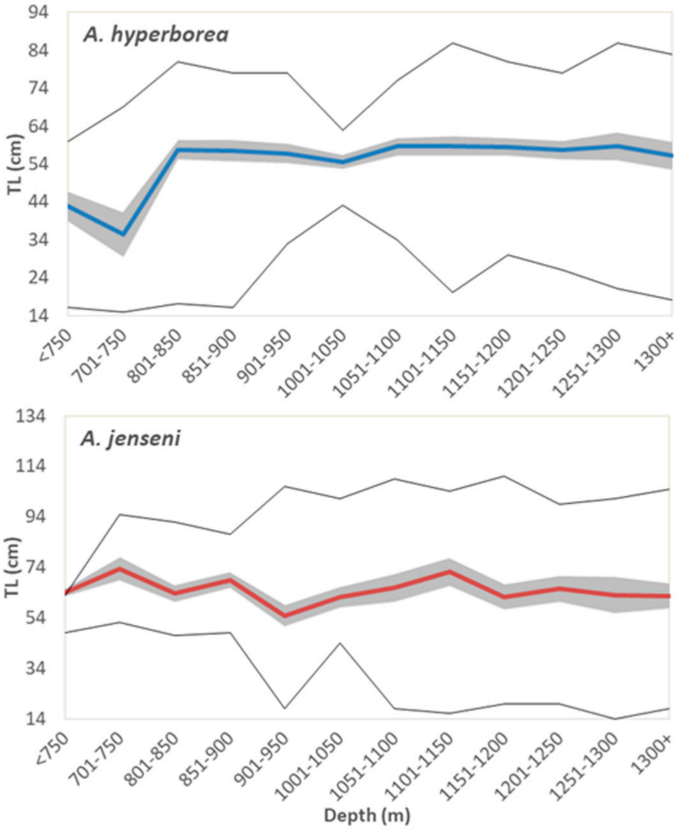


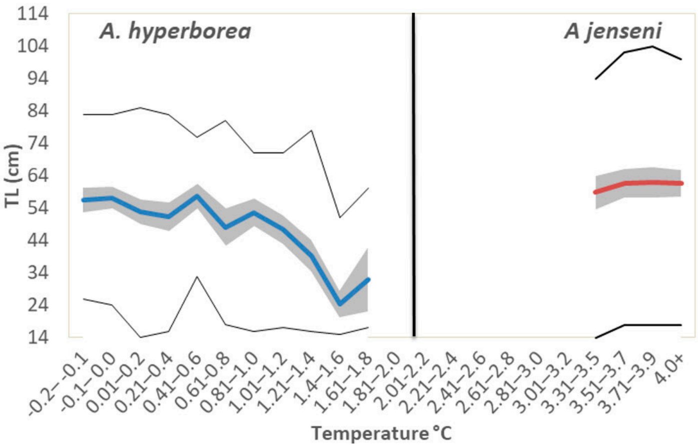
Figure 10. Fish density with respect to bottom temperature expressed as survey numbers per tow.

The mean size of *A. hyperborea* at depth averaged 52 cm and showed no trend (Figure 11a). A wide range of sizes was observed at all depths sampled, with one exception. At <750 m, smaller *A. hyperborea* averaging 40 cm were observed and fish > 61 cm were absent. However, abundance at those shallower depths was very low (see Figure 10) and only 7% of all specimens were captured at those depths. The average size of *A. jenseni*, 64 cm, was consistent over the entire depth range.



(**a**)

Figure 11. *Cont.*



(**b**)

Figure 11. (**a**) Average size of fish with respect to depth of capture and (**b**) average size of fish with respect to bottom temperature. Blue (*A. hyperborea*) and red (*A. jenseni*) lines are mean TL. Grey area is 95% CI and two black outer lines are minimum and maximum values of TL within each depth range. Black vertical line delineates temperature range of each species (see Figure 10).

The average size of *A. hyperborea* decreased with increasing temperature (Figure 11b). Fish averaged 56 cm at <0.5 °C decreasing to 31 cm > 1.5 °C and fish > 60 cm were absent at those higher temperatures. The relationship for *A. jenseni* was less apparent and there was a wide array of fish sizes at all temperatures. There were no associated temperature records for specimens of *A. jenseni* in <3.2 °C.

3.4. Maturity

A. jenseni are larger (TL) than *A. hyperborea* at each stage of maturity (Figure 12) but are very similar in size between sexes for each species. The increase in fish size decelerated at later stages of maturity with little increase in length in stage 3+ fish while the gonads are enlarging. The average sizes of stage 1 *A. hyperborea* and *A. jenseni* were 46 and 55 cm, respectively, increasing to 70–75 cm for stage 3+ *A. hyperborea* and 90+ cm for *A. jenseni*.

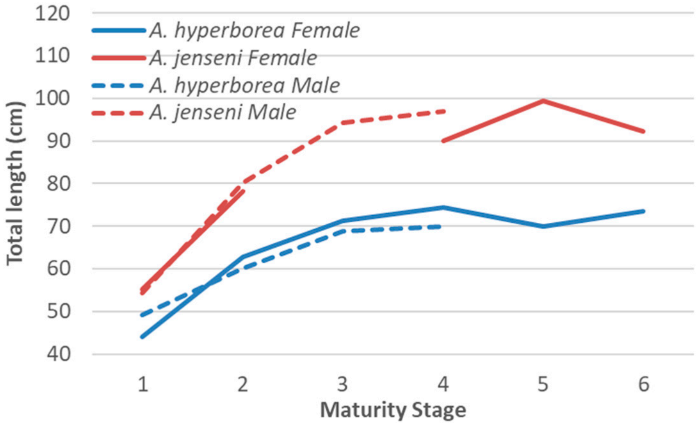


Figure 12. Average total length of fish by stage of maturity.

The average weight of the gonad increased with stage, weighing < 1% of body weight for stage 1 for both sexes and species, reaching 1.6% at stage 4 for *A. hyperborea* and 2% for *A. jenseni*. Gonad proportion reached a maximum of 3.4% at stage 5 for both species.

One hundred percent of *A. hyperborea* and *A. jenseni* were in stage 1 at <30 cm TL and <65 cm, respectively. *A. hyperborea* males started to mature (i.e., transition to stage 2) at 54 cm TL, *A. jenseni* males at 68 cm (Figure 13) while the onset of stage 2 entailed an acceleration in gonad weight. *A. hyperborea* females start to mature at 50 cm, *A. jenseni* females at 75 cm. Differences in size at the onset of maturity between sexes are considerably less than between species.

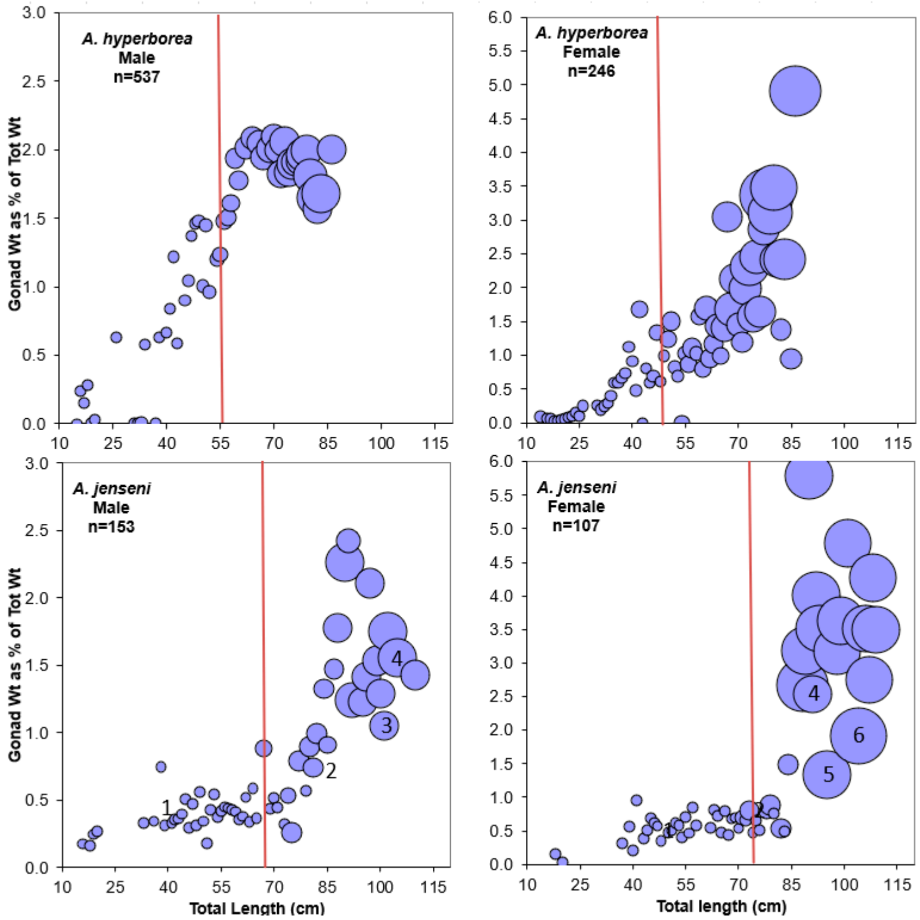


Figure 13. Bubble plots of gonad weight as a percent of total weight in relation to fish total length. Size of the expanding circle depicts maturity stage (see annotations within or near selected circles). Smallest circles, stage 1 indicate immature gonads and the largest circles for fully mature stage 4 males. For females, the largest circles are stage 6, resting/senescent (refer to [15] for maturity stages). Each circle may represent more than one fish and a mix of maturity stages. Red lines illustrate size of fish as they transition to stage 2 maturity.

Differences in (fully immature, length at 50% maturity and fully mature fish) were greater between species than between sexes within species: male *A. hyperborea*—(<52, 68, >84 cm), male *A. jenseni*—(<71, 90, >109 cm) and female *A. hyperborea*—(<46, 72, >89 cm) female *A. jenseni*—(<73, 84, >96 cm) (Figure 14). The ogives for *A. jenseni* were steeper, particularly for females indicating a more knife-edge pattern of maturity.

Maturity was also reflected in secondary reproductive characteristics, namely, alar rows, length of claspers, vas deferens, shell gland weight and uterus weight.

For males, alar row(s) were absent until the gonads started to mature, stage 1 transition to stage 2 (Figure 15). When *A. hyperborea* reached 53 cm TL, a single alar row started to develop on each outer wing and for *A. jenseni*, at 67 cm. The number of rows increased to a maximum of four rows for the largest, mature fish for both species.

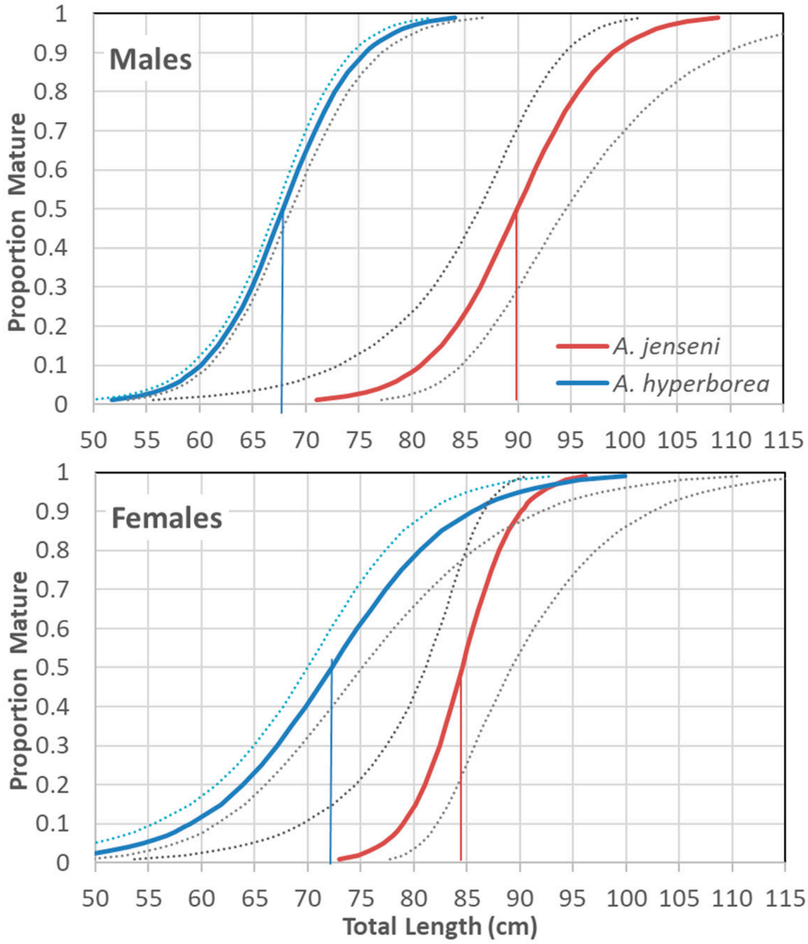


Figure 14. Length at 50% maturity (L_{50}) for *A. hyperborea* and *A. jenseni*, by sex as demarcated by the vertical lines. Dotted lines are 95% fiduciary intervals.

Clasper length was ≈0.2 cm in the smallest juveniles of both species, increasing in length as the fish increased in size, even prior to the onset of maturity (Figure 15). Clasper growth accelerated for *A. hyperborea* at >54 cm and was more pronounced for *A. jenseni* starting at >71 cm. Maximum clasper length was also longer in *A. jenseni* corresponding to its larger size.

Vas deferens weight in immature fish was <0.1 g for both species (Figure 15). For *A. hyperborea*, the weight of vas deferens relative to TL accelerated when the fish reached 54 cm at the onset of maturity and for *A. jenseni* at about 70 cm.

For both species, the shell gland weight of immature fish was <0.1 g (Figure 16). For *A. hyperborea*, shell gland weight started to increase at 56 cm TL, attaining a maximum weight of 38 g, and for *A. jenseni*, weight started to increase in 72 cm fish, reaching a maximum of 60 g. Similarly, uterus weight started to increase when *A. hyperborea* reached 56 cm and attained a maximum weight of 18 g; 71 cm and a maximum of 43 g for *A. jenseni*. This acceleration in weight increase corresponded to the onset of maturity.

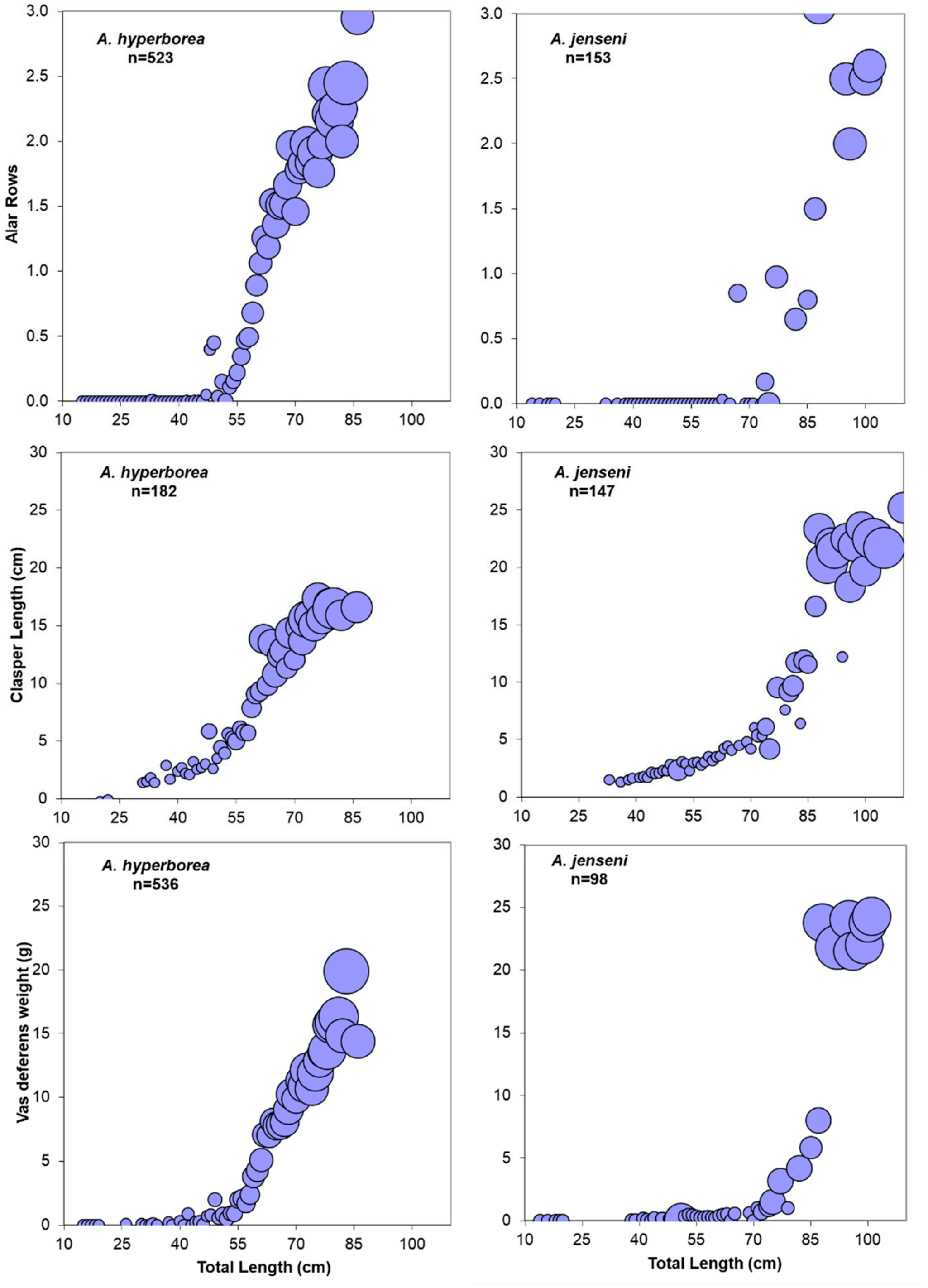


Figure 15. Bubble plots of male secondary reproductive characteristics, alar rows on the wings, clasper length and weight of the vas deferens in relation to total length and maturity stage. Partial alar rows were recorded to tenths. Maturity stage reflected by the size of the bubble was averaged by cm length grouping.

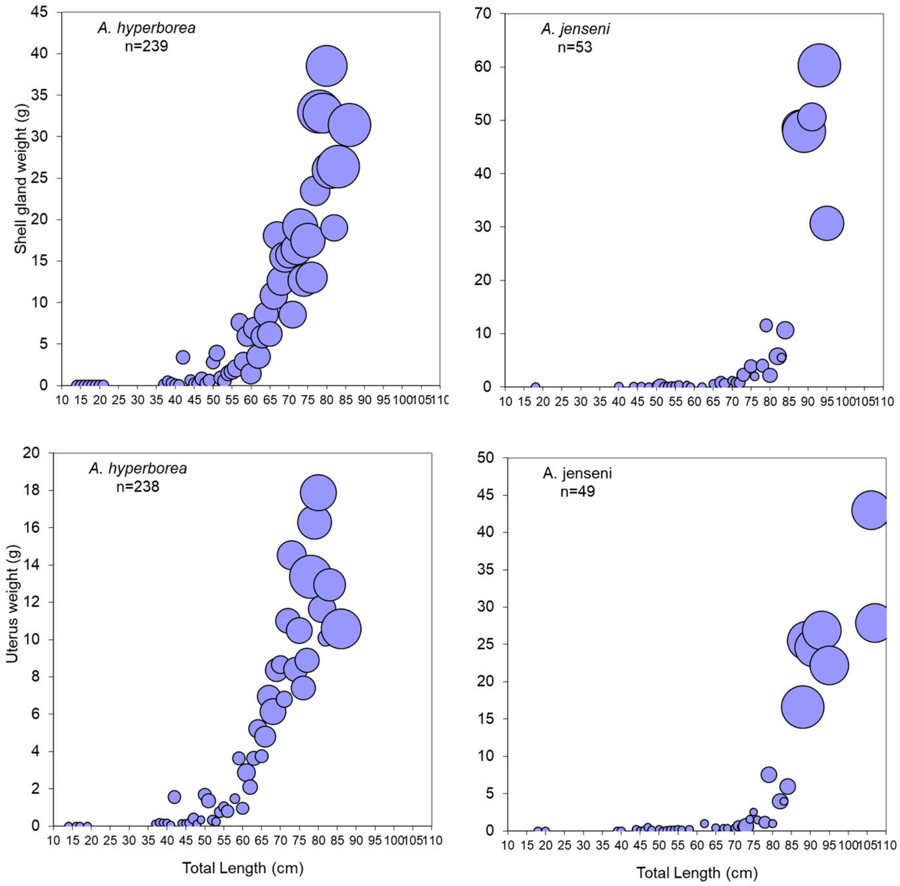


Figure 16. Bubble plots of female secondary reproductive characteristics, shell gland weight and uterus weight in relation to total length and maturity stage.

Table 4 summarizes the size at first maturity (initial appearance of stage 2 gonad) and compares those values to the various characteristics described above. For *A. hyperborea,* the average size at first maturity, size at the onset of alar row formation, and initial increase in clasper and vas deferens growth was 53–54 cm compared to 67–73 cm for *A. jenseni*. For females, the average for first maturity, shell gland width and uterus size was 56–57 cm for *A. hyperborea* compared to 71–75 cm for *A. jenseni*. Values at first maturity and secondary reproductive characteristics are higher for the larger *A. jenseni*.

Table 4. Summary of Maturity measures. 1st maturity refers to the point where gonads transitioned from stage 1 to stage 2. Average 1st maturity refers to the average of when growth in the secondary reproductive characteristics started to accelerate.

Attribute	Sex	*A hyperborea* (cm)	*A jenseni* (cm)	Difference (cm)
50% Maturity	Male	68	90	22
1st Maturity	Male	55	68	14
Alar rows	Male	53	67	14
Clasper	Male	54	71	21
Vas deferens	Male	54	73	19
Avg 1st maturity	Male	54	71	17
Max. obs. size	Male	86	110	24
50% Maturity	Female	72	84	12
1st Maturity	Female	57	75	18
Shell gland	Female	56	72	16
Uterus	Female	56	71	15
Avg 1st maturity	Female	56	73	17
Max. obs. size	Female	86	109	23

Five specimens, 1.3% of total female *A. hyperborea* collected, were in stage 4 maturity, containing partially formed purses in the uterus, and 24 specimens, 6.3% of total specimens collected, were stage 5, containing fully developed purses in the uterus. Nineteen specimens, 17% of total female *A. jenseni*, were in stage 5 maturity, with none at stage 4. Those females, ready to lay purses, were located throughout the sampled area, thus indicating that production/laying of purses occurred throughout the study area overlapping with immature and maturing stages 1–3 (Figure 17). There is no evidence of separation of stages within the bounds of their distribution for both species.

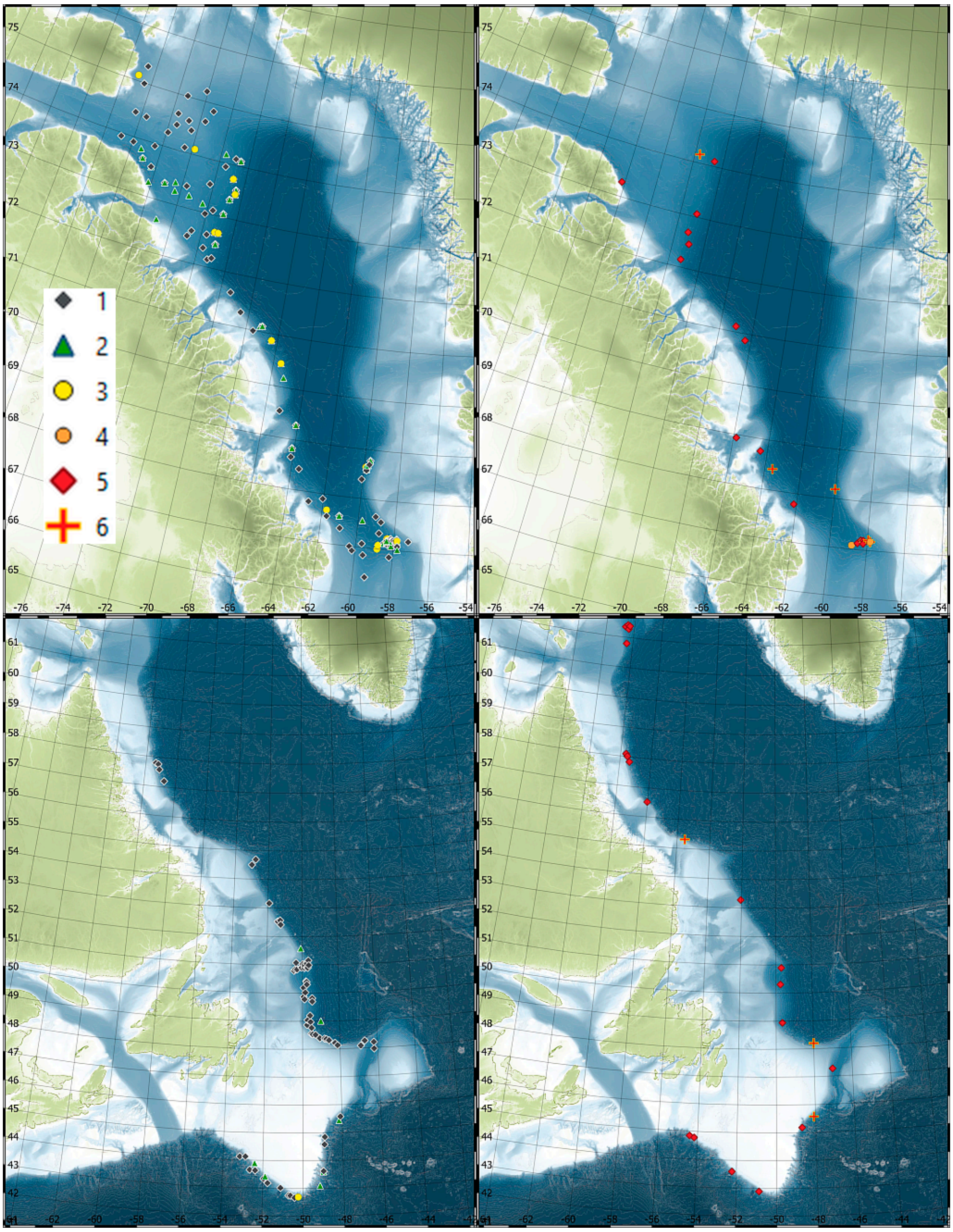


Figure 17. Distribution of female maturity Stages for *A. hyperborea* (upper panels) and *A. jenseni* (lower panels): (**Left**) panels depict immature and juvenile stages 1–3, (**Right**) panels depict fully mature stages 4–6.

However, although widely intermixed along the slope with no latitudinal separation among stages/sizes of fish (Figure 17), *A. hyperborea* size (TL) was structured by depth along the slope with a high degree of separation of fish < 20 cm (approximating YOY) and fish ≥ 20 cm (Figure 18). Ninety-two percent of *A. hyperborea* ≤ 20 cm were distributed at depths <900 m, their density peaking in 550–700 m, while 84% of fish > 20 cm (immature fish 1+ and adults) and 97% of fish >79 cm were located in > 900 m, concentrating mainly in > 1250 m. The distance between 650 m, where YOY reached their highest density, and 1100 m was 10–25 km, as much as 125 km northwest of Baffin Basin where there is a large relatively flat area < 900 m occupied primarily by fish < 20 cm. A similar separation of sizes was not observed for *A. jenseni* YOY. However, data taken from the lab samples for that species were limited. Only 9 *A. jenseni* < 20 cm were encountered.

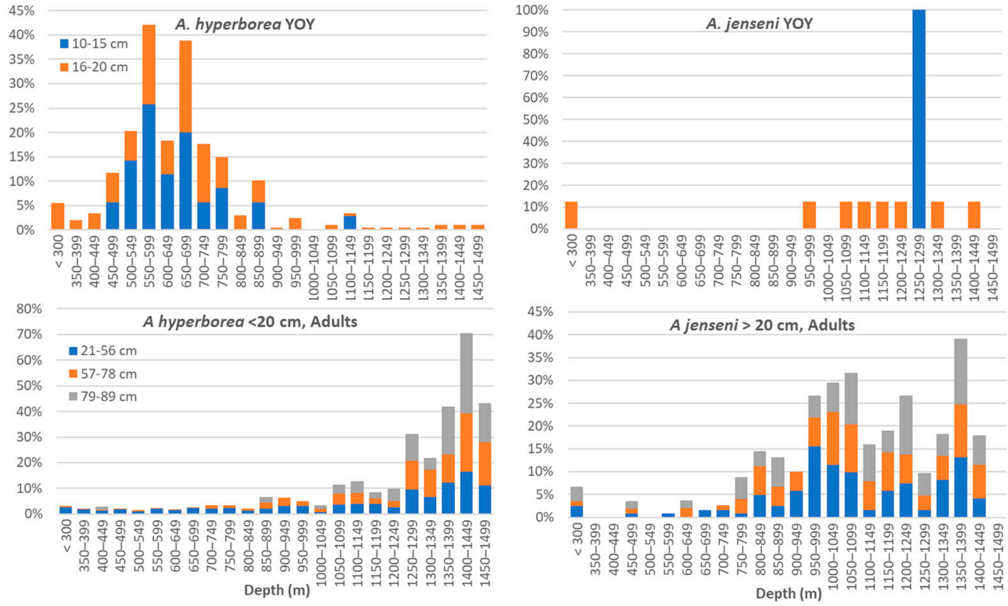


Figure 18. Length frequencies of *A. hyperborea* and *A. jenseni* at depth separated by size classes. *A. hyperborea* frequencies are based on fish that were measured during the Arctic surveys (n = 3329) while *A. jenseni* frequencies are based on specimens collected for lab analysis (n = 301). That species was not measured during the surveys.

Of the 389 *A. hyperborea* females examined, all collected from >850 m, only 4 were found with purses inside: 6 fully-formed and 2 partial purses. Of the 118 *A. jenseni*, all collected at >1000 m, 7 contained purses, 6 complete purses and 1 partially formed. Those *A. hyperborea* females were found with two purses inside, whereas four *A. jenseni* had one fully formed purse, indicating that the latter had already extruded one of the pair of purses. The average length of the *A. hyperborea* purses with/without horns was 173/105 mm and the average purse width was 58 mm. For the larger *A. jenseni*, the average purse length with/without horns was 235/122 mm with an average width of 76 mm.

4. Discussion

4.1. Morphometrics, Meristics, and Maturity

A. hyperborea and *A. jenseni* exhibit significant but trivial differences (due to large sample size) in spine counts with high degrees of overlap in values rendering those meristics of little use in differentiating species. Our study also identified several changes in morphology with growth. For example, the disc of both species became wider as the fish grew, so disc width/disc length would be informative as an identifying feature only relative to TL. Thus, in addition to highly similar spine counts between species, changes in their shape with growth render the body measurements of *A. hyperborea* and *A. jenseni* ineffective in differentiating the two species.

From DNA barcoding, including samples from our study area, mitochondrial DNA analysis was unable to differentiate *A. hyperborea* and *A. jenseni* [19]. Noting the close phenotypic resemblance, ref. [6] concluded that they are possibly the same species. However, ref. [5] noted that the two species, while easily confused, can be distinguished by teeth row count stating "one has to take a look in the mouth!" in order to differentiate species. Our analyses confirm a nearly complete separation in counts of upper jaw teeth rows between species. Furthermore, previously unreported, we observed a difference in maximum size, size at maturity and size of spines on a patch on the mid-rear portion of each wing in larger *A. hyperborea* juveniles, becoming more pronounced in adults and that difference can be used as a diagnostic in addition to teeth row counts to differentiate the two species in larger fish.

With similarities to studies in other areas, our spine and teeth row counts and morphometrics encompassed and extended ranges reported in past studies and identification manuals in most cases given our large sample size (Table 5). For example, the single value of disc width/disc length reported by [20,21] for *A. jenseni* fell within our reported range. An *A. hyperborea* disc width of 1.2–1.3 times disc length [6] falls within our observed range for both species. In addition, disc length as a proportion of TL (0.63) for both species was slightly higher than the 0.57 reported for *A. jenseni* in the North Atlantic [12,20]. However, such differences likely relate to a different mix of fish sizes in the sample between studies because we determined that those dimensions change as the fish grow.

We also found significant differences in maximum size reported in other studies (Table 5, in red). Although [5,6] indicated a maximum size of 112 and 100 cm, respectively, for *A. hyperborea*, very likely this was a result of *A. jenseni* being included in their samples as both authors specified that *A. hyperborea* distribute on the Atlantic slope where our study confirmed their absence. In the Norwegian Sea Deep [22] and in the Barents Sea [23], maximum TLs of 91 cm and 97 cm respectively were reported. Also, a maximum size of 85 cm in commercial catches and 91 cm in surveys were reported for the Barents Sea [24,25]. Thus, it appears that the species reaches a maximum size of 90 cm in the Northwest Atlantic (Baffin Basin) and slightly larger, 91 cm, possibly as high as 97 cm, in the Northeast Atlantic, but all smaller than the reported *A. jenseni* maxima. Nonetheless, in the Northwest Atlantic, Barents Sea and Norwegian Sea, *A. hyperborea* > 85 cm were rare: length frequencies from [13,22,23] are largely consistent with our results. For *A. jenseni*, values of maximum length reported by other authors were similar to our findings as summarized in Table 5.

For the Norwegian Sea slope, ref. [26] and Barents Sea [23,24,27,28] studies, characteristics used to determine species were not specified. However, the bottom temperature was primarily < 0° C, consistent with the *A. hyperborea* thermal habitat.

Given the difference in growth, the two species also matured at different sizes: *A. hyperborea* L_{50}'s of 68/72 cm TL for males/females and 90/84 cm for *A. jenseni*. Similar values were reported for *A. hyperborea*, 62/68 cm for males/females off Iceland and 65/75 cm for males/females in the Barents Sea (Table 5). There are no previous maturity studies for *A. jenseni*. Furthermore, we found differences in purse lengths and widths between species, with the larger species *A. jenseni* containing larger egg cases. Although our study was limited by a small number of pregnant specimens, this finding supports the fact that larger-sized skate species produce larger purses.

Table 5. Comparison of morphometrics, meristics and temperature with other studies. Numbers highlighted in red show where values from past studies differ from our findings.

Paper	Teeth Row Count	Median Spines	Spines Eye	Spines Shoulder Scapula	Thorns between Dorsal Fins	Disc Width/Disk Length	Max Size cm	Disk Width % of TL	Disk Length % if TL	Males 50% Mature (cm)	Females 50% Mature (cm)	Temperature (° C)
A. hyperborea												
[6] N Atl.	35–48 (30–58)	22–32 (19–38)	3 (1–5)	2–3 (1–4)	0–2 (0–2)	1.2–1.3 (1.04–1.66)	112 (90)			80–90 (68)		
[5] N. Atl.	35–48 (30–58)	25–32 (19–38)		2–3 (1–4)	0–2 (0–2)		100 (90)					−1 to 1.5 (−1.1 to 4.0)
[29] NW Atl.		22–37 (19–38)					86 (90)					
[4] NW Atl.	35–48 (30–58)	22–32 (19–38)					87 (90)					−0.4 to 3.5 (−1.1 to 4.0)
[11] Iceland										62 (68)	75 (72)	
[11] Barents Sea										65.4 (68)	68 (72)	
[24] Barents Sea							91 (90)					−1.0 to 2.0 (−1.1 to 4.0)
[30,31] Barents Sea							80, 85 (90)					
[22] Norwegian Sea							97 (90)					< 0 (−1.1 to 4.0)
A. jenseni												
[6] N Atl.	52–66 (52–71)	20–31 (21–40)	3–4 (2–7)	2–4 (1–4)			112 (112)			83 (90)		
[5] N Atl.	52–66 (52–71)	20–31 (21–40)		2–4 (1–4)			112 (112)					3.6–3.9 (3.0–6.2)
[29] NW Atl.	54–71 (52–71)		2–4 (2–7)	3–4 (1–4)	0–2 (0–2)							
[4] NW Atl.	58–66 (52–71)	24–31 (21–40)			0–2 (0–2)		85 (112)					2.7–4.0 (3.0–6.2)
[20] N. Atl.	52–64 (52–71)	20–31 (21–40)	1–3 (2–7)		0–1 (0–2)	1.31 (1.04–1.44)	111 (112)	74.2 (74.1)	57.1 (62.6)			
[12] NW Atl. MAR	54–61 (52–71)	20–26 (21–40)	3–4 (2–7)	3–4 (1–4)	0–1 (0–2)		85 (112)	73.9 (74.1)	56.6 (62.6)			
[21] MAR	52–64 (52–71)	20–31 (21–40)	2–5 (2–7)	3–4 (1–4)		1.31 (1.04–1.44)	111 (112)					

Some species of elasmobranchs, particularly highly mobile pelagic sharks, are known to occupy separate, usually shallower locations during the early stages of life (i.e., [32–34]). A reproductive strategy seemingly less likely for relatively sessile demersal species and one previously not reported for Amblyraja, we found that *A. hyperborea* < 20 cm (YOY) occupied a largely separate depth range than larger sizes, <900 m, effectively a separate nursery ground. This observation implies that females with developing purses must migrate to shallower depths to lay their purses returning soon after to greater depths. Tagging experiments could help to clarify the mechanism. A nearly fully spatial separation of stages in a rajid species was first noted by [35] in the Bering Sea for a species of Bathyraja. This pattern was not observed for *A. jenseni,* although the sample size of YOY was limited. Consistent with our study, ref. [12,21] indicated that *A. jenseni* size did not vary with the depth of capture, although we did observe a decreasing average size with increasing temperature, indicating a partial separation of stages. For both species, various stages of maturity were spread over their entire latitudinal distribution, indicating that reproduction occurred throughout their range.

4.2. Distribution and Habitat

The literature is not consistent as to whether the distributions of *A. hyperborea* and *A. jenseni* overlap. For example, refs. [5,6] indicated extensive overlap in the distribution of the two species in the North Atlantic and ref. [7] stated that the two species overlap in Arctic waters. On the contrary, ref. [36] listed *A. hyperborea* but not *A. jenseni* from the Grand Banks. None of those papers indicated how they reconciled the taxonomy leaving open the possibility of mixing species. However, the two species while cognate are likely allopatric [4,8]; our analysis, using teeth row counts and spine patches on the body determined that the two species do not overlap within our study area. Their distributions are divided by a biogeographic break, the Davis Strait, separating the Arctic from Atlantic waters, each area with different thermal conditions and different mixes of demersal fish [5,7,10,11,36–39]. *A. hyperborea* distribute on the slope in Arctic waters in Baffin Basin while *A. jenseni* inhabits the Atlantic Basin slope. In the Northeast Atlantic, referring to *A. hyperborea* as a cold-water species, refs. [30,31] stated that any records south of Arctic waters from the North Sea and eastern English Channel as reported by England, Wales and Northern Ireland are likely the result of misidentification or incorrect use of species codes. Those fish were likely misidentified as *A. jenseni*.

Consistent with our study, on the western side of Baffin Basin, *A. hyperborea* but not *A. jenseni* were recorded [9,10,38,39] and on the eastern side of Baffin Basin in Greenlandic waters only *A. hyperborea* were recorded [11,40]. Thus, *A. hyperborea* occupy all slope waters of the Basin, at least down to 1500 m, the greatest depths sampled. The deepest point in Baffin Basin is 2400 m and given that the known depth range of this species is 140 to 2500 m [41,42], it is likely that *A. hyperborea* occupy most if not all of Baffin Basin.

They were also found in deep Arctic bays and passages west of the Basin; in Hudson Strait (our study), Cumberland Sound [13], Ungava Bay and west into Hudson Strait (our study, [7]) but at much lower densities in those shallower waters. Three captures were recorded north of Baffin Basin in James Sound and Nares Strait, leading to the Arctic Ocean, at Lat 78° constituting the most northerly records of *A. hyperborea* [7]. In western North American waters, *A. hyperborea* were recorded in the Beaufort Sea [43,44]. If connected, this suggests that this species may also occupy some of the deepest passages of the Canadian Arctic Archipelago that separates Baffin Bay from the Beaufort Sea.

In addition to occupying Arctic waters of western and eastern Canada and Greenland, *A. hyperborea* have been recorded north of Iceland, the Spitsbergen/Svalbard Archipelago to the Greenland–Iceland Ridge, along the coasts of northern Norway and in the Norwegian Deep [26,30,45–47]. Also, *A. hyperborea* are cosmopolitan in Russian seas, the second most abundant species in the Barents Sea [23], Franz Josef Land and northern Novaya Zemliya Archipelagos, Kara, Laptev, East Siberian, Chukchi, Okhotsk and Bering Seas, northern Kuril Islands and western Kamchatka [47–49]. Thus, it appears to have a circumpolar distribution and is likely the most abundant cartilaginous fish species in the Arctic.

Less is known of the distribution of *A. jenseni*. The holotype was described from the waters of New England as *Raja jenseni* [2]. Subsequently, infrequent records were recorded just south of our study area in northern USA waters and on the Scotian Shelf slope [5,50–52]. Occasional captures of *A. jenseni* were also reported on the Grand Banks slope [8,53,54] in the southern part of our study area. These earlier scattered records combined with our study extending from the Grand Banks to northern Labrador show that in the Northwest Atlantic, *A. jenseni* distributes along the slope, likely continuously, from the mid-Atlantic Bight to the northernmost edge of the Atlantic slope but not north of Davis Strait. In the Northeast Atlantic, *A. jenseni* are recorded infrequently from south of Iceland and on the mid-Atlantic Ridge [12,14,21,55,56]. Scattered records have been reported west of the British Isles and as far south as waters off France and Portugal [57–64]. These records suggest that the species is widespread in the slope waters of the eastern (as well as the western) North Atlantic, although not commonly encountered, likely due to their deep distribution.

These sibling species inhabit similar depths along the slope, mainly in >650 m and, in both cases, they reached maximum density at the greatest depths sampled (1500 m). This suggests that they would be distributed at a high density well beyond sampled depths. Previous studies referred to *A. jenseni* as rare, i.e., [8,12]. However, our study shows that *A. jenseni* is a relatively common species reaching its highest density at the deepest depths sampled, likely occupying areas well beyond sampled depths in most of the northern North Atlantic Basin.

Previously, little was known about the thermal preferences/associations of the two species. We showed that they occupy different locations separated by a 200 km gap in Davis Strait with a highly overlapping depth range but different thermal habitats. In our study area, *A. hyperborea* are located almost exclusively in <2.5 °C in Baffin Bay and surrounds, *A. jenseni* in >2.6 °C on the Northwest Atlantic slope. In Cumberland Sound just west of Baffin Bay, five specimens of *A. hyperborea* were captured in 1.2 and 2.9 °C waters [13], corresponding to the upper range of temperatures that we recorded for this species. Nearly all *A. hyperborea* were captured in <2 °C in colder parts of the Barents Sea [23]. Survey catch rates of *A. hyperborea* decreased with decreasing latitude and increasing temperature near Iceland and were generally absent at latitudes < 65° [11]. Catches in southern Norway (Lat 62–73.5°) were lower to the south relating to the unsuitable (warmer) bottom water temperatures there. We observed a thermal range of 2.6–5.5 °C where nearly all captures occurred for *A. jenseni*, very similar to 2.7–4.0 °C reported for other parts of its range [5,6].

Biogeographic breaks with different thermal conditions are known to contribute to population genetic structuring of marine fishes, i.e., [65,66], and colder Arctic (*A. hyperborea*) versus warmer Atlantic (*A. jenseni*) slope conditions may have affected sufficient genetic separation manifested in the morphometric differences observed. The sequence divergence between not only *A. hyperborea* and *A. jenseni* but also *A. badia* (North Pacific) and *A. robertsi* (south Atlantic) is minimal (0.2–0.3%) [19]. Thus, [67] suggested that they may possibly be conspecific despite the physical differences. Nonetheless, in the Northern Hemisphere, we described not only the physical differences (teeth row count, spine patches on mid-rear wings, growth and maturity) between *A. hyperborea* and *A. jenseni* but also demonstrated their geographic separation and different thermal habitats.

From slope waters of Australia and New Zealand, formerly *A. badia*, synonymized with *A. hyperborea* [5,6,67], are found in thermal conditions more closely aligned with those of the North Atlantic slope [68] where only *A. jenseni* distribute rather than the colder Arctic waters inhabited by *A. hyperborea*, further complicating the understanding of the relationships of these very similar species of *Amblyraja*. Nonetheless, the (formerly) four species occupy vastly different distributions. Recent divergence seems the most logical explanation at least for *A. hyperborea* and *A. jenseni*, possibly resulting from disparate thermal conditions. It was suggested that for *Amblyraja hyperborea/jenseni*, more rapidly evolving markers (i.e., ITS, microsatellites and potentially adaptive markers) could be more effective in assessing whether or not they represent distinct species [19].

5. Conclusions

A. hyperborea and *A. jenseni* are sibling species with exclusive distributions, the smaller *A. hyperborea* occupying colder Arctic seas, the larger *A. jenseni* inhabiting warmer North Atlantic Basin waters but in a similar range of depths. The two distinct species, as presently classified, are nearly morphologically identical, but a combination of teeth row count, mid-rear wing spines in larger individuals, size at maturity, location and habitat (temperature range) can be used to differentiate the species.

However, based on DNA barcoding they are currently indistinguishable in their genetic makeup suggesting a number of possibilities, the most likely, that, once a single species, they would have undergone recent divergence, with insufficient time for reciprocal monophyly to have occurred, although more rapidly evolving markers may better detect differences between species [19]. This divergence may have come about by the formation of a biogeographic break causing differentiation of habitat and physical separation of what was once possibly a single species. The physical distance separating the two species is small, ≈200 km in the Davis Strait, but thermal conditions in the areas north and south of the break are very different. Such differences, coupled with reproductive isolation, may have caused the divergence.

What is less certain is the global phylogeny of the species. The synonymized group of species in the Southern Hemisphere, now referred to as *A. hyperborea,* is separated by vast distances from those in Arctic waters and occupies a very different habitat. In [67], it states:

> *"Although various species of Amblyraja hyperborea-like appearance have been described from several areas (A. badia, frerichsi, georgiana, jenseni, reversa, robertsi and taaf), distinct morphological interspecific differences hardly exist. Accordingly, all these species are possibly conspecific, with A. hyperborea (as the oldest valid name), having a worldwide distribution in cold, deep waters (Ebert & Stehmann, 2013)".*

Our analyses demonstrated separate distributions, significant habitat differences and different morphology between *A. hyperborea* and *A. jenseni*. In terms of maximum size, four South Pacific specimens of *A. hyperborea*, three captured near New Zealand (Te Papa) and one from west of Tasmania were 110–112.8 cm TL (Dr. Simon Weigman, pers. comm.). This is much larger than the maximum size of *A. hyperborea* from our study area and near the maximum size of *A. jenseni*. It would seem unlikely that the smaller *A. hyperborea* located in Arctic waters and separated by vast distances from what are currently referred to as *A. hyperborea* located in warmer conditions in the Southern Hemisphere, their disjunct distributions interposed by larger *A. jenseni* in the North Atlantic, are the same species. A global re-examination of teeth rows and mid-rear wing spines, growth and maturity, habitat and genetic analyses with rapidly evolving markers, particularly for synonymized specimens from the Southern Hemisphere might well provide clarity globally. There is also the fundamental question of whether distributional separation, unique meristics (teeth rows and wing spines), growth and maturity differences constitute sufficient evidence of distinct species.

Author Contributions: Conceptualization, D.W.K. and C.M.M.; methodology, D.W.K., C.M.M. and S.A.; validation, D.W.K., C.M.M. and S.A.; formal analysis, D.W.K. and S.A.; investigation, C.M.M. and D.W.K.; resources, Fisheries and Oceans; data curation, C.M.M. and D.W.K.; writing—original draft preparation, D.W.K. writing—review and editing, D.W.K., C.M.M., M.R.S. and S.A.; visualization, D.W.K.; supervision, D.W.K. and M.R.S.; project administration, D.W.K., C.M.M. and M.R.S.; funding acquisition, D.W.K. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Ethical review and approval were waived for this study since it dealt only with frozen specimens.

Data Availability Statement: Annual Fisheries and Oceans Canada survey data were used for these analyses. Open Fisheries and Oceans data are available at https://open.canada.ca/en.

Acknowledgments: The authors wish to thank Fisheries and Oceans Canada staff who participated in Canadian research surveys and Canadian Fisheries Observers who collected specimens and data onboard commercial vessels over many years. We are also grateful to Trevor Maddigan, Chris Holloway, Frank Dawson Jr, Jennifer Mercer, Lindsay Simms, Dennis Rice, Barry MacDonald and the late Dave Sears for conducting meticulous specimen dissections and data recordings in the lab.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Donovan, E. *The Natural History of British Fishes, Including Scientific and General Descriptions of the Most Interesting Species, and an Extensive Selection of Accurately Finished Coloured Plates*; F. and C. Rivington Publisher: London, UK, 1802; pp. 1–516.
2. Bigelow, H.B.; Schroeder, W.C. New and little known cartilaginous fishes from the Atlantic. *Bull. Mus. Comp. Zool.* **1950**, *103*, 385–408.
3. Collett, R. Fiske fra Nordhavs-Expeditionens sidste Togt, Sommeren 1878. *Forh. Vidensk. Selsk. Christiania* **1878**, *14*, 45–77.
4. Sulak, K.J.; MacWhirter, P.D.; Luke, K.E.; Norem, A.D.; Miller, J.M.; Cooper, J.A.; Harris, L.E. Identification guide to skates (family Rajidae) of the Canadian Atlantic and adjacent regions. *Can. Tech. Rept. Fish. Aquat. Sci.* **2009**, *2850*, 1–34.
5. Ebert, D.A.; Stehmann, M.W.F. Sharks, batoids and chimaeras of the North Atlantic. In *FAO Species Catalogue for Fishery Purposes*; FAO: Rome, Italy, 2013; p. 523. ISSN 1020-8682.
6. Last, P.; White, W.T.; De Carvalho, M.R.; Séret, B.; Stehmann, M.F.W.; Naylor, G.J.P. (Eds.) *Rays of the World*; Comstock Publishing Associates: Ithaca, NY, USA, 2016; p. 790.
7. Alphonso, N.R.; Coad, B.W.; Sawatsky, C.D.; Reist, J.A. *Distributional Records of Marine Fishes of Arctic Canada*; Fisheries and Oceans Canada, Central and Arctic Region: Winnipeg, MB, Canada, 2018; Volume 1287, p. 319.
8. Templeman, W. Rare Skates of the Newfoundland and Neighbouring Areas. *J. Fish. Res. Bd. Canada* **1965**, *22*, 259–279. [CrossRef]
9. Jørgensen, O.A.; Hvingel, C.; Møller, P.R.; Treble, M.A. Identification and mapping of bottom fish assemblages in Davis Strait and southern Baffin Bay. *Can. J. Fish. Aquat. Sci.* **2005**, *62*, 1833–1852. [CrossRef]
10. Jørgensen, O.A.; Hvingel, C.; Treble, M.A. Identification and mapping of bottom fish assemblages in northern Baffin Bay. *J. Northw. Atl. Fish. Sci.* **2011**, *43*, 65–79. [CrossRef]
11. Climent, R.L. Distribution, Reproductive Ecology, and Colouration of the Arctic Skate *Amblyraja hyperborea* (Collett, 1879) in the North Atlantic Ocean. Faculty of Biosciences, Fisheries and Economics, Department of Arctic and Marine Biology; BIO-3950; Master's Thesis, UiT Norges Arktiske Universitet, Tromsø, Norway, 2021.
12. Orlov, A.M.; Cotton, C.M. New data on the rare deep-sea skate *Amblyraja jenseni* (Rajidae) from the North Atlantic Ocean. *J. Ichthyol.* **2015**, *55*, 478–496. [CrossRef]
13. Peklova, I.; Hussey, N.E.; Hedges, K.J.; Treble, M.A.; Fisk, A.T. Movement, depth and temperature preferences of an important bycatch species, Arctic skate *Amblyraja hyperborea*, in Cumberland Sound, Canadian Arctic. *Endang. Species Res.* **2014**, *23*, 229–240. [CrossRef]
14. Stehmann, M.; Bürkel, D.L. Rajidae. In *Fishes of the North-Eastern Atlantic and Mediterranean*; Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., Tortonese, E., Eds.; UNESCO: Paris, France, 1984; Volume 1, pp. 163–196.
15. Gallagher, M.; Nolan, C.P.; Jeal, J. Age, Growth and Maturity of the Commercial Ray Species from the Irish Sea. *J. Northw. Atl. Fish. Sci.* **2005**, *35*, 54575529. [CrossRef]
16. Bishop, C.A. MS Revisions and additions to stratification schemes used during research vessel surveys in NAFO Subareas 2 and 3. *Nafo. Scr. Doc.* **1994**, *94*, 10.
17. Siferd, T.; Legge, G. *Modifications to the Campelen 1800 Shrimp Survey Trawl*; Fisheries and Oceans Canada: Winnipeg, MB, Canada, 2014; Volume 24, iv+38p.
18. DFO. *Assessment of Northern Shrimp, Pandalus borealis, and Striped Shrimp, Pandalus montagui, in the Eastern and Western Assessment Zones, February 2019*; Center for Science Advice (CSA), Central and Arctic Region, Fisheries and Oceans Canada: Winnipeg, MB, Canada, 2019; Volume 11.
19. Coulson, M.W.; Denti, d.; Van Guelpen, L.; Miri, C.; Kenchington, E.; Bentzen, P. DNA barcoding of Canada's skates. *Mol. Ecol. Resour.* **2011**, *11*, 968–978. [CrossRef] [PubMed]
20. Orlov, A.M.; Cotton, C.M. Sexually Dimorphic Morphological Characters in Five North Atlantic Deepwater Skates (Chondrichthyes: Rajiformes). *J. Mar. Biol.* **2011**, *2011*, 842821. [CrossRef]
21. Orlov, A.M.; Cotton, C.M.; Byrkjedal, I. Deepwater skates (Rajidae) collected during the 2004 cruises of RV G.O. Sars and M.S. Loran in the MidAtlantic Ridge area. *Cybium* **2006**, *30*, 3548.
22. Skjaeraasen, J.E.; Bergstad, O.A. Notes on the distribution and length composition of *Raja lintea, R. fyllae, R. hyperborea* and *Bathyraja spinicauda* (Pisces: Rajidae) in the deep northeastern North Sea and on the slope of the eastern Norwegian Sea. *ICES J. Mar. Sci.* **2001**, *58*, 21–28. [CrossRef]
23. Wienerroither, R.; Johannesen, E.; Dolgov, A.; Byrkjedal, I.; Aglen, A.; Bjelland, O.; Drevetnyak, K.; Eriksen, K.B.; Høines, Å.; Langhelle, G.; et al. *Atlas of the Barents Sea Fishes Based on the Winter Survey*; IMR-PINRO Joint Report Series 2; IMR-PINRO: Saint-Hubert, QC, Canada, 2013; 220p, ISSN 1502-8828.

24. Dolgov, A.V.; Drevetnyak, K.V.; Gusev, E.V. The Status of Skate Stocks in the Barents Sea. *J. Northw. Atl. Fish. Sci.* **2005**, *35*, 249–260. [CrossRef]
25. Dolgov, A.V.; Grekov, A.A.; Shestopal, I.P.; Sokolov, K.M. By-catch of Skates in Trawl and Long-Line Fisheries in the Barents Sea. *J. Northw. Atl. Fish. Sci.* **2005**, *35*, 357–366. [CrossRef]
26. Blindheim, J. Ecological Features of the Norwegian Sea. In Proceedings of the Sixth Conference of the Comité Arctique International, Fairbanks, Alaska, 13–15 May 1985; Rey, L.R., Ed.; Brill Publishers: Leiden, The Netherlands, 1989; pp. 366–401, ISBN 90-04-08281-6.
27. Jørgensen, L.L.; Spiridonov, V. *Effect from the King- and Snow Crab on Barents Sea Benthos. Results and Conclusions from the Norwegian-Russian Workshop in Tromsø 2010*; Fisken og Havet nr. 2013, 8/201; Institute of Marine Research: Bergen, Norway, 2013; 41p.
28. Wienerroither, R.; Johannesen, E.; Dolgov, A.; Byrkjedal, I.; Bjelland, O.; Drevetnyak, K.; Wenneck, T. *Atlas of the Barents Sea Fishes*; IMR/PINRO Joint Report Series 1; IMR-PINRO: Saint-Hubert, QC, Canada, 2011.
29. Corke, J. *Identification Guide to Sharks, Skates, Rays and Chimaeras of Atlantic Canada*; WWF: Toronto, ON, Canada, 2012.
30. Ices Advisory Committee Ices CM 2017/Acom:16 Report of the Working Group on Elasmobranch Fishes (WGEF). Ices Wgef Report: Lisbon, Portugal; 2017; p. 1018.
31. Ices Advisory Committee Ices CM 2013/Acom:19 Report of the Working Group on Elasmobranch Fishes (WGEF). Ices Wgef Report: Lisbon, Portugal, 2013; p. 680.
32. Driggers, W.B., III; Ingram, G.W., Jr.; Grace, M.A.; Gledhill, C.T.; Henwood, T.A.; Horton, C.N.; Jones, C.M. Pupping areas and mortality rates of young tiger sharks Galeocerdo cuvier in the western North Atlantic. *Ocean. Aquat. Biol.* **2008**, *2*, 1610170. [CrossRef]
33. Heupel, M.R.; Carlson, J.K.; Simpfendorfer, C.A. Shark nursery areas: Concepts, definition, characterization and assumptions. *Mar. Ecol. Progr. Ser.* **2007**, *337*, 287–297. [CrossRef]
34. Bangley, C.W.; Paramore, L.; Shiffman, D.S.; Rulifson, R.A. Increased Abundance and Nursery Habitat Use of the Bull Shark (*Carcharhinus leucas*) in Response to a Changing Environment in a Warm-Temperate Estuary. *Sci. Rep.* **2018**, *8*, 6018. [CrossRef]
35. Hoff, G.R. Identification of multiple nursery habitats of skates in the eastern Bering Sea. *J. Fish Biol.* **2016**, *88*, 1746–1757. [CrossRef]
36. Nogueira, A.; Paz, X.; Gonzalez-Troncoso, D. Changes in the exploited demersal fish assemblages in the Southern Grand Banks (NAFO Divisions 3NO) 2002–2013. *ICES J. Mar. Sci.* **2015**, *72*, 753–770. [CrossRef]
37. Guadalupe del Mar Villagarcta, M. Structure and Distribution of Demersal Fish Assemblages on the Northeast Newfoundland and Labrador Shelf. Master's Thesis, Department of Biology, Memorial University of Newfoundland, St. John's, NL, Canada, 1995.
38. Coad, B.W.; Reist, J.D. *Annotated List of the Arctic Marine Fishes of Canada*; Fisheries and Oceans Canada: Winnipeg, MB, Canada, 2004; Volume 2674, pp. 1–118.
39. Coad, B.W.; Reist, J.D. *Marine Fishes of Arctic Canada*; University of Toronto Press: Toronto, ON, Canada, 2018; xiii+618p.
40. Møller, P.R.; Nielsen, J.G.; Knudsen, S.W.; Poulsen, J.Y.; Sünksen, K.; Jørgensen, O.A. A check list of the fish fauna of Greenland waters. *Zootaxa* **2010**, *2378*, 1–84.
41. Artuykhin, Y.U.B.; Sheyko, B.A. (Eds.) *Catalog of Vertebrates of Kamchatka and Adjacent Waters*; Rossiyskaya Akademiya Nauk: Moscow, Russia, 2000.
42. Orlov, A.M. On the justification of commercial measure for the Far East skates (fam. Rajidae) for an example of mass western Bering Sea species. *Tr. Vniro* **2006**, *146*, 252–264.
43. Majewski, A.R.; Atchison, S.; MacPhee, S.; Eert, J.; Niemi, A.; Michel, C.; Reist, J.D. Marine fish community structure and habitat associations on the Canadian Beaufort shelf and slope. *Deep-Sea Res.* **2017**, *121*, 169–182. [CrossRef]
44. Thorsteinson, L.K.; Love, M.S. (Eds.) *Alaska Arctic Marine Fish Ecology Catalog Prepared in cooperation with Bureau of Ocean Energy Management, Environmental Studies Program (OCS Study, BOEM 2016-048)*; Scientific Investigations Report; U.S. Department of the Interior, U.S. Geological Survey: Reston, VA, USA, 2011; pp. 2016–5038.
45. Dolgov, A.V. Annotated list of fish-like vertebrates and fish of the Kara Sea. *J. Ichthyol.* **2013**, *53*, 914–922. [CrossRef]
46. Jørgensen, O.A.; Hvingel, C.; Møller, P.R. Bottom Fish Assemblages at the Shelf and Continental Slope off East Greenland. *J. Northw. Atl. Fish. Sci.* **2015**, *47*, 37–55. [CrossRef]
47. Mecklenburg, C.W.; Lynghammar, A.; Johannesen, E.; Byrkjedal, I.; Christiansen, J.S.; Dolgov, A.V.; Karamushko, O.V.; Mecklenburg, T.A.; Møller, P.R.; Steinke, D.; et al. Marine fishes of the Arctic Region. Vol. I. Conservation of Arctic Flora and Fauna, Akureyri, Iceland. *CAFF Monit. Ser. Rep.* **2018**, *28*, 1–454.
48. Lynghammar, A.; Christiansen, J.; Mecklenburg, C.; Karamushko, O.; Møller, P.; Gallucci, V. Species richness and distribution of chondrichthyan fishes in the Arctic Ocean and adjacent seas. *Biodiversity* **2013**, *14*, 57–66. [CrossRef]
49. Dyldin, Y.V. Annotated checklist of the sharks, batoids and chimaeras (Chondrichthyes: Elasmobranchii, Holocephali) from waters of Russia and adjacent areas. *Publ. Seto Mar. Biol. Lab.* **2015**, *43*, 40–91. [CrossRef]
50. Moore, J.A.; Hartel, K.E.; Craddock, J.E.; Gallbraith, J.K. An annotated list of deepwater fishes from off the New England region, with new area records. *Northeast Nat.* **2003**, *10*, 159–248. [CrossRef]
51. Halliday, R.G.; Themelis, D.E.; Hickey, W.M. Demersal fishes caught with bottom gillnets and baited gears at 500–2800 m on the continental slope off Nova Scotia, Canada. *J. Northw. Atl. Fish. Sci.* **2012**, *44*, 31–40. [CrossRef]
52. Halliday, R.G.; Van Guelpen, L.; Themelis, D.E. Demersal fish fauna of the continental slope off Nova Scotia, Canada, based on exploratory bottom trawl surveys in 1994–1995. *J. Northw. Atl. Fish. Sci.* **2012**, *44*, 41–60. [CrossRef]

53. Kenchington, E.; Power, D.; Koen-Alonso, M. Associations of demersal fish with sponge grounds on the continental slopes of the northwest Atlantic. *Mar. Ecol. Prog. Ser.* **2013**, *477*, 217–230. [CrossRef]
54. Vázquez, A.; Casas, J.M.; Brodie, W.B.; Javier Murillo, F.; Mandado, M.; Gago, A.; Alpoim, R.; Bañón, R.; Armesto, Á. List of species as recorded by Canadian and EU bottom trawl survey in Flemish Cap. *Nafo. Scr. Doc.* **2013**, *13*, N6154.
55. Cousins, N.J.; Linley, T.D.; Jamieson, A.J.; Bagley, P.M.; Blades, H.; Box, T.; Chambers, R.; Ford, A.; Shields, M.A.; Priede, I.G. Bathyal demersal fishes of Charlie Gibbs Fracture Zone region (49–54° N) of the MidAtlantic Ridge: II. Baited camera lander observations. *Deep Sea Res. Part II* **2013**, *98*, 397–406. [CrossRef]
56. ICES Working Group on Elasmobranch Fishes (WGEF). *ICES Sci. Rep.* **2021**, *3*, 822. [CrossRef]
57. Gordon, J.D.M.; Duncan, J.A.R. Deepsea bottom living fishes at two repeat stations at 2200 and 2900 m in the Rockall Trough, northeastern Atlantic Ocean. *Mar. Biol.* **1987**, *96*, 309–325. [CrossRef]
58. Gordon, J.D.M.; Duncan, J.A.R. A note on distribution and diet of deepwater rays (Rajidae) in an area of the Rockall Trough. *J. Mar. Biol. Ass.* **1989**, *69*, 655–658. [CrossRef]
59. Quero, J.C.; Lorance, P.; Tardy, E. Observations ichtyologiques effectuees en 1999 a bord du navire de recherche "Thalassa". *Ann. Soc. Sci. Nat. Chart. Marit.* **2000**, *8*, 1047–1058.
60. Wheeler, A.C.; Merrett, N.R.; Quigley, D.T.G. Additional records and notes for Wheeler's (1992) list of the common and scientific names of fishes of the British Isles. *J. Fish Biol.* **2004**, *65* (Suppl. SB), 1–40.
61. George, M.R.; Zidowitz, H. Checkliste der europäischen Knorpelfisharten mit wissenschaftlichen und deutschen Namen. *Z. Fischkund* **2006**, *8*, 71–81.
62. Neat, F.; Burns, F.; Drewery, J. The deepwater ecosystem of the continental shelf slope and seamounts of the Rockall Trough: A report on the ecology and biodiversity based on FRS scientific surveys. In *Fisheries Research Services Internal Report*; Joint Nature Conservation Committee: Aberdeen, Scotland, 2008; No 02/08.
63. Johnston, G.; O'Hea, B.; Dransfeld, L. Fish species recorded during deepwater trawl survey on the continental shelf and the Porcupine Bank, 2006–2008. *Ir. Nat. J.* **2010**, *31*, 130–134.
64. Séret, B. *Guide des Requins, des Raies et des Chimères des Pêches Françaises*; IRD: Paris, France, 2010.
65. Knutsen, H.; Jorde, P.E.; Sannæs, H.; Hoelzel, A.R.; Bergstad, O.A.; Stefanni, S.; Johansen, T.; Stenseth, N.C. Bathymetric barriers promoting genetic structure in the deepwater demersal fish tusk (*Brosme brosme*). *Mol. Ecol.* **2009**, *18*, 3151–3162. [CrossRef]
66. Lamichhaney, S.; Barrio, A.M.; Rafati, N.; Sundström, G.; Rubin, C.-J.; Gilbert, E.R.; Berglund, J.; Wetterbom, A.; Laikre, L.; Webster, M.T.; et al. Population-scale sequencing reveals genetic differentiation due to local adaptation in Atlantic herring. *Proc. Natl. Acad. Sci. USA* **2012**, *109*, 19345–19350. [CrossRef]
67. Weigmann, S. Annotated Checklist of the Living Sharks, Batoids and Chimaeras (Chondrichthyes) of the World, with a Focus on Biogeographical Diversity. *J. Fish Biol.* **2016**, *88*, 837–1037. [CrossRef]
68. Chiswell, S.M.; Bostock, H.C.; Sutton, P.J.H.; Williams, M.J.M. Physical oceanography of the deep seas around New Zealand: A review. *N. Z. J. Mar. Freshw. Res.* **2015**, *49*, 286–317. [CrossRef]