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LIFE HISTORY PARAMETERS OF BLUE SHARKS

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LIFE HISTORY PARAMETERS OF BLUE SHARKS

BY

KATHERINE VIDUCIC

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE

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MASTER OF SCIENCE

OF

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2018

ABSTRACT

The blue shark, *Prionace glauca*, is a pelagic elasmobranch that is found globally in tropic, sub-tropic, and warm temperate seas including the Mediterranean. Blue shark populations are not considered to be threatened, but a rapidly changing climate and uncertainties in fishing mortality are causing concern for changes in life history characteristics. Yet, no studies have examined such parameters for this species in over 35 years. We used 858 blue shark specimens, ranging from 1971 to 2016, to determine fork length, age, and weight at maturity, as well as measurements of reproductive organs (e.g., teste length, egg diameter) for both sexes. Males ranged from 62 to 300 cm and females ranged from 63 to 273 cm in fork length (FL). Ogives showed that males currently reach length at maturity (L_{50}) at 211.2 cm and weight (W_{50}) at 62.3 kg. Female blue sharks were smaller and lighter at maturity, with an L_{50} of 190.9 cm and W_{50} of 50.1 kg. Statistical models confirmed that L_{50}, W_{50}, and age at maturity all increased through time for males, while females showed only a significant increase in age at maturity and some organ measurements. Differences between individual reproductive organs for males and females were also present through time. These findings provide a current estimate of blue shark life-history parameters and demonstrate that there can be differential changes in life-history parameters between males and females through time.

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PREFACE

The following thesis has been submitted in manuscript format following the formatting guidelines of the journal *Fisheries Research*.

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CHAPTER 1

LIFE HISTORY PARAMETERS FOR THE BLUE SHARK (*PRIONACE GLAUCA*) IN THE NORTH ATLANTIC OCEAN

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Manuscript in preparation for *Fisheries Research*

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ABSTRACT

The blue shark, *Prionace glauca*, is a pelagic elasmobranch that is found globally in tropic, sub-tropic, and warm temperate seas including the Mediterranean. Blue shark populations are not considered to be threatened, but a rapidly changing climate and uncertainties in fishing mortality are causing concern for changes in life history characteristics. Yet, no studies have examined such parameters for this species in over 35 years. I used 858 blue shark specimens, ranging from 1971 to 2016, to determine fork length (FL), age, and weight at maturity, as well as measurements of reproductive organs (e.g., teste length, egg diameter) for both sexes. Males ranged from 62 to 300 cm and females ranged from 63 to 273 cm in FL. Ogives showed that males currently reach length at maturity (L_{50}) at 211.2 cm and weight (W_{50}) at 62.3 kg. Female blue sharks were smaller and lighter at maturity, with an L_{50} of 190.9 cm and W_{50} of 50.1 kg. Statistical models confirmed that L_{50}, W_{50}, and age at 50 % maturity increased through time for males, while females only showed a significant change in age at 50% maturity and organ measurements. Differences between individual reproductive organs for males and females were also present through time. These findings provide a current estimate of blue shark life-history parameters, which are critical for fisheries management in the context of multispecies food web models. Current results also demonstrate that there can be differential changes in life-history parameters between males and females through time.

1. INTRODUCTION

Marine species exhibit differences in life-history traits related to body size, reproduction, age, and growth (Cortes, 2008*)*. Intensive exploitation of marine fish has led to substantial changes in the life-history characteristics of populations that generally show increased growth rates and time to maturity (Greenstreet & Hall 1996; Jennings, Greenstreet and Reynolds, 1999). Large or slow-growing species with late maturity often decline in abundance more rapidly than their smaller and faster-growing counterparts (Jennings, Greenstreet and Reynolds, 1999). Thus, differences or changes in life-history traits over time can be used as an indicator to assess the exploitation of a species. Pelagic sharks are generally K-selected species with slow growth rates and late maturation and viviparous reproduction with few offspring. These life-history characteristics together with certain behavioral traits, such as the formation of aggregations, make them particularly vulnerable to overexploitation and thus changes in life-history traits (Pratt and Casey, 1990; Smith et al., 1998; Frisk et al., 2001; Dulvy et al., 2008). Yet, there is a poor understanding of how this is reflected in shark populations through time due to a lack of long-term data.

Abundance, size and age structure, and changes to life-history parameters may all be consequences of not only fishing, but also fluctuations in the physical and biotic environment. In other words, life-history impacts over time may be due to changing ocean temperatures, primary productivity, and/or currents (Brander, 1995; Blindheim and Skjoldal, 1993). For example, cod (*Gadus morhua*) have a weight-at-age relationship that has been shown to be highly temperature-dependent (Brander, 1995).

This ripples through the foodweb to also impact prey species of herring and capelin (Blindheim and Skjoldal, 1993). How environmental factors ripple through the ecosystem is difficult to untangle from fishing impacts, but life-history responses need to be evaluated in light of other physical and biotic changes taking place in the ecosystem. One example is from Ricker's (1981) study of changes in weight of Pacific salmon species. He concluded that there was evidence for reductions in weight from the 1950's onward that were attributable to size-selective fishing and not temperature or salinity. This is in contrast to McAllister and colleagues (1992) who showed that environment had a large effect on British Columbia pink salmon populations (*Oncorhynchus gorbuscha*).

The blue shark, *Prionace glauca,* is a pelagic elasmobranch that has circum-global distribution and occurs in tropic, sub-tropic, and warm temperate seas, including the Mediterranean (Bigelow and Schroder, 1948; Aasen, 1966; Nakano and Stevens, 2008). This species migrates throughout the North Atlantic Ocean (NA) (Compagno, 1984) and is considered the most abundant species among the pelagic sharks (Bigelow and Schroeder 1948, McKenzie and Tibbo, 1964). The blue shark is a placental viviparous species, with litters usually consisting of 25 to 50 pups after a gestation period of approximately 12 months (Pratt, 1979; Castro, 2011). Female blue sharks arrive on the continental shelf off southern New England in late May and early June to copulate with males (Pratt, 1979). The pupping season is thought to occur between March and July, and the apparent lack of "young of the year" (YOY) blue sharks off New England suggest an offshore pupping (Pratt, 1979). Different phases of their reproductive cycle have been shown to occur in different areas of the NA. There is strong evidence from tagging data and catch records that blue sharks in the NA constitute a single stock (Kohler et al., 2002).

The blue shark is not believed to be overfished in the NA, however, the International Commission for Conservation of Atlantic Tuna (ICCAT) acknowledges that there still remains a high level of uncertainty (SCRS, 2016). This uncertainty stems from the fact that there are no international catch quotas for pelagic shark species and reporting of shark catches by member nations is recommended, but not required (Campana, 2016). Blue sharks are the most frequently discarded fish species during commercial pelagic longline fishing operations worldwide (Campana et al., 2009). Several nations bordering the Atlantic Ocean specifically target blue sharks for their fins and meat (Mejuto et al., 2002; Neves dos Santos et al., 2001). Data reported by ICCAT shows that the estimated catches of the blue shark in the North Atlantic Ocean have increased between 1991-2015 (SCRS, 2016). The total NA catch of blue sharks reported to ICCAT in 2015 was 43,708 metric tons (NMFS, 2016). While blue shark populations are generally not considered to be threatened, it is not clear how uncertainties in fishing mortality may be impacting populations. Blue sharks experience a predictable recruitment rate similar to that of most other elasmobranchs due to late age at first reproduction and low numbers of offspring; therefore, there can be no rapid improvement to stock status once populations are depleted (Musick, 1999; Campana et al., 2015). Recovery times from even modest overfishing can be expected to take decades for many elasmobranch species, including blue sharks (Musick, 1999).

There is growing evidence that decades of size-selective harvesting has led to the reduction in body sizes of many species and that such artificial selection against large body size affects not only the targeted species but also the surrounding community (Fenberg and Roy, 2008). Such harvesting pressures coupled with changes in the environment and prey availability may be causing changes in life-history parameters for species such as the blue shark. Here, we question how life history parameters have changed over time. We hypothesized that blue sharks would reach length at maturity (L_{50}) at smaller fork lengths (FL) than previously found (Pratt 1979), as well as mature at earlier ages. We also hypothesized that these changes would also be reflected in the reproductive organs for both males and females.

2. METHODS

Blue sharks for this study were collected along the east coast of the United States and Canada from 1971 to 2016 through NMFS-APP. Specimens were obtained from cooperating commercial and recreational fishermen, and scientists on research vessels and at shark tournaments. Our samples included those used in the Pratt (1979) study, which were archived at NMFS-APP, and as well as new ones taken since that study. Sampling continuity was insured by using standardized techniques established by Pratt (1979). The primary sampler at NMFS-APP after H. Pratt was L. Natanson, who was trained by H. Pratt to ensure continuity in measurements. Additional samplers were trained by L. Natanson; data was only used after the sampler underwent rigorous training. If any measurement was in question, it was removed from the study using methods from Natanson and Gervelis (2013).

Data collected on each blue shark specimen included the location where it was caught, along with the sex of the individual. Fork length in centimeters (cm) was also measured (from the tip of the snout to the fork of the tail, over the curvature of the body) in the field following Kohler et al. (1996). Individuals were weighed (lbs) when possible and converted to kilograms (kg). All lengths from other studies converted to FL using the relationship equations from Kohler at al. (1996). Reproductive terminology follows Hamlett (1999) and Hamlett and Koob (1999).

For analyses to determine if life history parameters changed throughout time, samples were divided into discrete time periods (TP). These were:

TP1 = 1971- 1977

TP2 = 1978-2002

TP3 = 2003-2016.

TP1 data were collected and used for the Pratt (1979) study. TP2 data were collected with an overlap of Pratt and the current sampler L. Natanson. TP3 data were primarily collected by L. Natanson. Along with these logistical checks for sample processing accuracy, TP2 also allows several (n = 4) generations of blue sharks to turn over so that changes over time are observed from TP1 to TP3. TP 2 and TP3 allow for multiple generations to be observed in each time period.

2.1 REPRODUCTION

A detailed necropsy was performed on each individual to evaluate sexual maturity in both sexes. Organs on the right side of the body were used to ensure consistency and because only the right ovary is present and functional in female blue sharks (Pratt 1979). Organ measurements were taken in millimeters (mm).

External characteristics of the male blue shark included: degree of clasper calcification and rotation, and measurement of clasper length. The degree of clasper calcification was determined by firmness and classified as either soft, plastic, or hard. Clasper rotation was determined if there was easy rotation or resistance when clasper was manipulated. Clasper length was measured posterior to the free tip to the free trailing edge of the pelvic fin lateral to each clasper. The siphon sac, which lies between the skin and the body cavity, was measured by making a vertical incision forward of the proximal end of the clasper. Internal measurements included: testis length and width, epididymis width, and ampulla epididymis width. Testis weight (gm) was taken when possible. Presences or absence of sperm packets was noted; if present, the length and width of an average sperm packet was measured.

Female blue sharks were examined for the presence or absence of external mating scars or injuries. Internal measurements included: the width of the upper oviduct and oviducal gland, uterus width and length, and ovary width and length. The ovary was weighed (gm) when possible. If ovarian eggs were present, the width of the largest egg was measured and a rough count of like-sized eggs was obtained. The presence or absence of the vaginal membrane was determined by insertion of a probe. All measurements were taken from each individual when possible.

In general, maturity stage was determined during necropsy. However, in some cases maturity stage was not noted; for those samples maturity stages were assigned based on plots of organ measurement in relation to FL (Pratt, 1979). All reproductive organ measurements were plotted relative to body length or weight to evaluate if an inflection was shown in the data. An inflection in this relationship was assumed to represent size at 50% maturity (Jensen et al., 2002); however, if an inflection point was not observed then these measurements were eliminated from further maturity analysis.

2.2 MATURITY INDICIES

Maturity status was defined as immature, unknown, or mature for males. For females, maturity status was defined as immature, mature, gravid, postpartum, mature virgin, ovulating, or unknown. Status was determined by size and condition of reproductive organs (e.g., fully differentiated organ systems that are actively developing, embryos, or both with robust ovaries and the uterus when empty is long and flaccid). Unknown statuses were assigned for both male and female blue sharks when there was no clear determination of maturity. Specimens with an unknown maturity status were not used in ogive analyses but were kept in the scatterplots for visualization purposes and to represent sizes transitioning from immature to mature individuals. Males and females were categorized as either immature or mature for ogive analyses.

2.3 AGE

The 15th – 20th vertebrae were removed from each shark below the fifth gill arch for ageing (Skomal and Natanson, 2003). Vertebral samples were immediately transported to the lab, frozen and then thawed at a later date when ready to process. Vertebrae were thin-sectioned in a sagittal plane following the methods of Skomal and Natanson (2003).

To determine age, band pairs were counted from digital images of each section. Sections were immersed in water in a glass petri dish which was placed on a black background with reflected white light. Each section was photographed using a Nikon SMZ1500 stereomicroscope attached to a Nikon DSR12 camera. Magnification was adjusted based on the size of the vertebrae and noted in each photograph. Photographs were edited in Adobe Photoshop Elements to highlight and mark the band pairs.

2.4 BAND PAIR COUNTS

Inter-calibration between the primary reader K. Viducic (Reader 1) and G. Skomal (Reader 2) was undertaken to determine and ensure consistency in band pair count criteria. A band pair was defined as crossing the corpus calcareum through the intermedialia with contouring on the external surface, the first opaque band which shows an angle change of the band (Figure 1; Skomal and Natanson, 2003). To ensure correct interpretation of band pairs, readers simultaneously examined images from 48 sections from various sized individuals. Subsequently, both readers independently recounted the 48 vertebrae two times each.

Inter-reader comparisons were calculated using the second counts of both readers. Bias and precision was examined for counts of inter-calibration and intra-calibration using average percent error (APE; Beamish and Fournier, 1981), bias graphs (Campana et al., 1995), and three tests of symmetry (Bowker, 1948; McNemar, 1947; Evans and Hoenig, 1998; McBride et al., 2014). Coefficient of variation (CV; Chang, 1982) was also calculated; a less than 10% difference between readers was assumed precise and showed that definition of criteria was maintained (Natanson et al., 2018).

After the inter-reader calibration, Reader 1 counted all the vertebrae in this study three times. Bias calculations were conducted on counts 2 and 3 (K2, K3) and final ages were based on count 3. All calculations where conducted in R and (R Core Team, 2017; FBP: Precision Templets for Calculating Ageing Precision, 2017). For the purposes of this study, band pairs are assumed to deposit annually based on the OTC information from Skomal and Natanson (2003). However, with recent information suggesting that this relationship may not persist in larger specimens (Natanson et al., 2018), we understand that annual deposits may represent a bias in the results for the larger specimens.

2.5 STATISTICAL ANALYSIS

To determine 50% maturity of blue sharks, ogives were derived using direct ages, FL, weight, and organ measurements associated with reproductive condition of mature and immature specimens. Measurements of 50% maturity for both males and females were derived using a generalized linear model with a binomial distribution and logit link function. Binomial distributions with logit link functions are suitable for data that is either “yes” or “no”, or in this case, mature or immature (Zuur et al. 2009). The differences in ogives by time period were calculated using generalized linear models (GLM) and organ models were calculated based on generalized additive models (GAM). Model fit was evaluated based on Akaike Information Criterion (AIC_c; Burnham and Anderson, 2002). The best fitting model was considered to be the model with the lowest AIC_c value. The AIC_c difference between each model (Δ_i) was calculated by $\Delta_i = AIC_{c,i} - AIC_{c,min}$ (Burnham and Anderson 2002). The models with values of $\Delta_i \leq 2$ showed that there was no evidence of a statistical difference between time periods. Models with Δ_i values >10 are indicative of poor fit relative to the best fitting model and are generally unsupported. If the AIC_c value had a difference $\Delta_i > 2$ then there was a statistical difference between time periods and changes are occurring over time in the maturity. All models were examined for normality using residual plots to detect for violation of independence or mean-variance assumptions. All models were fit using the *mgcv* package (Wood 2011) in R (R Core Team, 2017.)

3. RESULTS

A total of 858 specimens were used in this study and vertebra were collected from 188 of these samples. No vertebral samples from TP1 were available, therefore vertebrae from TP2 and TP3 were used to determine age (Table 1). Blue sharks were collected mainly in June and July, though samples were collected year-round (Table 2). Recreational fishermen at shark fishing tournaments caught the majority of sharks, 66.6%, commercial fishermen caught 23.4%, scientists on research vessels collected 8.7%, and 1.3% were collected by unknown sources. Using data from this study we were able to define criteria to determine maturity status for both sexes from individual measurements and condition.

3.1 MALE MATURITY INDICATORS

There was a significant difference in both the L_{50} and W_{50} between all three time periods (Table 3; Table 4). Results of ogive comparisons between TP1, 2, and 3 showed a statistically significant increase in FL, WT, and age at maturity (Table 3). Additionally, significant differences were found between all three TPs in all organ measurements except left clasper length (Table 3; Table 5). Therefore, measurements for TP3 are used as current maturity indicators as this is the most recent data that represents the current population.

Based on TP3, clear inflections were seen in the relationships between FL and left clasper length while the epididymis width and teste length showed a more gradual change in size with FL (Figures 2, 3, 4). The point at which 50% of the specimens were mature in males was 211.2 cm FL (L_{50}) (Figure 5) and 62.3 kg (W_{50}) (Fig. 6). The smallest mature fish in this study was 181.0 cm FL and the largest immature is 220.5 cm FL. The smallest mature fish and largest immature in TP3 was 209.3 cm FL and 220.5 cm FL, respectively. This created a range in which sharks can be considered as transitional where there is an overlap of immature and mature fish.

Immature males in this study ranged from 62 to 220.5 cm FL. Mature males ranged from 181 to 300 cm FL. In TP3, immature sharks ranged in FL from 64.7 to 220.5 cm. Mature sharks in TP3 ranged in FL from 194 to 300 cm. Immature males had underdeveloped claspers that appeared to be uncalcified or “plastic,” while mature males had fully calcified clasper. However, in some cases where mature males had claspers which appeared to be plastic, the measurements of reproductive organs were taken into consideration to determine maturity. Mature males with plastic claspers were observed mostly in June (N=17) with only one to three found in each month from March – May and July – November. In these cases, where claspers were found to be plastic, the measurements of the epididymis and teste length were also taken into account to assign maturity: left clasper length at 50% maturity was 124.6 mm; epididymis width and teste length were 19.1 and 136.9 mm, respectively (Table 6).

3.2 FEMALE MATURITY INDICATORS

Results of ogive comparisons between time periods showed no significant difference between the L_{50} and W_{50} (Table 7; Table 8). However, statistical differences were calculated in four out of seven of the organ measurements used as maturity indictors (Table 7; Table 8). Due to no significant statistical differences in L_{50} and W_{50}, data from all time periods were combined and used in all analyses (Table 7).

Clear inflections were observed between FL and egg diameter, oviducal gland width, uterus width, and oviduct width (Figures 7 - 10). Gradual inflections were seen between FL and ovary width, ovary length, and uterus length (Figures 11 – 13). Females reached L_{50} at 190.9 cm FL (Figure 5) and W_{50} 50.1 kg (Figure 6). The largest immature fish was 206.0 cm FL and the smallest mature 173.0 cm FL. This created a range in which sharks can be considered as transitional where there is an over lap of immature and mature fish.

Female maturity is as described by Pratt (1979) as:

> *"They possess fully differentiated organ systems that are actively developing eggs, embryos, or both. The ovary is robust … the oviducal gland is large and heart- shaped with the anterior horns slightly coiled. The uterus when empty is long and flaccid."*

Only one mature female had an internal membrane (hymen). Immature females in this study ranged in FL from 63.1 cm to 206.0 cm and mature ranged from 173.0 cm to 273 cm. The measurement of 50% maturity of all organ measurements fell within the transitional zones (Table 6). Ovary length, oviducal diameter, and uterus diameter showed significant differences over time. Ovary length at which females reached 50% maturity increased from TP1 (183.6 mm) to TP3 (213.5 mm), while oviducal diameter decreased in size from TP1 (28.6 mm) to TP3 (25.0 mm) (Table 7; Table 10). Uterus length increased drastically from TP2 (274.0 mm) to TP3 (405.6 mm) (Table 7; Table 10). However, due to the elasticity of the uterus as it is stretched during pregnancy this measurement is highly variable.

3.3 BAND PAIR COUNTS

Inter-calibration indicated that both readers were following the same criteria. The APE (7.22) was in an acceptable range and although the CV (10.21) is slightly high, it was within 10. Bias data was on the 1:1 ratio until the larger counts (>11) which can be attributed to small sample sizes of these ages. (Figure 14). Tests of symmetry showed significant differences between counts in McNemar (1947; $\chi^2 = 9.78$, $df=1$, $n= 48$, $p= 0.0018$) and Evans and Hoenig (1998; $\chi^2= 10.0$, $df=3$, $n= 48$, $p= 0.019$) while Bowker (1948) unpooled method was found to be insignificant ($\chi^2=19.8$, $df=12$, $n= 48$, $p= 0.071$).

Intra-reader bias values were lower than inter-reader values, however, significant differences were still observed in tests of symmetry. Both the APE and CV were within acceptable range (4.32 and 6.11, respectively) indicating that definition of criteria was maintained. No bias was detected in the bias graph (Figure 15). Tests of symmetry showed significant differences between counts in McNemar (1947; χ^2=11.85, *df*=1, *n*= 188, *p*= 0.00058) and Evans and Hoenig (1998; χ^2=15.86, *df*=3, *n*= 188, *p*= 0.0012) while Bowker (1948) was insignificant (χ^2=30.25, *df*=20, *n*= 188, *p*= 0.066).

The results of the APE, CV, bias analysis, and Bowker's (1948) test of symmetry suggest that criteria are being maintained by both readers and within reader counts. However, McNemar (1947) and Evans and Hoenig (1998) tests show significant differences. All three tests of symmetry are sensitive to small changes. McNemars (1947) method is sensitive to small differences if there are many cells where differences accumulate which is the case ibn the current study. The Evans and Hoenig (1998) test shows that slightly more bands were counted on K3 versus K2, however, this is not observed in the bias graphs. Since the majority of tests showed no bias and both tests that showed bias had inherent issues, we chose to accept the counts from K3 for further analyses.

A significant difference is observed in age at 50% maturity over TPs 2 and 3 in both sexes (Table 3; Table 4; Table 7; Table 8). Male blue sharks were found to mature at 5.8 years in TP2 and in increased by 2.8 years to 8.6 years in TP3 (Table 3; Figure 16). Females reach 50% maturity at 5.0 years in TP2 and increase significantly to 11.0 years (Table 7; Figure 16). Due to both sexes having significant differences in age at 50% maturity between time periods current age at maturity age estimates are based on TP3.

4. DISCUSSION

Our 45-year dataset in this study allowed us to test hypotheses that changes in life-history parameters are occurring over time for blue sharks. We found evidence to support this, leading to the observation that differential changes have occurred in males and females. In particular, males currently reach length at maturity (L_{50}) at 211.2 cm and weight (W_{50}) at 62.3 kg, whereas females were 190.9 cm and 50.1 kg at L_{50} and W_{50}, respectively. Statistical tests confirmed that L_{50}, W_{50}, and age at maturity increased through time for males, while females only showed a significant change in age. Differences in individual reproductive organs for males and females were also present through time.

Despite their long evolutionary history, elasmobranchs are facing new and substantial anthropogenic threats including climate change and fisheries interactions, which cause acute and chronic stress that may exceed levels typically imposed by natural events (e.g., seasonal habitat changes, predator avoidance) (Skomal and Bernal, 2010). Blue sharks seem to prefer layers of waters from 12°-21°C (McKenzie and Tibbo 1964, Gubanov and Grigor’yev 1975, Sciarotta and Nelson 1977, Casey 1982, Nakano 1994, Nakano and Nagasawa 1996) but have been caught in oceans with sea surface temperatures ranging from 8° to 29.5°C (Gubanov and Grigor’yev 1975, Casey and Hoenig 1977, Nakano 1994, Castro and Mejuto 1995, Nakano and Nagasawa 1996), showing that slight temperature changes will not greatly affect the blue sharks’ distribution, however it can alter the movement patterns based on prey availability. Blue sharks consume cephalopods as a primary component of their diet (Strasburg, 1958; Tricas, 1979; Stevens, 1984; Kohler, 1987), along with various species of locally abundant pelagic and demersal teleosts as well as marine mammals and elasmobranchs (Bigelow and Schroeder, 1948; LeBrasseur, 1964; Stevens, 1973; Harvey, 1979; Kohler, 1987).

Density-dependent compensation potentially plays an important role in a population's ability to sustain or recover from fishing mortality (Natanson et al., 2014). Some researchers suggest sharks have the ability to compensate life history traits in response to stress induced by fishing or other pressure (Carlson and Baremore, 2003). However, only a few cases of density-dependent compensation have been empirically described for sharks and are most species are poorly understood (Cortés, 1998; 1999; 2007; Walker, 1998). Growth reportedly increased in both juvenile sandbar sharks, *Carcharhinus plumbeus*, in the NA (Sminkey and Musick, 1995) and Atlantic sharpnose sharks, *Rhizoprionodon terraenovae*, in the Gulf of Mexico (Carlson and Baremore, 2003) following fishery-induced decreases in abundance (Natanson et al., 2014). The ability to compensate for harvest-induced changes has important implications for the regulation and sustainability of populations (Johnson and Post, 2009). However, it seems that the blue shark does not have the need to compensate for pressures from fishing or other factors based on the the fact that the blue shark is not believed to be overfished in the NA (SCRS, 2016), as well as from the results of this study showing that the blue shark is not maturing at smaller sizes or earlier ages.

The L_{50} values for males in this study were generally higher than those found in other studies on blue sharks (Table 11). For example, Hazin and Lessa (1994, 2005) in the South-Western Atlantic calculated males reached $L_{50\ \mathrm{at}}$ 188.4 cm FL. Female size at L_{50} (190.9 cm) for this study in the Northern Atlantic was the same value found by Hazin and Lessa (2005) in the South-Western Atlantic Ocean, otherwise, our NA female L_{50} was generally smaller than those from other areas (Table 11).

Differences in the growth rates (k) between the same species of sharks have been found both regional (i.e. the blacknose sharks, Carcharhinus acronotus, in the Gulf of Mexico vs the western North Atlantic; Driggers et al., 2004) and oceanic (i.e. the porbeagle) in the western North Atlantic vs the South Pacific (Francis et al., 2008). Thus, it is not surprising that differences exist in the blue shark between oceans. These variations could be due to food availability, water temperature or salinity.

There was also an increase in L_{50} for female blue sharks between Pratt (1979) and the total L_{50} calculate herein. I reanalyzed the Pratt (1979) data designating the subadults as immature and produced an estimate of 190.6 cm as compared to Pratt’s original L_{50} of 185.0 cm. The L_{50} that was estimated in TP1 (190.6 cm) is statistically the same as the whole period of 190.9 cm. Differences in the 50% maturity of four female reproductive organs are showing that female blue sharks are undergoing changes overtime even though it has not been observed in the L_{50} and W_{50}. Measurement differences in uterus length, oviducal diameter, and ovary length may be the beginning to changes in life history parameters such as L_{50} and W_{50} males underwent.

Age at 50% maturity was higher in this study than in Pratt (1979) in both male and female blue sharks 8.6 and 11.0 years respectively. This differs from Pratt (1979), where it was estimated that blue sharks of both sexes mature at around 4 to 5 years old. Without having vertebrae from TP1 I were not able to make a direct comparison to the ages found by Pratt (1979). Pratt also did not directly age from vertebrae to assign an ogive that could also explain the differences.

It is common to process vertebrae using the methods in this study, but there are other methods used across different oceans (i.e. such as x-ray or whole vertebrae analysis). Differences in ages across other studies could be due to the preparation or experience of readers (Officer et al., 1996). Francis and Maolagain (2016) concluded that they were unable to assign ages in their study do to the amount of variability among readers. In a study by Skomal and Natanson (2003), the annual band pair deposition in blue sharks was validated up to 4^+ years in age using vertebrae from two oxytetracycline (OTC) injected fish. It was then assumed that the band pair deposits can show annual growth in immature fish to a certain point. However, the accuracy of band pair counts has come into question. In Natanson et al. (2018), band pairs in correlation to body size was investigated between seven different species of sharks, including the blue shark. Band pair counts varied along the vertebral columns in all but the smallest blue shark (Natanson et al., 2018); suggesting that band pair ages may not be appropriate throughout life for this species. However, variation in the blue shark was within 2 band pair counts which is not seen as a significant difference compared to other species of sharks in this study.

Marine fishes and invertebrates respond to ocean warming through distribution shifts, generally to higher latitudes and deeper waters (Cheung et al., 2013), resulting in possible migration pattern shifts in blue sharks that follow preferred food sources. Ocean climate trends indicate that temperature in the Northwest Atlantic Shelf warms at a rate nearly three times faster than the global average; this enhanced warming is accompanied by an increase in salinity due to a change in water mass distribution (Saba et al., 2016). Temperature and salinity increases may influence blue shark prey species, or influence other predator prey interactions. Blue sharks mainly consuming cephalopods, where it was found that sea–bottom temperature was closely linked to the extent of squid movement (Sims et al., 2001). Sea surface temperature increased during the 20th century and continues to rise. From 1901 through 2015, temperature rose at an average rate of 0.13°F per decade (EPA, 2016).

In addition to temperature changes and the availability of prey, blue shark life history traits may be influenced by size-selective harvesting. The mechanisms used by commercial, recreational and artisanal fisheries and hunters to preferentially remove large individuals are almost as diverse as the number of species affected by such harvesting practices (Fenberg and Roy, 2008). For example, commercial fisheries tend to select larger fish through the use of different kinds of fishing gear such as trawls and gillnets (based on mesh size), longlines and trap nets (Bohnsack et al. 1989; Policansky, 1993; Dahm, 2000; Law, 2000; Fenberg and Roy, 2008). Another example is recreational fisheries and shark tournaments that target large sharks as trophies and highly valuable. In general, selective harvesting of some species can increase the growth rate, size and abundance of other nonharvested species as well because of release from competitive pressure (Godoy & Moreno, 1989; Lindberg et al., 1998; Guidetti et al., 2004; Fenberg and Roy, 2008). Blue sharks are typically not the target in most fisheries because of the pliability of their meat and they share an environment with more valuable species.

The results of this study have shown that changes have taken place in the relationship of reproductive parameters and maturity of the blue shark. Males have seen a significant increase in FL and the main reproductive organs except for claspers over time periods as well as WT. The results from this study show that males are increasing in size at maturity through time. While female FL and WT have showed no change over time. Future research should investigate the mechanisms driving these changes such as temperature, fishing pressure, or changes in migration.

ACKNOWLEDGMENTS

Thank you to all the participants of shark tournaments over the years as well as cooperating fishermen for allowing the NOAA-National Marine Fisheries Service to sample their landed blue sharks over the years. I would like to thank every one past and present in the Apex Predators Program for all of their help on the blue shark projects throughout the years. Thank you to my committee members Drs. Graham Forrester and Terry Bradley for providing comments and suggestions that improved the manuscript. A special acknowledgement to those who have helped me with this project, especially Dr. Greg Skomal and Megan Winton. Thank you to everyone at the NOAA-National Marine Fisheries Service Lab, especially Dr. Nancy Kohler, Brian Gervelis, Cami McCandless, Kelsey James, and Kate Woolley. Thank you to Wes Pratt for initiating the blue shark project and for all of the data he collected over the years.

TABLES

Table 1: Sample data on sharks collected for this study including ranges in fork length (FL) in centimeters (cm) over time periods as well as the type of samples provided.

	Sample Type	TP1 Size Range (cm)	TP2 Size Range (cm)	TP3 Size Range (cm)	TP1-3 Size Range (cm)
Males	Reproductive Organs	102-279 (n=155)	62-285 (n=110)	64.7-300 (n=224)	62-300 (n=489)
	Vertebra for Ageing	n/a	62-282 (n=32)	64.7-298 (n=65)	62-298 (n=97)
Females	Reproductive Organs	108-263 (n=183)	114-273 (n=76)	63-257 (n=110)	63 – 273 (n=369)
	Vertebra for Ageing	n/a	114-273 (n=26)	63-232 (n=65)	63-273 (n=91)

Table 2: Sample sizes of when blue shark specimens were caught.

	Males (n=490)	Females (n=369)
January	0	1
February	2	4
March	8	8
April	3	4
May	44	5
June	176	112
July	150	69
August	29	32
September	47	66
October	25	64
November	5	4
December	1	0

Table 3: 50% maturity of fork length (FL), weight (WT), age, and reproductive measurements over time periods of male blue sharks. * indicate if a statistical difference ($p < 0.05$) between measurements was observed over time.

	50 % Maturity All Time Periods	50 % Maturity Time Period 1	50 % Maturity Time Period 2	50 % Maturity Time Period 3
Left clasper (mm)	112.8	105.7	116.6	124.6
Epidyimis width (mm)*	18.4	18.6	17.0	19.1
Teste length (mm)*	133.7	130.7	130.2	136.9
Fork length (cm)*	192.5	184.1	199.8	211.2
Weight (kg)*	48.6	35.6	40.2	62.3
Age (years)*	8.0	N/A	5.8	8.6

Table 4: Relative fit of model for male parameters, models are ranked from best- to worst-fitting. edf = total model estimated degrees of freedom;; AIC = Akaike information criterion; Δ = AIC difference.

Males				L_{50}				W_{50}			Age
Model	edf	AIC	Δ_i	Model	edf	AIC	Δ_i	Model	edf	AIC	Δ_i
matstatus(fork*TP)	6	115.48	0	matstatus(weight*TP)	6	103.03	0	matstatus(age+TP)	3	63.09	0
matstatus(fork+TP)	4	119.32	3.84	matstatus(weight+TP)	4	119.32	16.29	matstatus(age*TP)	4	63.5	0.41
matstatus(fork)	2	190.83	71	matstatus(weight)	2	138.72	19.4	matstatus(age)	2	68.35	4.85

Table 5: Relative fit of model for male organ parameters, models are ranked from best- to worst-fitting. edf = total model estimated degrees of freedom;; AIC = Akaike information criterion; Δ = AIC difference.

Males	Left clasper			Teste length				Epididymis width			
Model	edf	AIC	Δ	Model	edf	AIC	Δ	Model	edf	AIC	Δ
leftclasper~s(fork)+TP	11.01	3283.94	0	testelength~s(fork)+TP	7.57	2983.54	0	epididymiswidth~s(fork)+TP	8.88	1991.52	0
leftclasper~s(fork)	9.01	3285.66	1.72	testelength~s(fork)	6.11	2987.89	4.35	epididymiswidth~s(fork)	7.32	2019.8	28.28
leftclasper~s(fork,by=TP)	9.59	4007.84	722.18	testelength~s(fork,by=TP)	7.48	3056.26	68.37	epididymiswidth~s(fork,by=TP)	7.88	2074.16	54.36

Table 6: Maturity indices of male reproductive organs that show the size range of maturity statuses and size at 50% maturity.

	Maturity Status	Size (mm)	Size at 50% Maturity (mm)
Left clasper	Immature	≤ 115	
	Uncertain	> 115 - < 135	124.60
	Mature	≥135	
Epididymis width	Immature	≤ 15	
	Uncertain	> 15 - < 24	19.10
	Mature	≥ 24	
Teste length	Immature	≤ 126	
	Uncertain	> 126 - 176	136.92
	Mature	≥ 176	

Table 7: 50% maturity of fork length (FL), weight (WT), age, and reproductive measurements over time periods of female blue sharks. * indicate if a statistical difference ($p < 0.05$) between measurements was observed over time.

	50 % Maturity All Time Periods	50 % Maturity Time Period 1	50 % Maturity Time Period 2	50 % Maturity Time Period 3
Ovary length (mm)*	188.9	183.6	186.1	213.5
Ovary width (mm)	61.1	50.2	65.2	59.3
Egg diameter (mm)	10.6	11.0	10.0	9.1
Oviducal gland width (mm)*	29.0	28.6	29.0	25.0
Uterus width (mm)*	28.1	27.2	30.2	19.6
Uterus length (mm)*	400.0	N/A	274.0	405.6
Oviduct width (mm)	8.3	N/A	7.9	9.7
Fork length (cm)	190.9	190.6	191.8	189.8
Weight (kg)	50.0	50.8	52.3	43.5
Age (years)*	8.8	N/A	5.0	11.0

Table 8: Relative fit of model for female parameters, models are ranked from best- to worst-fitting. edf = total model estimated degrees of freedom;; AIC = Akaike information criterion; Δ = AIC difference.

	L_{50}				W_{50}				Age		
Model	edf	AIC	Δ_ι	Model	edf	AIC	Δ_ι	Model	edf	AIC	Δ_ι
matstatus(fork)	2	89	0	matstatus(weight)	2	67.35	0	matstatus(age*TP)	5	24.48	0
matstatus(fork+TP)	4	92.83	3.83	matstatus(weight*TP)	6	68.32	0.97	matstatus(age+TP)	4	25.54	1.06
matstatus(fork*TP)	6	94.64	1.81	matstatus(weight+TP)	4	69.3	0.98	matstatus(age)	2	74.97	49.43

Table 9: Maturity indices of female reproductive organs that show the size range of maturity statuses and size at 50% maturity.

	Maturity Status	Size (mm)	Size at 50% Maturity (mm)
Ovary length	Immature	≤ 136	
	Uncertain	< 136 - >240	188.89
	Mature	≥ 240	
Ovary width	Immature	≤ 40	
	Uncertain	< 40 - > 80	61.11
	Mature	≥ 80	
Egg diameter	Immature	≤ 6	
	Uncertain	> 6 - <16	10.62
	Mature	≥ 16	
Oviducal gland width	Immature	≤ 22	
	Uncertain	> 22 - < 35	29.09
	Mature	≥35	
Uterus width	Immature	≤ 22	
	Uncertain	> 22 - < 35	28.06
	Mature	≥ 35	
Uterus length	Immature	≤ 280	
	Uncertain	> 260 - < 540	400.02
	Mature	≥ 540	
Oviduct width	Immature	≤ 5	
	Uncertain	> 5 - < 12	8.36
	Mature	≥12	

Table 10: Relative fit of model for female organ parameters, models are ranked from best- to worst-fitting. edf = total model estimated degrees of freedom;; AIC = Akaike information criterion; Δ = AIC difference.

Females	Ovary length			Ovary width			
Model	edf	AIC	Δ_i	Model	edf	AIC	Δ_i
ovarylength~s(fork)+TP	6.94	1775.16	0	ovarywidth~s(fork)	5.39	1207.56	0
ovarylength~s(fork)	4.6	1787.94	12.78	ovarywidth~s(fork)+TP	7.43	1207.66	0.1
ovarylength~s(fork,by=TP)	5.77	1825.32	37.38	ovarywidth~s(fork,by=TP)	6.92	1267.66	60

Egg diameter				Oviducal gland width			
Model	edf	AIC	Δ_i	Model	edf	AIC	Δ_i
eggdiameter~s(fork)+TP	7.63	1290.66	0	oviducalglandwidth~s(fork)+TP	10.1	1490.92	0
eggdiameter~s(fork)	5.66	1291.75	1.09	oviducalglandwidth~s(fork)	7.88	1530.48	39.56
eggdiameter~s(fork,by=TP)	5.51	1451.28	159.53	oviducalglandwidth~s(fork,by=TP)	7.6	1760.93	230.45

Uterus width				Uterus length			
Model	edf	AIC	Δ_i	Model	edf	AIC	Δ_i
uteruswidth~s(fork)+TP	10.05	2032.94	0	uteruslength~s(fork)+TP	8.01	969.69	0
uteruswidth~s(fork)	7.97	2050.28	17.34	uteruslength~s(fork)	5.88	970.07	0.38
uteruswidth~s(fork,by=TP)	6.26	2477.65	427.37	uteruslength~s(fork,by=TP)	8.92	976.82	6.75

Oviduct width			
Model	edf	AIC	Δ
oviductwidth~s(fork)	6.45	444.05	0
oviductwidth~s(fork)+TP	7.47	445.52	1.47
oviductwidth~s(fork,by=TP)	3.52	587.74	142.22

Table 11: Comparison of blue shark life history studies. Length represented as fork length (FL). All lengths from other studies converted to fork length (FL) using the relationships from Kohler at al. (1996).

Study	Location	Female L_{50}	Male L_{50}
This study	North West Atlantic	190.9	211.2
Hazin and Lessa (2005)	South-Western Atlantic Ocean	190.9	188.4
Megalofonou et al (2009)	Mediterranean Sea	179.9	170.1
Carrera- Fernández et al. (2010)	Baja California Sur, Mexico	164.3	154.35
Bustamante and Bennett (2013)	South-East Pacific Ocean	167.0	159.6
Jolly et al (2013)	South Africa	163.0	168.8
Francis and Maolagain (2016)	New Zealand	179.4	194.0

FIGURES

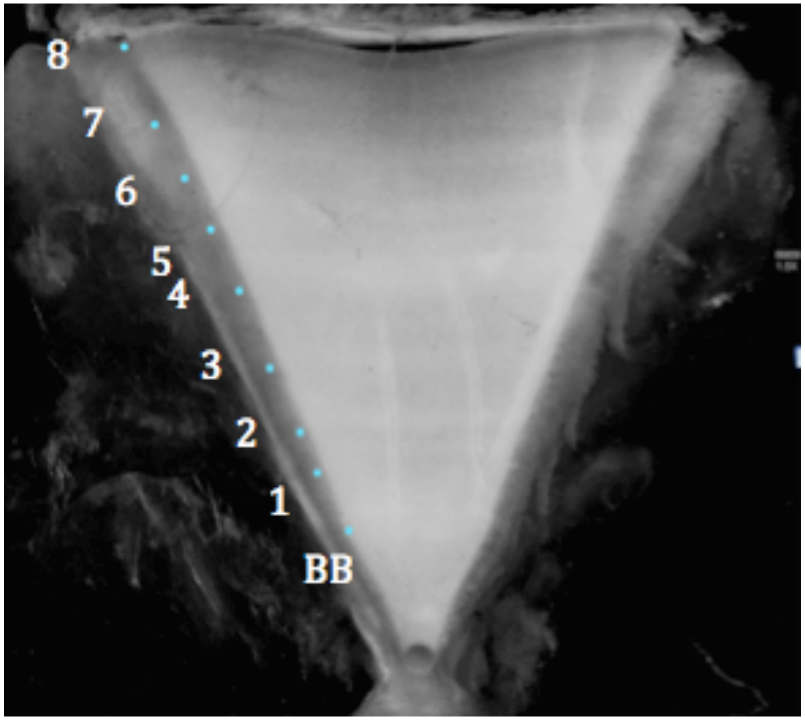

Figure 1: Section of blue shark vertebrae with band pairs marked beginning with the birth band (BB).

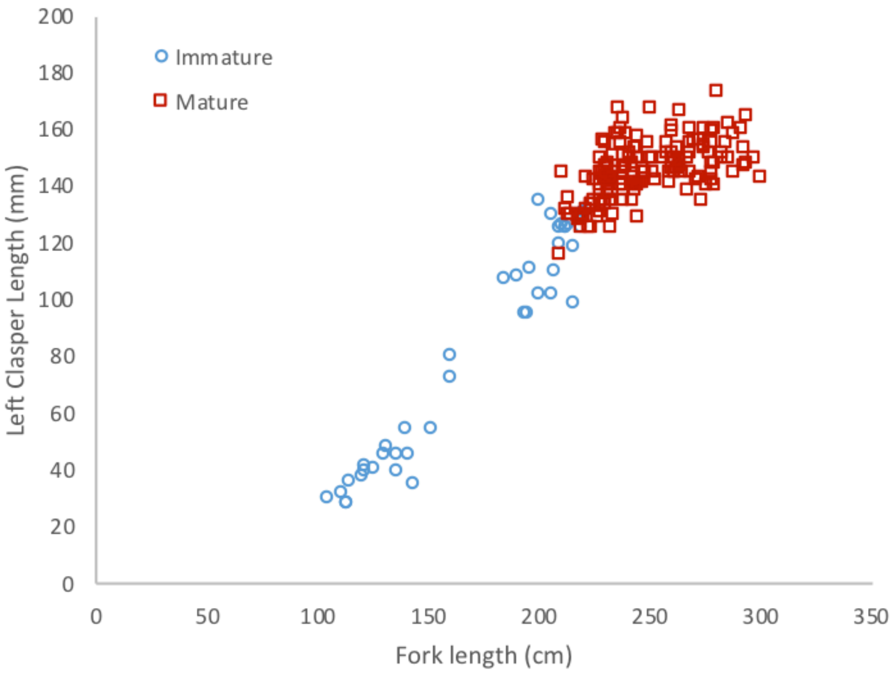

Figure 2: Relationship of left clasper length (mm) to fork length (cm).

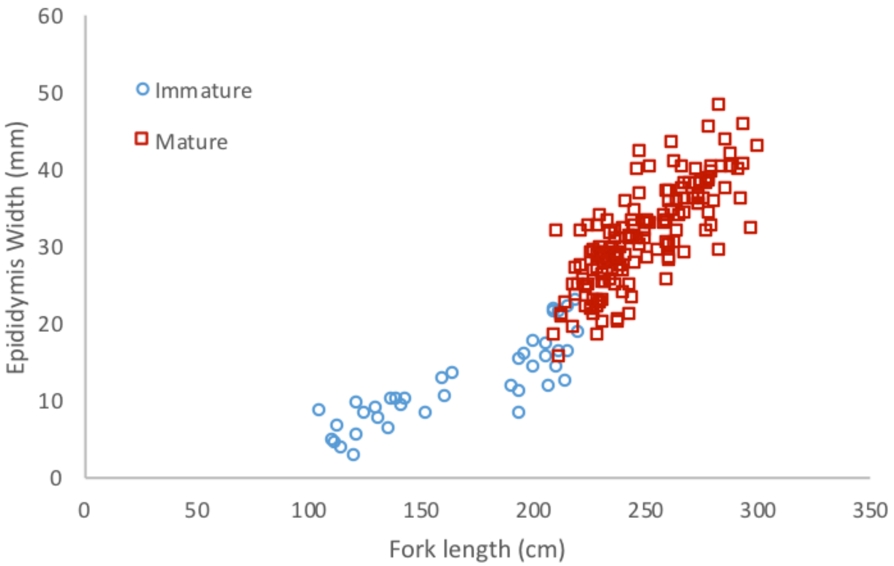

Figure 3: Relationship of epididymis width (mm) to fork length (cm).

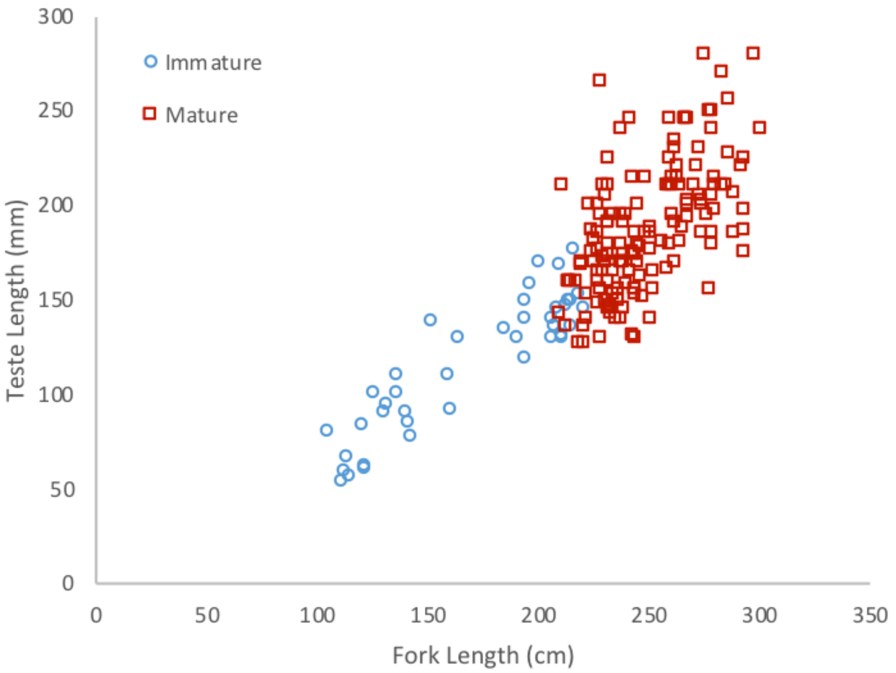

Figure 4: Relationship of teste length (mm) to fork length (cm).

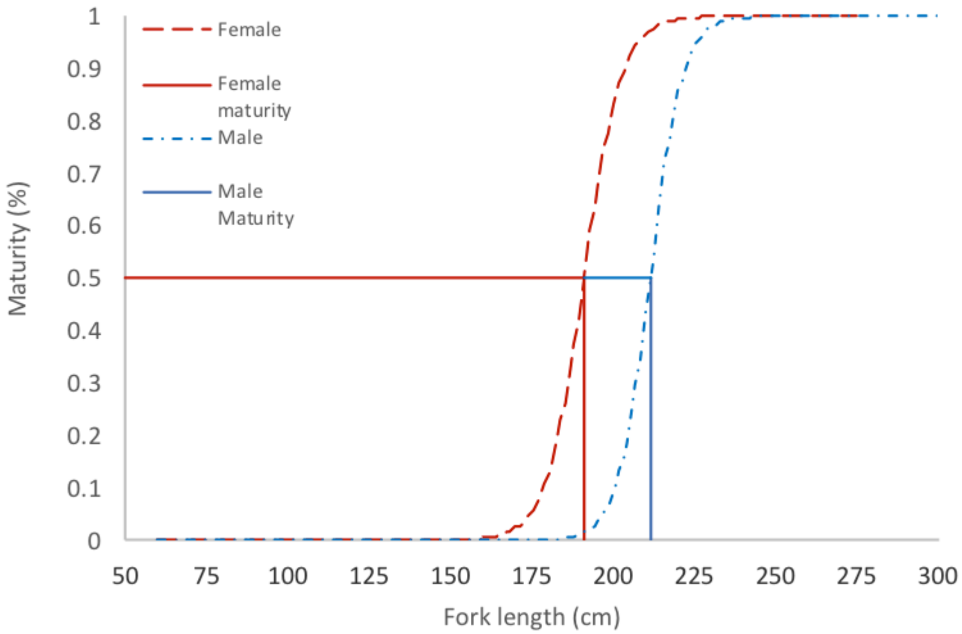

Figure 5: Relationship of fork length (cm) at 50% maturity (L_{50}) of male and female blue sharks.

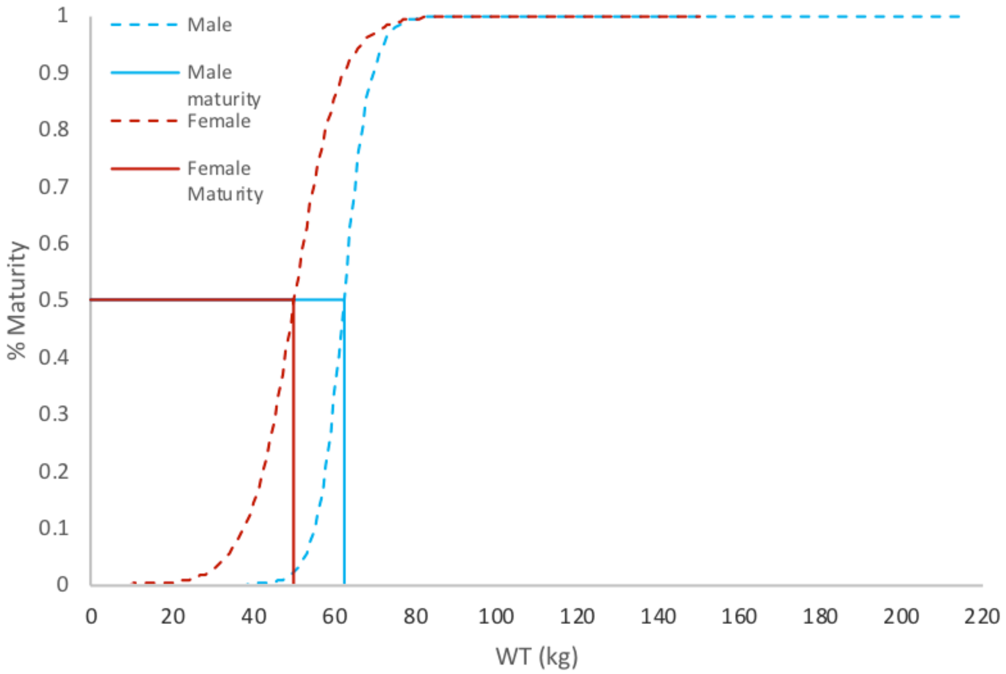

Figure 6: Relationship of fork length (cm) at weight at 50% maturity (W_{50}) of male and female blue sharks.)

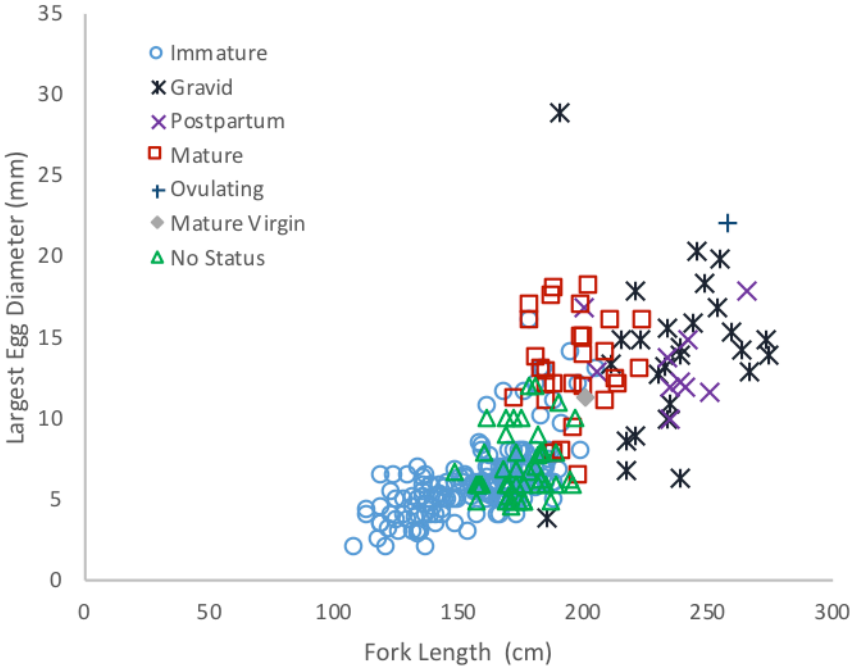

Figure 7: Relationship of egg diameter (mm) to fork length (cm).

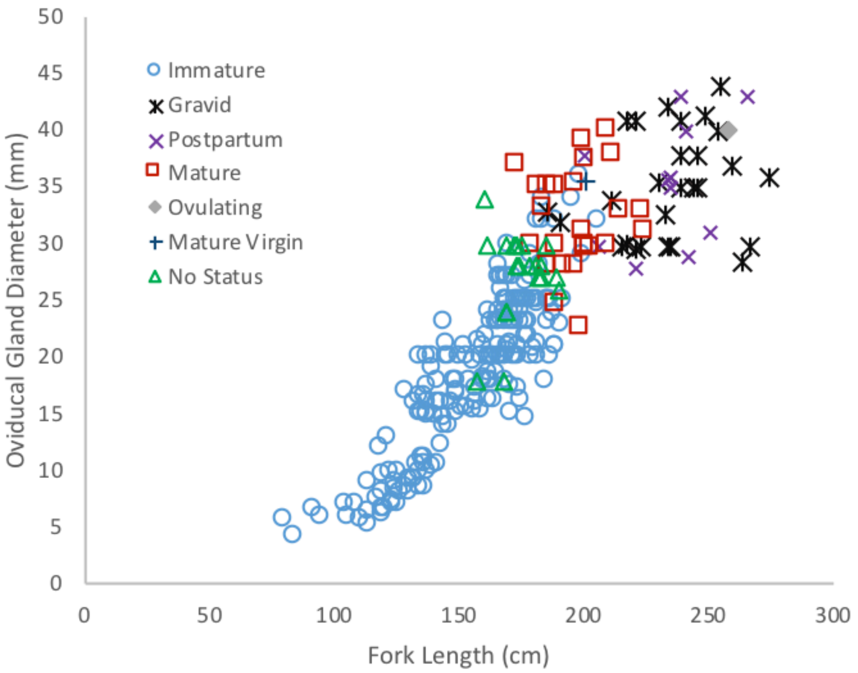

Figure 8: Relationship of oviducal gland (mm) width to fork length (cm).

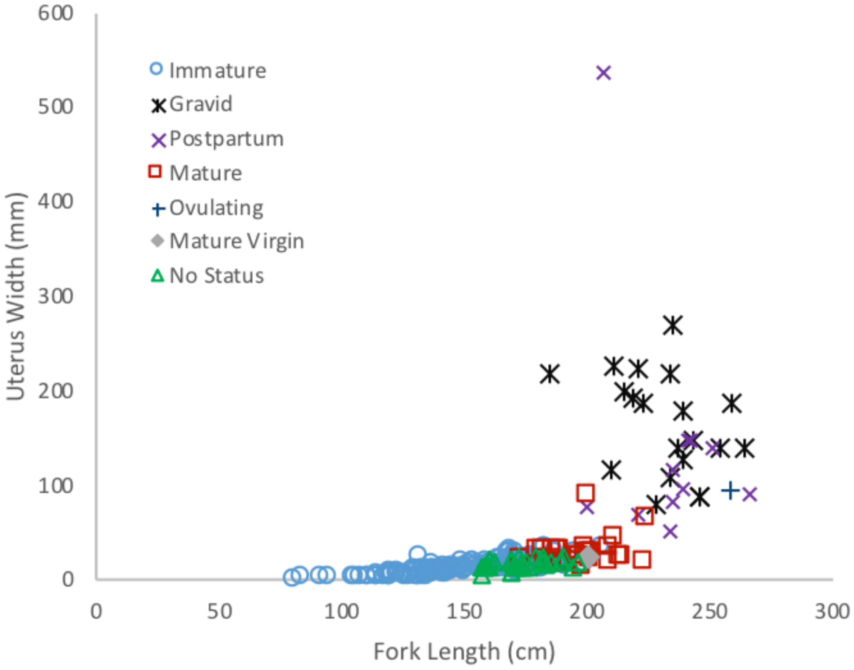

Figure 9: Relationship of uterus width (mm) to fork length (cm).

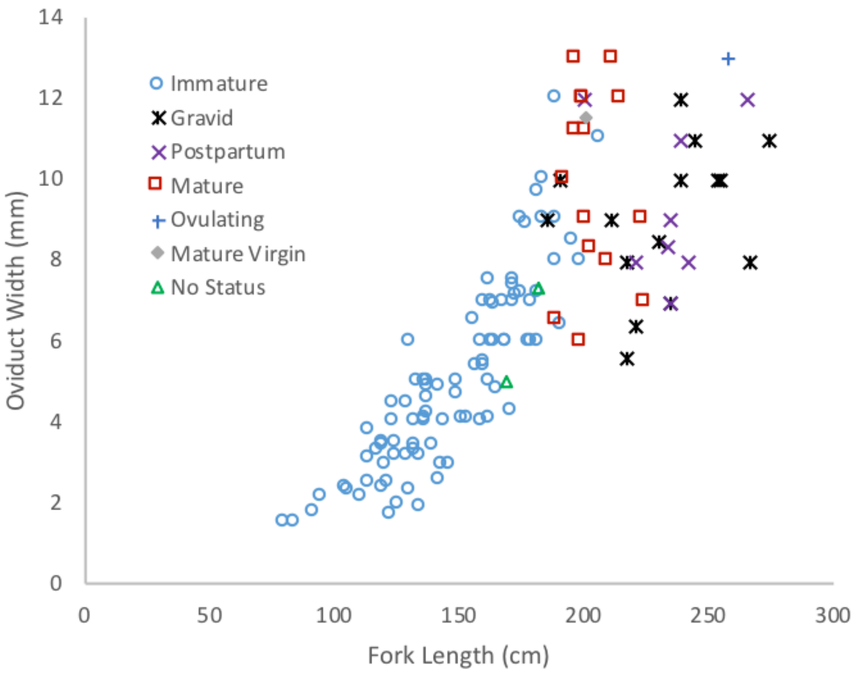

Figure 10: Relationship of oviduct width (mm) to fork length (cm).

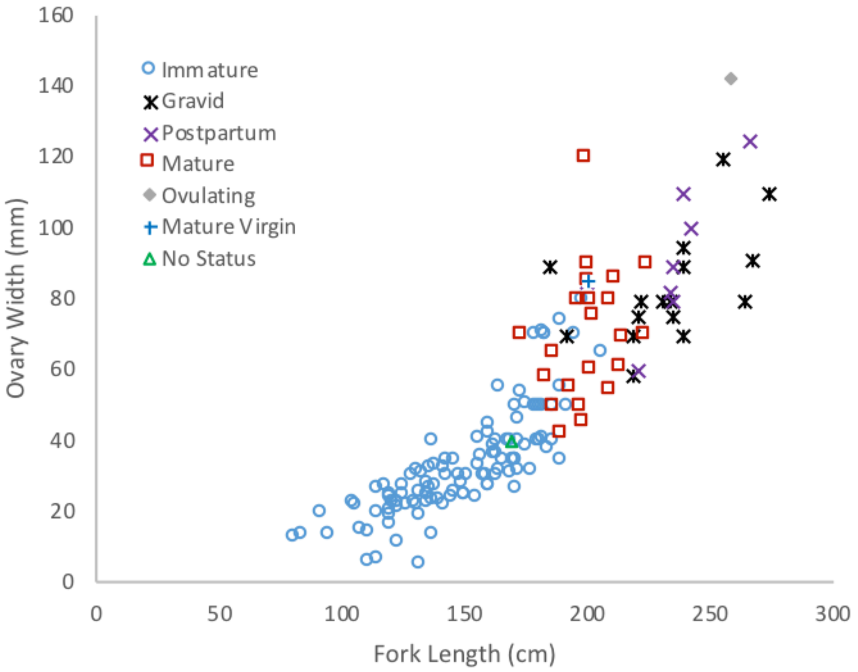

Figure 11: Relationship of ovary width (mm) to fork length (cm).

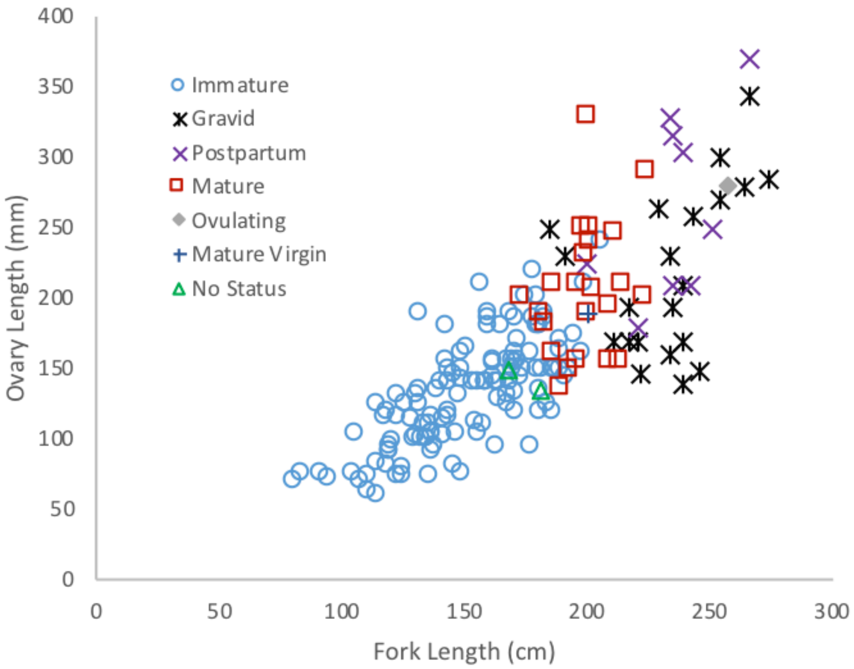

Figure 12: Relationship of ovary length (mm) to fork length (cm).

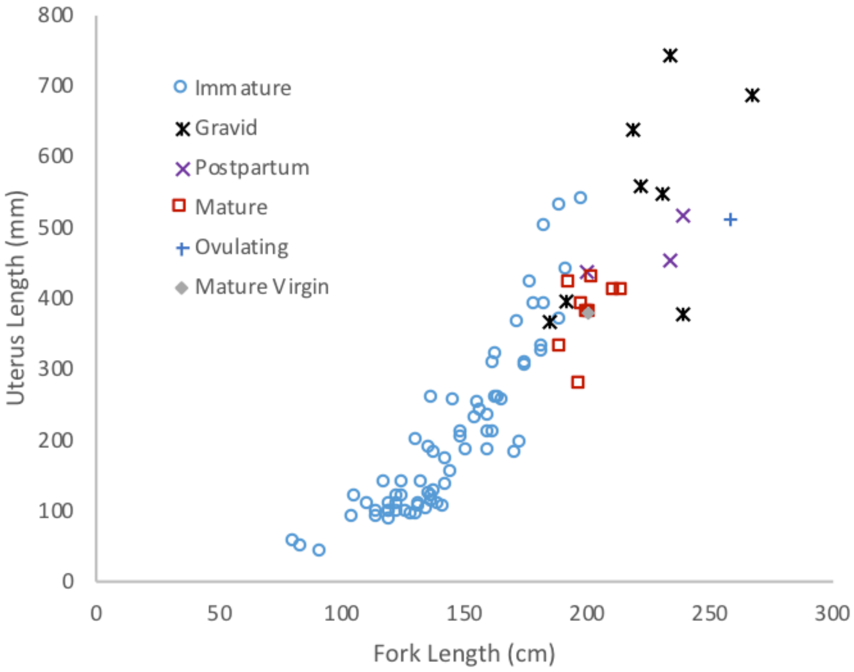

Figure 13: Relationship of uterus length (mm) to fork length (cm).

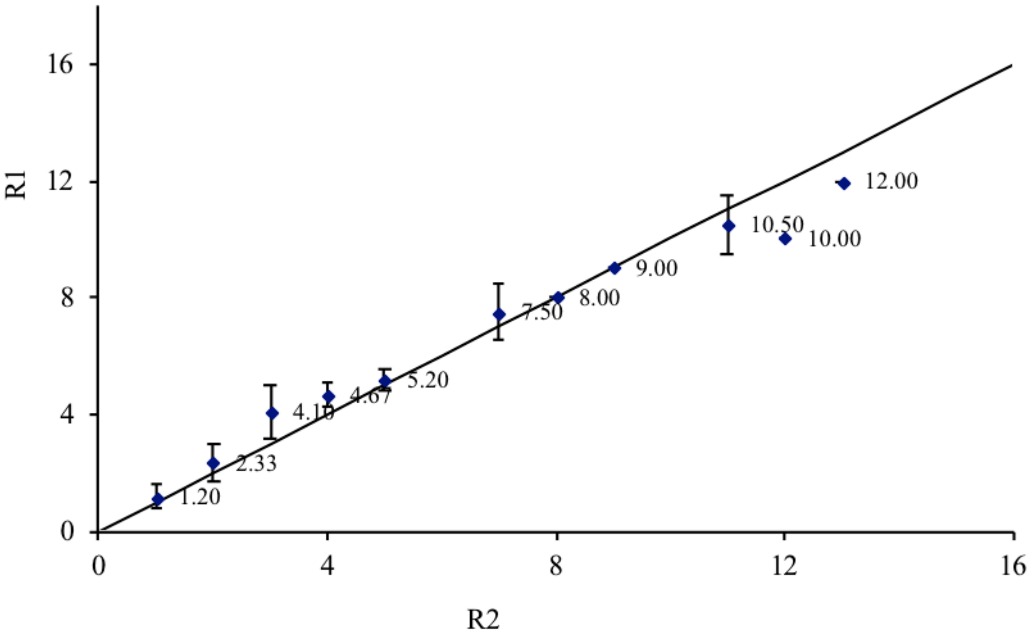

Figure 14: Bias graph showing relationship of Reader 2 to Reader 1 band pair counts of inter-calibration readings.

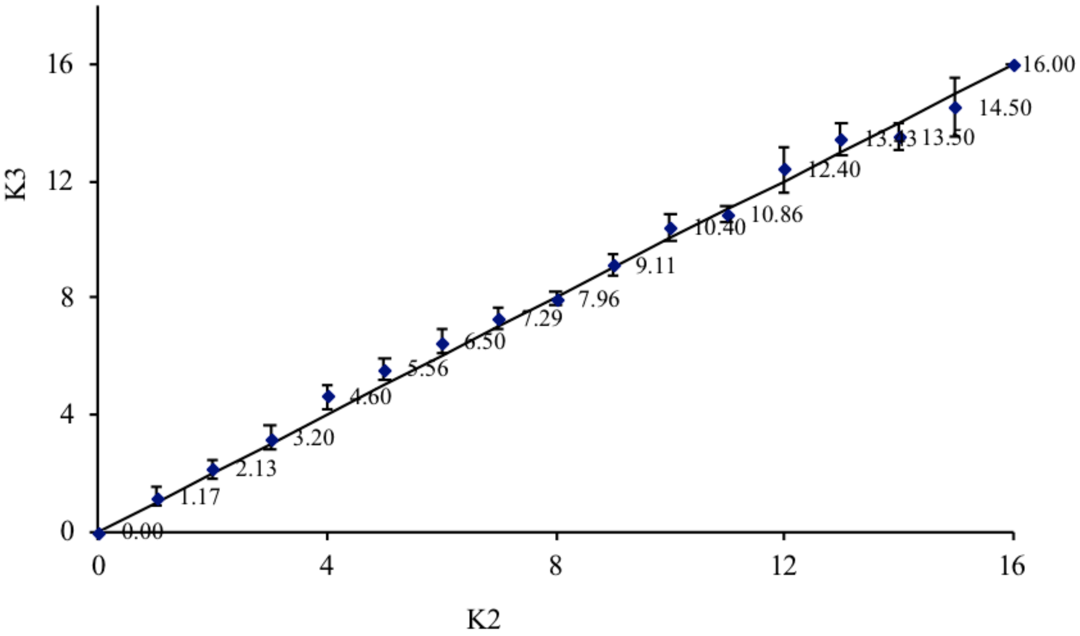

Figure 15: Bias graph showing relationship of band pair counts 2 and 3 (K2 and K3) of intra-reader counts.

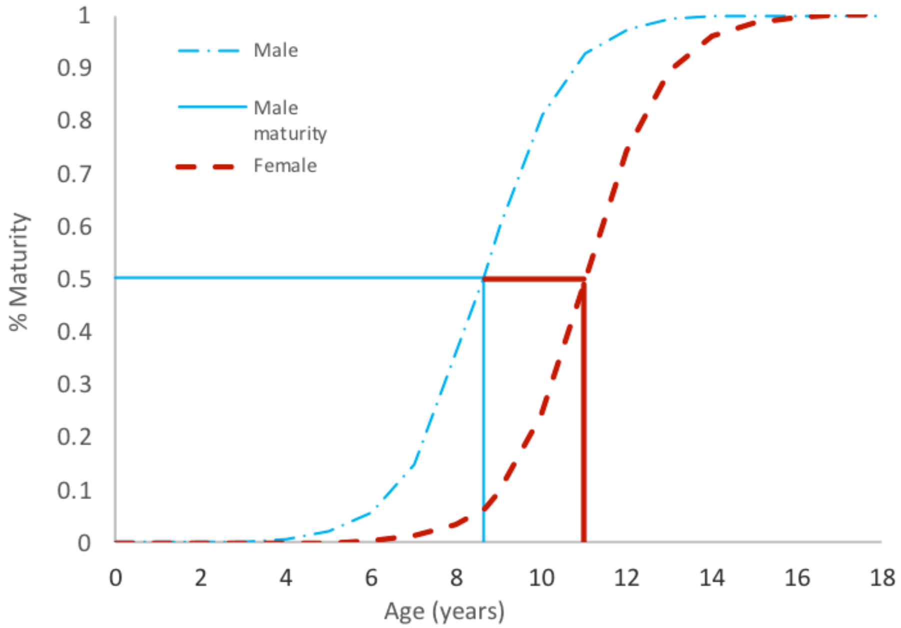

Figure 16: Relationship of age (years) to 50% maturity of males and females.

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