Temporal patterns of sex-specific size at maturity of porbeagle sharks (*Lamna nasus*)

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Abstract

Examining population dynamics within fisheries science is an effective way to investigate the size and age structure of a given fish population, and to understand how that stock might change over time. Porbeagle sharks are an endangered, pelagic shark species, for which there was an active Canadian food fishery until 2013. The objective of this research is to conduct a temporal study of size and maturity of porbeagle sharks before and after the fishery closure. Using longline fishing equipment at approximately 50 locations in the Northwest Atlantic Canadian waters, the sharks were caught, and body size and maturity were measured. Comparing length at maturity data from 1999-2001 (before fishery closure) and 2017 (after fishery closure) has provided insights into the changes that have occurred in the last 16 to 18 years. I used generalized linear models to analyse changes in size at maturity, and in body shape, and body size. I found that maturity was influenced by fork length, year, and sex. The difference among years may be due to a lack of data collected during some years of the study. In addition, body shape was affected by sex alone, whereby the relationship between fork length and interdorsal length was steeper for males than females. Overall, our results indicate that there has been a temporal change in life history traits of porbeagle sharks.

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Introduction

Population Dynamics and Effects of Fisheries

Population dynamics is the division of biology that investigates the size and age structure of a particular population in a given time and space. The size and age structure of a population are determined by birth, death, immigration and emigration rates. In a fisheries context, population dynamics describes the ways that a given stock might change over time and is used to determine sustainable yields for fishing fleets in the coming year. While immigration and emigration occur in wild fish populations, they are often not incorporated in fish stock analyses, due to how difficult they are to measure. When creating a stock analysis, there are three main rates that are observed: recruitment, growth and mortality.

Recruitment can be defined as the number of juvenile fish each year that grow to a certain age or size, becoming susceptible to catch in the fishery. Some of the juveniles are too small to be caught in a net, on a longline or through other fishing methods, while with some other species, they can be caught just after birth, due to the size at which they are born. This can be defined as active selectivity (Punt et al. 2014). Depending on the size of the gear that is being used (the size of hooks or mesh size in nets) different species could be caught at different life stages. In pelagic longline fishing, sharks become susceptible to a fishery depending on their availability, encounterability, and selectivity (Cortés et al. 2010). Availability is determined by the probability that a fishing boat will encounter their target species, while encounterability is the probability that one hook will catch the

target species (Cortés et al. 2010). For example, these would be affected by fishing in preferred habitats, and the availability of prey items in the surrounding area.

Mortality can be divided into two components: natural and fishing mortality. Natural mortality describes death that occurs without human interaction (old age, disease, or other natural factors). Fishing mortality can be classified as a death that occurs as the result of directed fishery catches or bycatch. Bycatch occurs when a fish or other marine species is unintentionally caught when fishers are targeting another species (Department of Fisheries and Oceans 2007a). This can also include individuals of the same target species, but those of an undesirable size, age, or sex. Bycatch mortality can also result from post-release mortality, whereby death occurs following release as a result of injuries obtained during handling or stress associated with being caught (Campana et al. 2016). For porbeagle specifically, the main source of fishing mortality was through directed fishing until 2013, when the fishery was closed. The current source of fishing mortality for this species is bycatch (Baum et al. 2003).

Fisheries can be intentionally or unintentionally size selective, due to size of fishing gear or location of fishing. There are many regulations that restrict fishers and protect small fish, but this practice represents a form of artificial selection and may result in fishery-induced evolution. This type of evolution may occur over very few generations if selection for large individuals is intense (Heino et al. 2015). Length data from a fishery or survey can give a general idea of the distribution of lengths for the entire population and inform whether or not fishery-induced evolution is occurring. While these measures do not include the number of juvenile fish that are not vulnerable to the fishery, it is representative of the older, larger portion of a population.

One example of how exploitation can have serious consequences on life history can be seen in Atlantic cod (*Gadus morhua*) and how they were affected by their fishery. Hutchings (2005) reported declines in age and size at maturity following heavy exploitation, as well as extensive reductions in abundance associated with changes in life history of two populations of Atlantic cod in the Northwest Atlantic. These life history changes negatively affected the potential for population growth at each generation (Hutchings 2005). They have not recovered in population size or changes to life history (Shelton et al. 2006).

Study Species

The porbeagle (*Lamna nasus*) is a large pelagic shark species, found in the north and south Atlantic, as well as the south Pacific oceans. Typically found in waters colder than 14°C, in the Northwest Atlantic they can range from Newfoundland and Labrador to New Jersey (Department of Fisheries and Oceans 2007b). Individuals living in the Northwest Atlantic are considered to be one population, with no crossover into any of the other populations around the world (Cassoff et al. 2007). This population spans from north of Newfoundland, in Canadian waters, down to the Sargasso Sea, around the United States, with currently unknown migration patterns throughout the year (Campana et al. 2015). Producing only 2 to 4 pups per year, young are born after a 8-9 month gestation period (Jensen et al. 2002) at a length of around 65-70 cm (Department of Fisheries and Oceans 2007b). These are fully formed juvenile sharks, which increases their survival rate at birth and reduces their chances of being targeted by predators. Males and females have similar growth rates until an approximate length of 170 cm fork length (FL), measured from anterior region of the head to the fork in the tail, which is the point at

which males mature (Natanson et al. 2002, Cassoff et al. 2007, Biais et al. 2017). From there, the growth rate of males begins to decline, while females continue to grow until approximately 215 cm FL (Natanson et al. 2002, Cassoff et al. 2007) when they reach sexual maturity.

A directed fishery targeting porbeagle in Canada was opened in 1994 and continued until 2013. As early as the 1960s, foreign fishing fleets came into Canadian waters and exploited the porbeagle, having no restrictions regarding the number caught. When the Canadian fishing fleet joined the porbeagle fishery in the early 1990s, the amount fished did not substantially increase until the early 2000s, remaining high until the fishery was closed several years later. From the beginning of exploitation, in the early 1960s, continuing in the mid-1990s to the closing in 2013, the fishing period spanned approximately three generations (COSEWIC 2014). Extensive exploitation of a population has the potential to cause changes in growth rates and maturity due to the size selective nature of the fishing practice (Cassoff et al. 2007). During the commercial fishery, the rate of decline of juveniles and adults was approximately 75% to 85% respectively (Cassoff et al. 2007). On the basis of this population decline, porbeagle has since been assessed and listed as endangered by COSEWIC (2014).

Many of the porbeagle were being caught at younger ages in the directed fishery, meaning they were often not sexually mature (COSEWIC 2014). Between 1963 and 2001, the selective pressure of the fishery is thought to have caused a decrease in age at maturity for males from 8 to 7 years, and from 19 to 14 years for females (Cassoff et al. 2007). This decrease in age at maturity corresponds with a decrease of 5 cm in length at maturity for males, with no significant change for females (Campana et al. 2015). Before

these decreases occurred, individuals were maturing later, which meant that the sharks were being caught before they could reproduce, which is many years after they became susceptible to the fishery. Juveniles were being recruited into the fishery at similar sizes as before, but notably younger ages of 2-3 years in 1993, which was significantly younger than the 6-7 years which had been previously observed (Campana et al. 2002). This change in size-at-age could be an indication that individuals were maturing at smaller sizes than the pre-fishery population.

Project Goals

The purpose of this study can be divided into two main objectives. First, I will examine whether the mean length distributions of the porbeagle have changed since the last study was completed in the early 2000s. This information could be used to determine the number of recruits that are entering the reproductive stage, which could lend insight into future population growth or decline. I will compare the size at maturity of porbeagles to determine whether it has changed, which would indicate changes in life-history following the fishery closure. I will be investigating whether there has been any decrease in the length at maturity, as seen in Cassoff et al. (2007), from 1999-2001 to 2017 due to past fishing pressure.

Methods

This project is based on biological data from porbeagle that was collected during two time periods. The first set of data were collected before the fishery closed, from 1999 to 2001. These early samples were taken on board commercial vessels during directed fishing for porbeagle, where, at this time, the fishermen would fish in Canadian waters

and further out into the ocean. Since there was an active fishery during the time of the first three years of data, a subsample of the fisheries data was collected and compiled to be used in this study. With fishing periods ranging from around February to November, there was a longer time frame in which the sharks were fished, and measurements collected. The sharks caught during this time were kept by the fishermen to be sold. Data were also collected during 2017, after the fishery had closed. Samples from 2017 came from a research survey that used the same gear type but differed from the fishery methods from the previous period in having fewer sections of gear used in each set, and the amount of time the gear soaked in the water for was much less. Three long line fishing boats were sent out to 50 pre-determined locations along the coasts of Nova Scotia and Newfoundland and Labrador, around the Bay of Fundy, the Scotian Shelf, the Grand Banks, and the opening to the Saint Lawrence Channel (Figure 1). Data in 2017 were collected within a three-week period, from the end of June to mid-July, while during the fishery it was collected from early spring, extending into late fall.

Gear Description

A pelagic longline set consists of three main components: the mainline, the gangions and the hooks. Straight or offset J-hooks were attached to gangions that were clipped on the mainline, and the mainline was held at varying depths in the water column using weights and floats (Figure 2). A gangion consists of a strong rope attached to a metal leader that holds the hook. These gangions are used to attach the hooks to the mainline. One set of gear was divided into sections, with each section beginning and ending with a high flyer (a vertical, floating pole that is deployed in the water to locate the beginning and end of a submerged long fishing line), which was attached to the

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monofilament line with a piece of rope. In each section, gangions were attached to the mainline in groups of 11, separated by a float. The floats were set up so that there were two long floats (the float attached to the line with a long rope), a short float (the float attached to the line with short rope), then another two long floats. This was done so that the hooks could be deployed at different depths in the water column, and at different temperatures. On the 6th gangion of each grouping, a weight was added so that the gear would stay submerged. When the last high flyer was released, the set was allowed to sit in the water and "soak". To retrieve the gear, the boat would return to the first high flyer deployed and retrieve it, allowing the mainline to be hauled in.

Biological Measurements

During retrieval of the fishing gear, the sharks would be brought on board to be measured. In 2017, live animals were subsequently released back into the water, while dead animals were dissected, and internal observations were added to the external measurements. In 1999-2001, all porbeagle were landed, so all animals had internal measurements taken.

Data on fork length, and interdorsal length, both of which were measured in centimetres, sex, and maturity were collected from each captured porbeagle. To find fork length, the end of a measuring tape was placed at the tip of the snout and, over the curve of the body, extended to the fork in the tail. Interdorsal length was measured from the base of the first dorsal fin, underneath the free rear tip, to the origin of the second dorsal fin (Figure 3). Both interdorsal and fork lengths were measured to the nearest half centimetre. Sex could be determined by the presence (male) or absence (female) of claspers extending from the pelvic fins.

There were several characteristics that could be used to help determine the maturity of an individual, including length, clasper turgidity, and internal anatomy. If the individuals were small (< 150 cm) they were assumed to be immature, and the opposite was true for very large individuals (> 190 cm for males, and > 225 cm for females). The second method involved determining the turgidity of the claspers for the males was an indicator of maturity. There were three main stages of stiffness of the claspers: rubbery or plastic (both immature), or stiff (mature). However, the best method to determine maturity was to examine the internal reproductive anatomy of each individual. Mature males had evidence of sperm packets and well-developed testes. Mature females had follicles, a developed uterus and shell gland.

Data Analysis

All data compilation and analyses were done in R Studio1.0.153 (R Core Team 2017). Generalized linear models (GLM) were used to explain the data. To assess the factors that may influence length at 50% maturity, I constructed an additive model with year, sex and fork length as possible predictors of maturity. These data were fit using a GLM with a binomial error structure because maturity is binary (immature or mature). Length at 50% maturity for 1999 and 2017 (the two temporal extremes) were predicted for each sex from the fitted relationship. In addition, I examined the relationship between fork length and interdorsal length to determine if there was a difference in body shape between the two sexes and among years using a Gaussian GLM. All possible models were compared in an information theoretic framework (Akaike Information Criterion) to determine the model that best fit the data. Parameters that were retained in the best model were considered to be the best predictors of the data. The McFadden pseudo R^2 value was

also calculated to find the goodness-of-fit for the logistic models. These were used to explain the variability and to determine the improvement from the null model to a fitted model. Models are ranked between 0 and 1 (McFadden 1977).

Results

Length Distributions

Sample sizes consisted of 682, 128, and 20 individuals in 1999, 2000 and 2001 respectively, totaling 830 individuals for the pre-closure data. Minimum and maximum size varied among years for all sharks, but the smallest that was caught was 85.5 cm for males, and 94 cm for females, while the largest was 246 and 260.5 cm respectively, across all three, early years. In contrast, the post-closure (2017) of the fishery (further referred to as post-closure) population consisted of only 178 individuals, divided into the same groups as earlier (Tables 1 and 2). The minimum size for males was 74 cm, which was 11.5 cm smaller than the minimum of the pre-closure population, and for females was 72 cm, which was 22 cm smaller. For both males and females, the maximum length was 230 cm, which was 15 cm smaller for males and 30.5 cm smaller for females than before, in the pre-closure data.

Frequency distributions for males and females varied among years, as did sample size, with the most data concentrated in 1999 (Figure 4). The majority of males sampled in 1999 were between 160 to 180 cm FL, with a second peak at 200 to 210 cm. Similar distributions can be observed in 2000 and 2017 concentrated around and before the 200 cm bin, while 2017 males also have a peak around 160 to 180 cm that 2000 does not. For the females, fluctuating curve can be seen in the 1999 data set. It peaks at 140, 170, and

between 210 to 250 cm, indicating that there were larger fish sampled in that year. In 2000, most females sampled were between 110 and 150 cm, while in 2017, most were 80 to 90 cm, and 160 to 180 cm. Data in 2001 were too sparse to draw inferences.

The length distribution of the samples was not the same among years, differing the most between 1999 and 2017 (Figure 5). For females in particular, there were proportionately more small sharks sampled, making the average fork length lower in 2017 than in 1999. Males also showed a lower average fork length in the 2017 data.

Length at Maturity

The best model for describing how the probability of maturity changes with fork length included both sex and year as factors (Table 3). The calculated McFadden pseudo-R^2 value was 0.78. For each year, males and females matured at different fork lengths (Figure 6), as can be seen by the difference at 50% maturity. Looking solely at 1999 and 2017, as they were the two furthest apart temporally as well as the years with the most data, there is a change in predicted length at 50% maturity among the males and females (Figure 6). There was a decrease of 12 cm for males (174 to 162 cm) and 17 cm for females (217 to 200 cm) from 1999 to 2017, respectively. It could be seen that the model that best fit the data incorporated differences in year (Table 4 and 5). Data from 2000 and 2001 were not included in this comparison, as there were low proportions of mature individuals for those two years (Tables 1 and 2).

Body Shape

There was a difference in body shape between males and females, demonstrated by changes in interdorsal distance with fork length (Table 6). Using a Gaussian GLM to compare the data, the preferred model included sex as a factor, but not year (Table 6).

This shows that, in general, males have a smaller interdorsal length at a given fork length than do females (Figure 7). The McFadden pseudo R^2 is 0.47.

Discussion

Length Distributions

Sampling for fisheries research is expected to provide a representation of the total stock or population (King 2007). However, multiple factors can affect the representativeness of a sample, including selectivity of the sampling gear, measurement variations among samplers (King 2007, Punt et al. 2014), and differences in sampling area (Punt et al. 2014). In my data set, the discrepancy in sample sizes is due to a change in sampling effort among years. The pre-closure data was sampled from the directed fishery for porbeagle, which had a much higher sampling effort than the survey in 2017. This difference could be attributed to the number of vessels participating, the number of sets done per vessel, the duration of the fishery compared to the survey, as well as the soak time. While the 2017 survey used similar gear and bait as compared to the directed fishery, there were differences in locations and in soak time. During the fishery, fishermen could fish within Canada's Exclusive Economic Zone (EEZ), the 200 nautical mile limit which Canada has exclusive exploitation rights to, in the Bay of Fundy, on the Scotian Shelf and the Grand Banks, or even further out into the ocean, and would often leave the gear to soak for long periods of time, sometimes overnight, to increase the probability of catch. The post-fishery survey fished at specific locations which were distributed throughout the Canadian range of the species, with a soak time of four hours,

which would have been much less than that of the pre-closure. This reduction in time and space could have affected the total collected sample size.

The minimum lengths of males and females captured in 2017 were lower than they had been in previous years (Table 1). This is unlikely to be due to hook size or bait types because these would have been the same among years (Bowlby, H. pers. comm.), while it could result from sampling differences between pre- and post-closure of the fishery. Instead, the sharks could be catchable because of where fishing was occurring during the survey. The length distributions of the samples also varied among years (Figure 4). In 1999, the majority of males caught had lengths between 150 and 200 cm, whereas the females fluctuated more, with more individuals with lengths below 150 cm and above 210 cm being caught. This difference could be an indication of where males and females migrate during certain times of the year (Campana et al. 2015). In 2000, a greater number of larger males and smaller females being caught. The data collected in 2017 shows even more fluctuation when compared to data from 1999. Male length tended to be between 150 to 200 cm. Most females caught were below 100 cm in length, then more around 150 cm. These female individuals were not yet sexually mature. Females had a lower average length distribution between 1999 and 2017 (Figure 5b), which could be due to the low number of mature individuals measured in 2017. If the 1999 and 2017 length distributions are representative of the population in those years, these patterns may indicate that smaller females being recruited into the population. Alternatively, these trends could indicate sampling that was concentrated at temperatures which immature or mature porbeagle prefer (Jensen et al. 2002). These sharks are known to migrate up and down the Northwest Atlantic coast, as well as changing depth throughout the year (Aasen

1961). In spring and summer, porbeagle move north into waters surrounding Canada, and they tend to stay near the surface (Aasen 1961, Jensen et al. 2002). During the colder months, they tend to move southwards to the Sargasso Sea, as well as swimming at depths of around 200 m (Aasen 1961). Depending on the season that the sharks were being fished in, this could influence the size and numbers that were collected in a particular region.

Length at Maturity

Males and females mature at different lengths (Figure 6; Cassoff et al. 2007). This difference in fork length at maturity between the sexes is well known (COSEWIC 2014). Jensen et al. (2002), reported that length at 50% maturity for males was at 174 cm, and at 218 cm for females, using data collected between 1979 and 2001. These data are similar to the data collected from 1999 to 2001. However, length at 50% maturity in the post-closure data declined to 162 cm for males and to 200 cm for females (Figure 6). This reduction in size at maturity is consistent with a continuing downward trend in length at maturity, previously noted in Cassoff et al. (2007). This could have been caused by a large decline in abundance and high mortality due to the fishery. This decline in porbeagle length at maturity could represent increased growth and investment in reproduction in younger stages in response to the reduced population abundance (Heino et al. 2015). This early investment in reproduction could be an adaptive response to the high mortality rates during the fishery. One negative possibility of reproducing at smaller sizes when they first produce pups, is that the females are restricted by their size to produce and accommodate larger embryos (Cassoff et al. 2007) and would not be able to produce as many young. While not a large sample in 2017, the females also appear to

have declined in length at maturity. Although there has not been a previous observation of such decline (Cassoff et al. 2007), this could indicate a downward trend for females, as well as males. However, the data in 2017 did not have many mature females to be able to definitively indicate how strong the trend was. The amount of data that were collected in 1999 made up 67% of the total data collected, which had the potential to skew the age at maturity and sex relationship.

Body Shape

At a given interdorsal length, males have a slightly smaller fork length than females. Because males mature earlier than females, this difference could be due to the higher growth rate of females that continues after the male growth slows down. This trend could also be a result of the necessary optimal size and shape for reproduction in females (Hassell et al. 2012). While the reason for this relationship is largely unknown, one of these factors could be predation at a young age, meaning that they might grow differently than the females to reduce the risk. Although there is a similar predation risk associated with females, it has been found in other live-bearing fish, such as *Brachyrhaphis rhabdophora*, that female body shape will converge to reduce the chance of predation, while optimizing their body shape for reproduction (Hassell et al. 2012).

Future Directions

While the directed fishery has been closed for several years and porbeagle sharks are not being actively targeted, they are still susceptible to bycatch in other fisheries, including those that target groundfish, swordfish and tuna. Bycatch of individuals in the Northwest Atlantic population that live in the ocean surrounding Canada's EEZ is unregulated and unknown (Campana et al. 2015). The effects of bycatch could still be a

factor on the life history of the porbeagle, although catches are much reduced from those of the active fishery. Future work could focus on better determination of mortality rates associated with bycatch on Canadian vessels, and temporal patterns of maturity, and how it is affected by the current bycatch rates. These variations in the life history of the porbeagle could increase our understanding of how bycatch might effect the recovery potential of this shark species (Gibson and Campana 2005). Further investigation on how body shape differs between males and females could increase our knowledge concerning sexual dimorphism and the biological significance of growth with respect to sex. While other species of animals have been studied for their body shape, little focus has been given to sharks, and specifically the porbeagle. Possible ecological explanations for body size differences include predation (fishery), or the necessity of optimal size for bearing live young in females (Hassell et al. 2012).
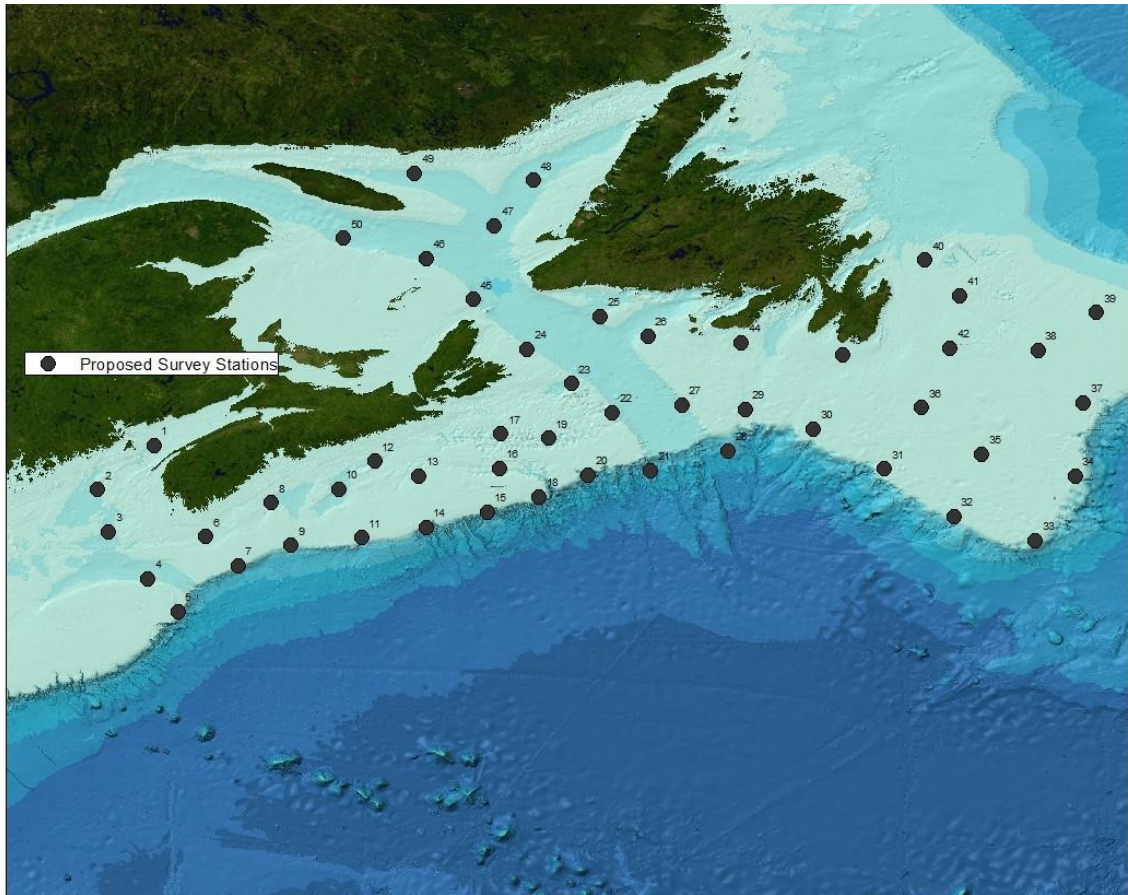
Figures and Tables

Figure 1. Map showing the 50 locations fished in the 2017 porbeagle survey. Locations were not fished in chronological order.
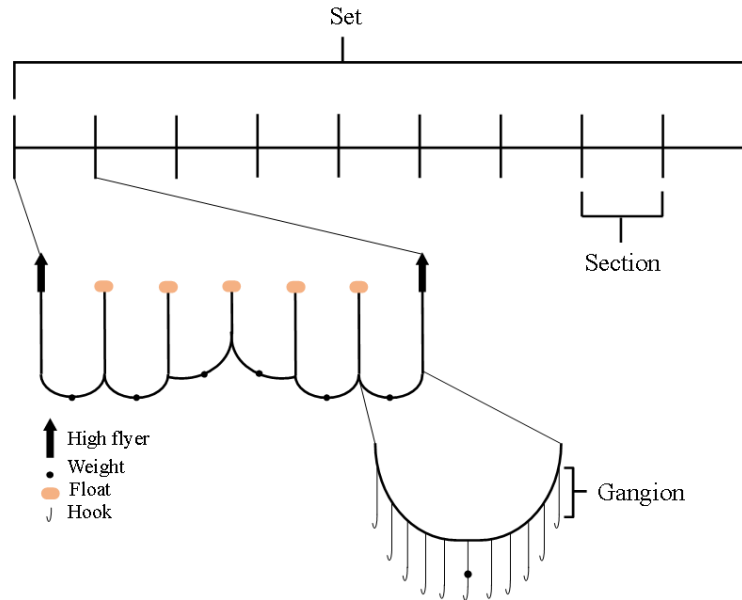
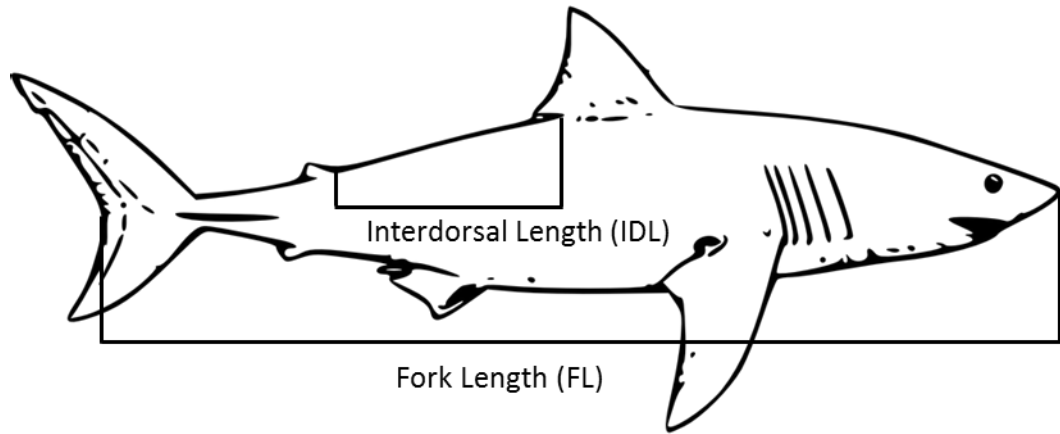Figure 2. Example of how long line fishing gear was deployed for the survey.

Figure 3. Diagram showing where the length measurements were taken. Fork length was taken over the curve of the body, from the tip of the nose to the fork in the tail. Interdorsal length was taken from under the free rear tip of the first dorsal fin to the origin of the second dorsal fin. Each measurement was taken to a half centimetre.
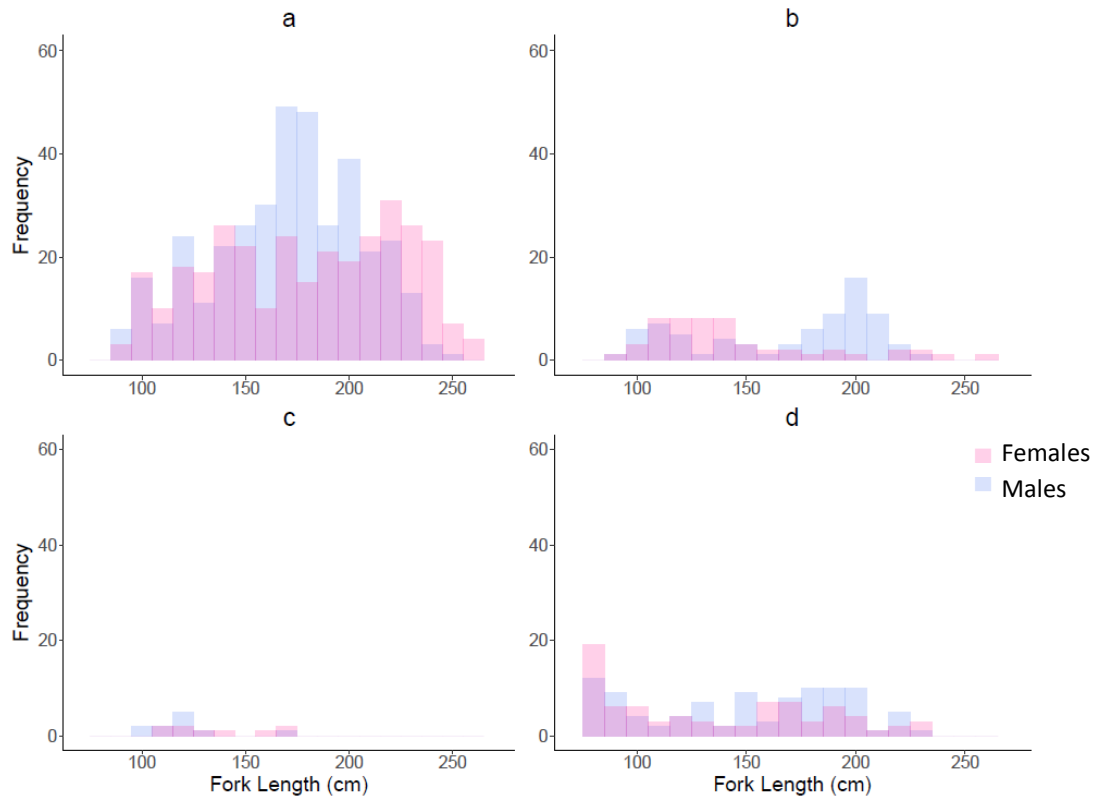
Figure 4. Length-frequency distributions of males and females across years, where a) 1999 b) 2000 c) 2001 and d) 2017. Individuals were organized in 5 cm bins. The dark pink shows where the two colours overlapped.
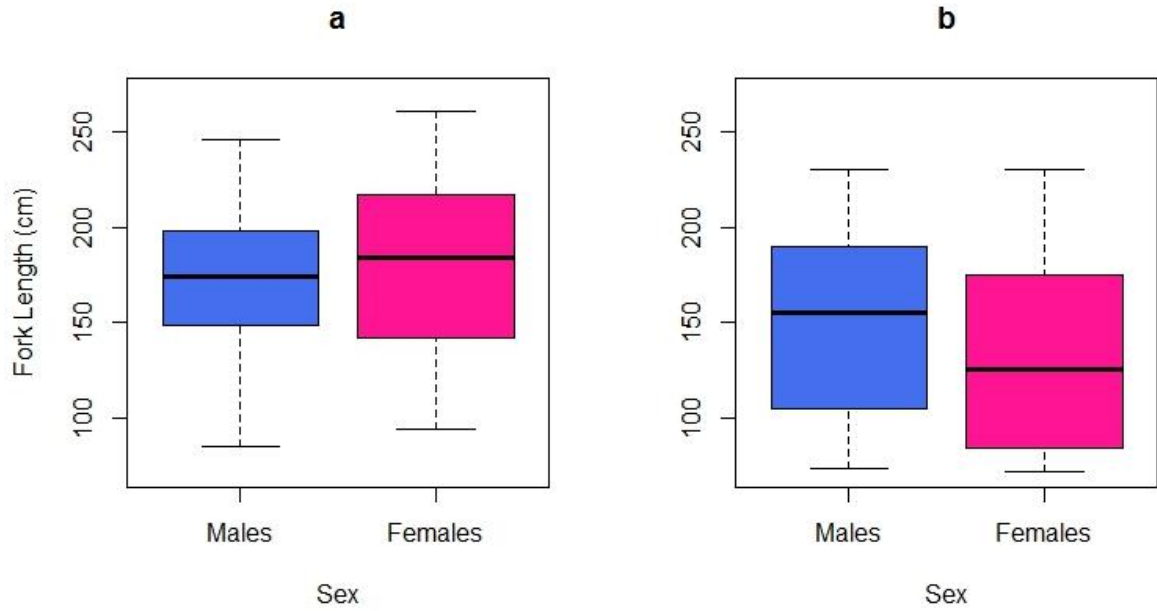
Figure 5. Boxplots showing the median, and 25th and 75th quartiles of the sampled fork lengths for males and females in a) 1999 and b) 2017. Years 2000 and 2001 are not shown due to lacking data.
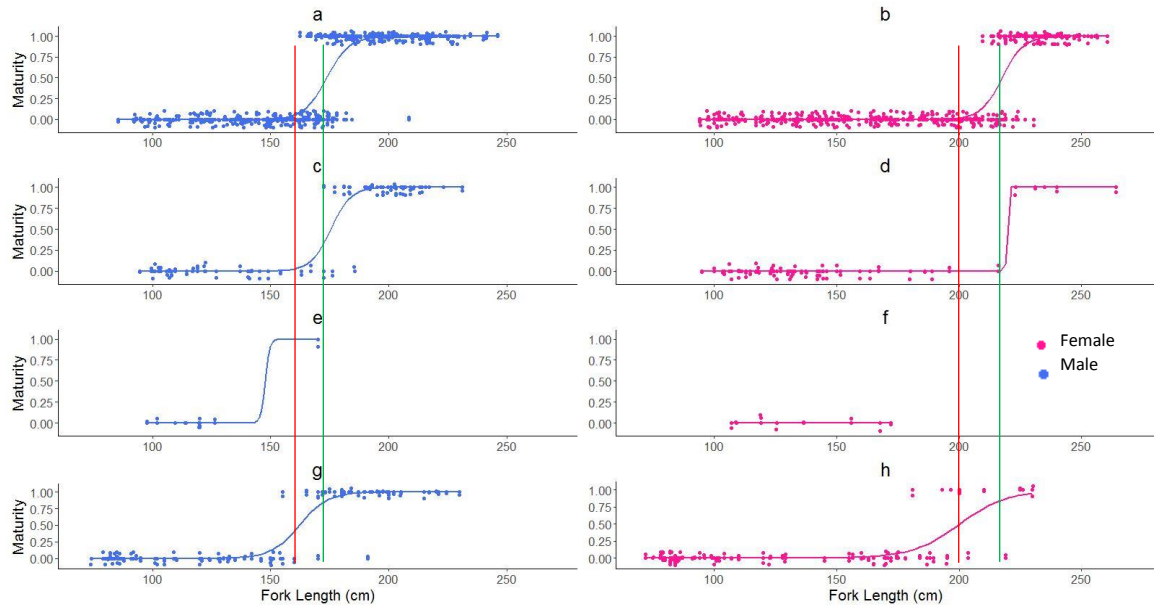
Figure 6. The predicted relationship between fork length at maturity for male (blue circle) and female (pink circle) porbeagle shark, based on a binomial GLM (curved lines) in a) 1999 males b) 1999 females c) 2000 males d) 2000 females e) 2001 males f) 2001 females g) 2017 males and h) 2017 females. Points are jittered to show individuals. Vertical lines show length at 50% maturity for 1999 (green) and 2017 (red).
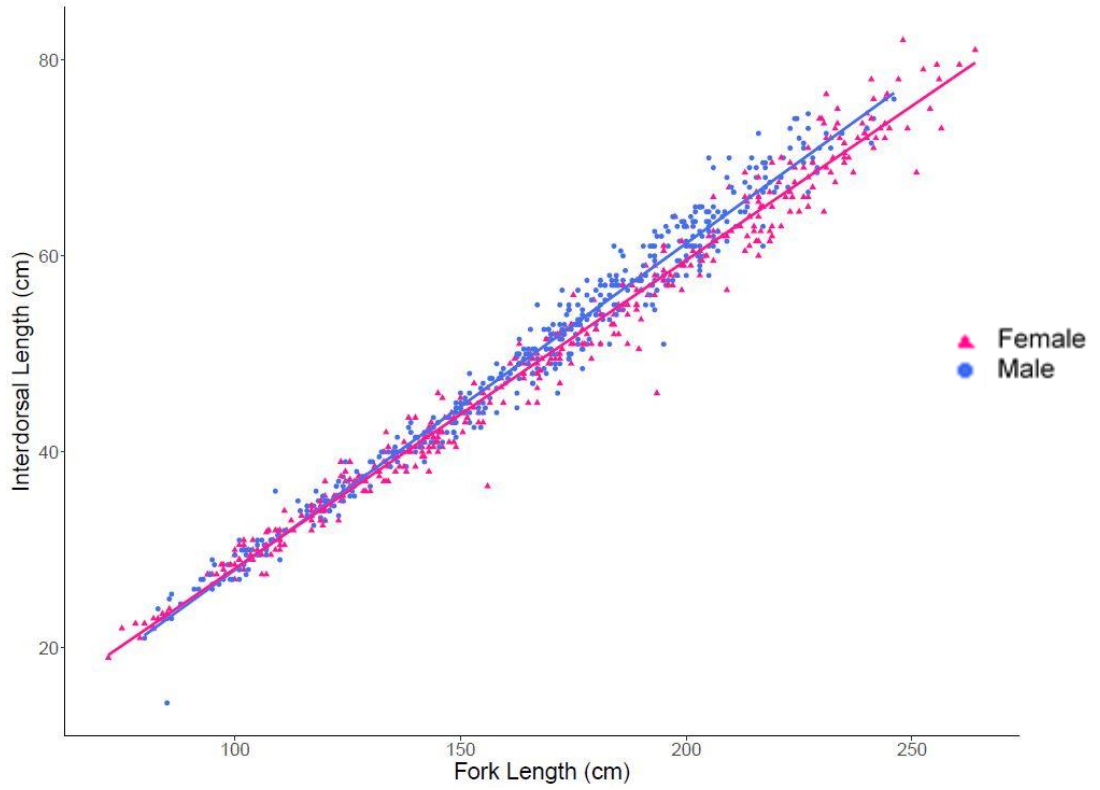
Figure 7. The predicted relationship between interdorsal length and fork length for male (blue circles) and female (pink triangles) porbeagle shark, based on a Gaussian GLM (lines) for all years.

Table 1. Summary of the male data used to analyse the pre-closure (1999-2001) and post-closure (2017) effects of the fishery on the Northwest Atlantic population of porbeagle (*Lamna nasus*).

Year	Sample Size			FL (cm)	
	Immature	Mature	Total	Min	Max
1999	184	181	365	85.5	246
2000	32	43	75	94.5	231
2001	10	1	11	97.5	170
2017	52	46	98	74	230
Total	278	271	549	-	-

Table 2. Summary of the female data used to analyse the pre-closure (1999-2001) and post-closure (2017) effects of the fishery on the Northwest Atlantic population of porbeagle (*Lamna nasus*).

Year	Sample Size			FL (cm)	
	Immature	Mature	Total	Min	Max
1999	235	82	317	94	260.5
2000	48	5	53	95	264
2001	9	0	9	107	172
2017	70	10	80	72	230
Total	362	97	459	-	-

Table 3. Model selection table of fork length to maturity among all years. The best model in this table shows that both sex and year are factors in determining a change in length at maturity. Models ranked by AICc, with the best being at the top. A '+' indicates that the argument is contained in the model.

FL	Sex	Year	df	logLik	AICc	delta	weight
+	+	+	6	-142.606	297.3	0.00	1
+	+		3	-159.311	324.6	27.35	0
+		+	5	-322.063	654.2	356.89	0
+			2	-331.960	667.9	370.64	0

Table 4. Model showing how length at maturity for males in 1999 and 2017 show significant differences at 50% maturity. This model was run solely with 1999 and 2017 data. Models ranked by AICc, with the best being at the top. A '+' indicates that the argument is contained in the model.

FL	Year	df	logLik	AICc	delta	weight
+	+	3	-81.101	168.3	0.00	0.997
+		2	-87.990	180.0	11.75	0.003

Table 5. Model showing how length at maturity for females in 1999 and 2017 show significant differences at 50% maturity. This model was run solely with 1999 and 2017 data. Models ranked by AICc, with the best being at the top. A '+' indicates that the argument is contained in the model.

FL	Year	df	logLik	AICc	delta	weight
+	+	5	-298.355	606.8	0.00	1
+		2	-309.944	623.9	17.12	0

Table 6. Model selection table of body shape, determined by the relationship between fork length and interdorsal length among all years. The best model used sex as a factor, but not year. Models ranked by AICc, with the best being at the top. A '+' indicates that the argument is contained in the model.

FL	Sex	Year	df	logLik	AICc	delta	weight
+	+		4	-1901.516	3811.1	0.00	0.928
+	+	+	7	-1901.027	3816.2	5.10	0.072
+			3	-1931.861	3869.7	58.67	0.000
+		+	6	-1931.156	3874.4	63.33	0.000

Acknowledgements

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