LCS05/06-DW-47

NURSERY GROUNDS AND MATURATION OF THE SANDBAR SHARK IN THE WESTERN NORTH ATLANTIC

BY

REBEKA RAND MERSON

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE

REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

BIOLOGICAL SCIENCES

UNIVERSITY OF RHODE ISLAND

1998

Manuscript 4

Maturation of the sandbar shark in the western North Atlantic

ABSTRACT

Sandbar sharks from the western North Atlantic and Gulf of Mexico were sampled between 1995 and 1997 to describe development of the reproductive tract, determine range in the length-at-maturity , reassess litter size and outline seasonal gonadal cycle to assess frequency of pregnancy. In males and females marked increases in reproductive tract anatomy occurs at about 140 cm fork length (FL), indicating the transition between juvenile and subadult stages. The smallest mature female was 148 cm FL and the largest immature was 175 cm FL. The smallest mature male was 139 cm FL and the largest immature was 153 cm FL. Probit analysis was used to produce maturity schedules for males and females. There was no difference in maturity schedules of either sex produced by data collected during this study and data from the National Marine Fisheries Service reproduction database (1971-1996). Length-at-maturity in both female and male sandbar sharks are consistent with reports in the literature, but the maturity schedules produced here describe the range in length-at-maturity. Females produce a mean litter size of eight pups possibly less frequently as every other year.

INTRODUCTION

The sandbar shark, *Carcharhinus plumbeus*, is distributed in warm-temperate and tropical oceans (Compagno, 1984). This species is targeted by commercial and recreational fishers and is currently managed by a quota system under the National Marine Fisheries Service Fishery Management Plan for Sharks of the Atlantic Ocean (National Marine Fisheries Service, 1993). This management plan and the Magnuson-Stevens act of 1996 mandate collection of scientific data for stock assessment and resource management. Length-at-maturity and offspring production are two parameters included in these initiatives because of their utility in fisheries models. Additionally, length-at-maturity is used to set minimum landed size limits; by setting the minimum larger than the length-at-maturity, individuals are given the opportunity to reproduce at least once before being subjected to fishing mortality.

Reproductive biology of the sandbar shark has been described from geographically isolated populations (western North Atlantic, Springer, 1960; East China Sea, Taniuchi, 1971; Hawaii, Wass, 1973; Taiwan, Joung and Chen, 1995). A comparison of these studies reveals differences in length-at-maturity, length-at-birth and litter size. Population differences in reproductive parameters were reported for the bonnethead shark (*Sphyrna tiburo*) (Parsons, 1993). Therefore, estimates of fecundity and maturity schedules used for management should be population specific.

Sandbar sharks in the western North Atlantic and Gulf of Mexico comprise one interbreeding population (Heist et al., 1995). Springer (1960) reported the length at first maturity of this population; females mature at 150 cm FL and males mature at 148 cm FL. Although this information is useful, it does not begin to describe the probability of maturity at a given length.

Mean litter size was reported to be nine pups per litter (Springer, 1960; Colvocoresses and Musick, 1989). Springer (1960) reported gestation duration was nine months and that females produce a litter every other year. The percent of mature females gravid was reported to be 17% off the Florida coast (Springer, 1960) and 27 % in the Gulf of Mexico (Clarke and von Schmidt, 1965). This suggests the reproductive cycle is longer than two years. A female would produce less offspring over a lifetime if the frequency of litter production were not every other year.

Given the lack of a complete maturity schedule and the need for good estimates of offspring production, the objectives of this study were to describe the development of reproductive tracts for baseline data, determine the range in length-at-maturity, reassess litter size, and outline the seasonal gonadal cycle to assess the frequency of pregnancy in sandbar sharks from the western North Atlantic.

MATERIALS AND METHODS

Reproductive tracts from 93 male and 242 female sandbar sharks (81-235 cm FL) were collected in the western North Atlantic and Gulf of Mexico by observers on commercial fishing vessels, and by fisheries biologists during National Marine Fisheries Service nursery research and longline surveys between January 1995 and October 1997. Because the majority of the samples were obtained from commercial fishing operations, relatively few or no samples were collected when the large coastal fishery was closed. Samples were examined immediately after capture, within 24 hours of capture (held on ice), or thawed after being frozen. Data from 93 male and 161 female sandbar sharks (59-212 cm FL) examined between June 1971 and August 1996 by National Marine Fisheries Service Apex Predators Program biologists was analyzed for comparison to data collected during this study.

Several measurements and observations of female and male reproductive tracts were made to outline patterns of development. Ovary length and width, largest oocyte diameter, oviducal (shell or nidamental) gland width, and uterus diameter were measured with dial calipers to the nearest millimeter. The ovary and uteri were closely examined for presence of vitellogenic oocytes (containing yolk) or degenerating (atretic) follicles, hymen (vagina-cloacal membrane), and remains of placenta indicative of recent parturition. Litter size and embryo lengths were recorded from pregnant females. On males, clasper and testis lengths were measured to the nearest millimeter using a ruler.

Degree of clasper calcification was observed. Testis diameter, upper epididymis width, and seminal ampulla diameter were measured with dial calipers to the nearest millimeter.

Females were classified mature if the shark was pregnant or if placental remains or egg cases were observed in the uteri. Additionally, females were classified mature if the uterine diameters were equal to or larger than those of pregnant and postpartum sandbar sharks (Springer, 1960; Wass, 1973). Male sandbar sharks were determined to be mature if the claspers were completely calcified and rotatable.

Maturity schedules were constructed using probit analysis (Finney, 1971) with the SAS program on data collected during this study and data from the National Marine Fisheries Service reproduction database. When 95% fiducial limits of the ogives overlapped, the datasets were combined to produce a robust maturity schedule. Age was assigned to lengths based on the von Bertalanffy parameters of Casey and Natanson (1992) and Sminkey and Musick (1995).

Results were qualitatively compared to published literature. Lengths reported in literature were converted from reported lengths using the reported conversion equations (precaudal length (PCL) to total length (TL)), and TL were converted to FL using the equation $FL=0.9722 + 0.8157(TL)$, based on a regression of 908 sandbar sharks ($r^2=0.98$, $p<0.01$) (Manuscript 2).

RESULTS

Development

The length and width of the ovary of female sandbar sharks gradually increased with shark length (Fig. 1). The oviducal gland width exhibited a sharp increase when females were between 140 and 150 cm FL (Fig. 2). At a length of 110 cm FL, the diameter of the uteri gradually increased until about 140 cm FL when uterine diameters increased dramatically (Fig. 2). The minimum uterine diameter in postpartum sharks was 23 mm.

It was possible to determine the presence or absence of the hymen (vagina-cloacal membrane) in 198 females examined during this study. Intact hymena were observed in 145 females. All pregnant and postpartum females and females with uterine diameters equal to or larger than 23 mm had no intact hymena. Nine females (140 to 158 cm FL) with intact hymena had developing oocytes in the ovaries, an indication that they were maturing. The uterine diameters in these maturing females ranged from 10 to 20 mm (mean 13 mm).

In males, the testis length and diameter increased gradually with the length of the shark (Fig. 3), and also varied seasonally in mature sharks (see Seasonal Cycle). Both the upper epididymis width and ampulla diameter (Fig. 4) increased when sharks were 140 cm FL. Clasper length showed a sharp increase between 130 and 150 cm FL (Fig. 5). All males larger than 153 cm FL had calcified claspers.

Maturity

Maturity status was assigned to 386 female and 151 male sandbar sharks. The smallest mature female was 148 cm FL and the largest immature was 175 cm FL. The smallest mature male was 139 cm FL and the largest immature was 153 cm FL. Separate maturity ogives were produced with the NMFS reproduction database and the data from this study. The 95% fiducial limits overlapped on both the male and female maturity ogives produced from the two data sets (Fig. 6), and then were combined (Fig. 7, Table 1, Table 2).

Seasonal Cycle

In mature females two conditions of oocyte development were observed. Either the ovary was resting or the ovary was active with oocytes increasing in diameter over the year. Pregnant, postpartum, and another group of mature females (Fig. 8) had resting ovaries. Active ovaries were observed in a group of non-pregnant females (Fig. 8). The largest oocytes were observed between March and May.

Litters of 10 pregnant females were examined and information from 27 litters recorded in the National Marine Fisheries Service reproduction database was analyzed. The smallest pregnant female was 156 cm FL. Litter size ranged from 2-11 pups (mean 8, SE 0.8) and was not correlated with maternal length (regression, $p>0.05$). Encased eggs were observed in three females in July and September. The first visible embryos were detected in July, and the lengths of embryos increased until July (Fig. 9).

In mature males, testis length and width show a seasonal cycle. The smallest testis diameters occur between June and September and gradually increase between January and May when the maximum diameter and length were 53 mm (Fig. 10) and 230 mm, respectively. This trend is mirrored by ampulla diameter where the maximum diameters occur between May and July with a significant decrease in August (t-test, $p<0.01$)).

DISCUSSION

Conservative indicators of maturity were used to assign maturity status in this study. In males, calcification of the claspers is an unambiguous criterion. In females, pregnant and postpartum conditions are definitive indicators of maturity. In this study a minimum uterus diameter of 23 mm was used as an indicator of maturity in female sandbar sharks because mature resting females show no other evidence of maturity. This criterion was used for the sandbar shark by Springer (1960) and Wass (1973). Confirmation that this criterion is valid comes from the observation that maturing sandbar sharks with intact hymena had a mean uterus diameter 10 mm less than the minimum postpartum uterus diameter.

The smallest mature female observed in this study (148 cm FL) is consistent with the length reported by Springer (1960) (150 cm FL). The smallest mature female reported by Sminkey and Musick (1995) (139 cm FL, 126 cm PCL) is 9 cm smaller than what we report. Our smallest mature male was smaller than that reported by Springer (1960). The maturity schedules produced during this study give more information about the range in length-at-maturity and will therefore allow for varying degrees of conservation by management.

A minimum size limit larger than the L_{99} would be the most conservative, allowing all sandbar sharks the opportunity to reproduce at least once before being subjected to fishing mortality. Based on the findings of this study, the minimum size limits should be 173 cm FL and 161 cm FL for female and male sandbar sharks, respectively. A minimum size limit of 157 cm FL for females and 149 cm FL for males would allow at least half of the sandbar sharks to reproduce at least once. An overall minimum size of 150 cm FL would allow only 15-20% of females and 55-60% of males to reproduce. Given the differences in length-at-maturity between the sexes, the minimum length limit should be set separately for males and females or be based on the female maturity schedule.

The reproductive anatomy of male and female sandbar sharks is similar to other carcharhinoid sharks. Size of the male and female gonads in immature sandbar sharks gradually increases with shark length. The increase probably reflects growth of the epigonal organ where the gonads are embedded. In males and females, marked increases in many parts of the reproductive anatomy (epididymis, ampulla, claspers, oviducal gland) occur around 140 cm FL. This indicates transition from a juvenile status to a subadult stage. Several females were observed to be maturing between 140 cm and 158 cm FL.

Springer (1960) reported a two year reproductive cycle in female sandbar sharks. Three reproductive conditions in mature female sandbar sharks were observed over the course of the year during the present study; pregnant with a resting ovary, non-pregnant with a resting ovary and non-pregnant with an active ovary containing developing oocytes. This may indicate a reproductive cycle longer than two years. More samples during the mating season are needed to make quantitative comparisons between reproductively active and resting females.

Oocyte diameters larger than the full size (25-30 mm) reported by Springer (1960) were observed in females between February and May. These data, combined with the timing of first detectable embryos and testis diameter maxima, place time of mating and fertilization between March and July. This does not necessarily mean the mating season is that extensive. Pratt (1993) showed that the females of several species of sharks, including the sandbar shark, store sperm in the oviducal gland. This makes possible a specific mating period with a flexible fertilization schedule.

In summary, female sandbar sharks were mature between 148 and 175 cm FL and give birth to an average of eight pups. The frequency of pregnancy is no less than every other year, but the evidence of a two year resting period warrants further investigation. Male sandbar sharks were mature between 139 and 153 cm FL. The differences in the maturity schedules of male and female sandbar sharks show that when minimum size limits are used for management the sexes should be managed independently or the female maturity schedule should be used.

ACKNOWLEDGMENTS

I thank very much Chris Jensen and Matthew Callahan from the Gulf and South Atlantic Fisheries Foundation, Inc., and Eric Sander for collecting most of the reproductive tract samples used in this study. Access to the National Marine Fisheries Service sandbar shark reproduction database and use of the Narragansett Bay Laboratory facilities was made possible by Dr. Nancy Kohler and very much appreciated. I am grateful for the guidance of Wes Pratt during the course of this study.

Funding for this research was provided by NOAA/NMFS Highly Migratory Species and the American Museum of Natural History Lerner-Gray Fund for Marine Research.

LITERATURE CITED

Casey, J. G., and L.J. Natanson. 1992. Revised estimates of age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. Can. J. Fish. Aquat. Sci. 49:1474-1477.

Clark, E. and K. von Schmidt. 1965. Sharks of the central Gulf coast of Florida. Bull. Mar. Sci. 15:13-83.

Colvocoresses, J. A. & J. A. Musick. 1989. Reproductive biology of the sandbar shark, Carcharhinus plumbeus, in the Chesapeake Bight. Proceedings of the 69th Annual Meeting American Society of Ichthyologists and Herpetologists. San Francisco State University, San Francisco, CA 17-23 June, 1989.

Compagno, L. J. V. 1984. FAO species catalogue. Vol. 4. Sharks of the world. Part 2- Carcharhiniformes. FAO Fish. Synop. 4(2):250-655.

Finney, D. J. 1971. Probit analysis. Third edition. Cambridge University Press. Cambridge, England.

Heist, E. J., J. E. Graves and J. A. Musick. 1995. Population genetics of the sandbar shark (*Carcharhinus plumbeus*) in the Gulf of Mexico and mid-Atlantic bight. Copeia 1995:555-562.

Joung, S. J. and C. T. Chen. 1995. Reproduction on the sandbar shark, *Carcharhinus plumbeus*, in the waters off northeastern Taiwan. Copeia 1995:659-665

Magnuson-Stevens Fishery Conservation and Management Act. 1996. Public Law 94-265, Amended 11 October 1996.

National Marine Fisheries Service. 1993. Fishery management plan for sharks of the Atlantic Ocean. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Washington.

Ott, R. L. 1993. An Introduction to Statistical Methods and Data Analysis. Duxbury Press. Belmont.

Parsons, G. R. 1993. Geographic variation in reproduction between two populations of the bonnethead shark, *Sphyrna tiburo*. Env. Biol. Fish. 38:25-35.

Pratt, H. L., Jr. 1993. The storage of spermatozoa in the oviducal gland of western North Atlantic sharks. Env. Biol. Fish. 38:139-149.

Sminkey, T. R. and J. A. Musick. 1995. Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. Copeia 1995:871-883.

Springer, S. 1960. Natural history of the sandbar shark *Eulamia milberti*. Fish. Bull. 61:1-38.

Taniuchi, T. 1971. Reproduction of the sandbar shark, *Carcharhinus milberti*, in the east China Sea. Jap. J. Ichthyol. 18:94-98.

Wass, R. C. 1973. Size, growth, and reproduction of the sandbar shark *Carcharhinus milberti*, in Hawaii. Pac. Sci. 27:305-318.

Table 1. Probability of maturity-at-length for female sandbar sharks from probit analysis of combined data (data from sharks examined during this study and the National Marine Fisheries Service reproduction database). Age A is based on von Bertalanffy parameters of Sminkey and Musick (1995) and Age B is based on von Bertalanffy parameters of Casey and Natanson (1992).

Table 1. Probability of maturity-at-length for females.
Age 1 classification based on Sminkey and Musick (1985)
Age 2 classification based on Casey and Natanson (1992)

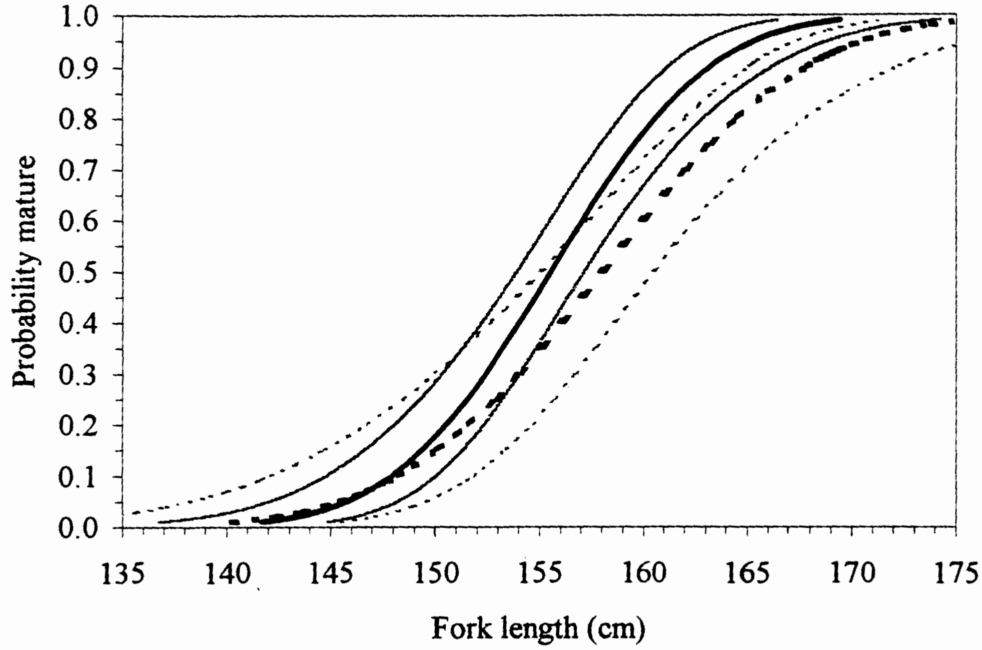
Females					
		Fiducial limits			
Probability of maturity	Fork Length (cm)	Lower 95%	Upper 95%	Age 1	Age 2
0.01	140	135	144	13	24
0.05	145	141	148	14	26
0.10	148	144	150	15	28
0.15	149	146	151	15	28
0.20	151	148	153	16	30
0.25	152	150	154	17	30
0.30	153	151	155	17	31
0.35	154	152	156	17	32
0.40	155	153	156	18	32
0.45	156	154	157	18	33
0.50	157	155	158	19	34
0.55	157	156	159	19	34
0.60	158	157	160	19	35
0.65	159	158	161	20	35
0.70	160	159	162	20	36
0.75	161	160	163	21	37
0.80	162	161	165	21	38
0.85	164	162	166	22	40
0.90	165	163	168	23	41
0.95	168	165	171	25	44
0.99	173	169	177	30	51

Table 2. Probability of maturity-at-length for male sandbar sharks from probit analysis of combined data (data from sharks examined during this study and the National Marine Fisheries Service reproduction database). Age A is based on von Bertalanffy parameters of Sminkey and Musick (1995) and Age B is based on von Bertalanffy parameters of Casey and Natanson (1992).

Table 2. Probability of maturity-at-length for males.
Age 1 classification based on Sminkey and Musick (1985)
Age 2 classification based on Casey and Natanson (1992)

Males					
		Fiducial limits			
Probability of maturity	Fork Length (cm)	Lower 95%	Upper 95%	Age 1	Age 2
0.01	137	131	141	12	22
0.05	141	136	143	13	24
0.10	142	139	145	13	25
0.15	144	140	146	13	26
0.20	145	142	147	14	26
0.25	146	143	148	14	27
0.30	146	144	148	14	27
0.35	147	145	149	14	27
0.40	148	146	150	15	28
0.45	148	146	150	15	28
0.50	149	147	151	15	28
0.55	150	148	152	15	29
0.60	150	148	153	15	29
0.65	151	149	153	16	30
0.70	152	150	154	16	30
0.75	153	151	155	16	31
0.80	153	151	156	16	31
0.85	154	152	158	17	32
0.90	156	153	159	18	33
0.95	157	155	162	18	34
0.99	161	158	167	19	37

Figure 6. Probability of maturity-at-length from probit analyses of female sandbar sharks (upper panel) and male sandbar sharks (lower panel). Solid lines are sharks examined during this study, dashed lines are sharks recorded in the NMFS reproduction database. Black lines are values, gray lines are 95% lower and 95% upper fiducial limits. All probit analyses have Chi-square goodness-of-fit probability>0.90. Fiducial limits were calculated using a t-value of 1.96.


1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Probability mature
135
140
145
150
155
160
165
170
175
Fork length (cm)

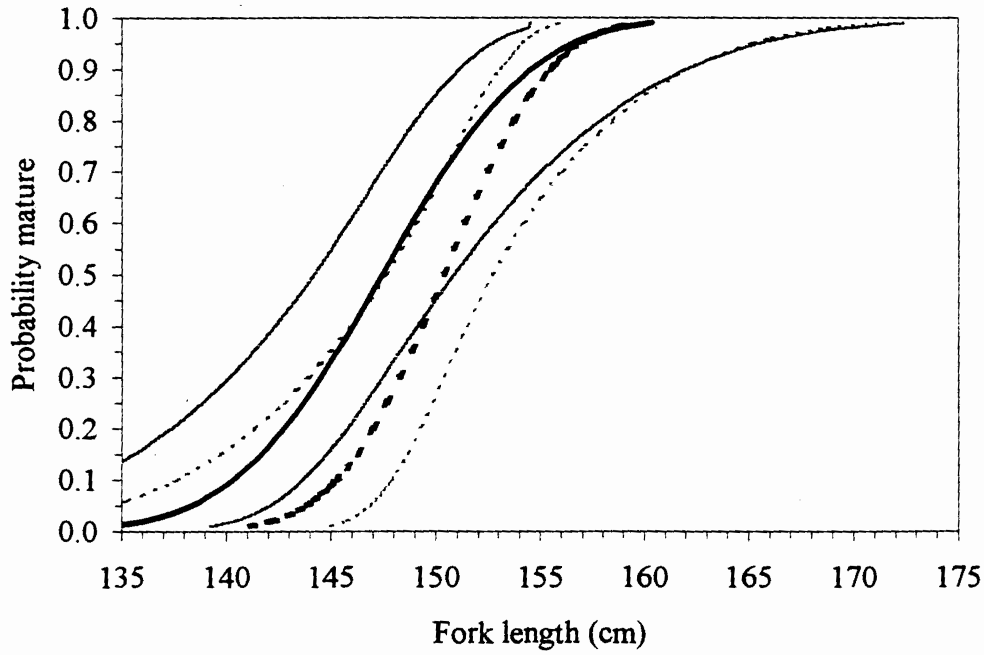
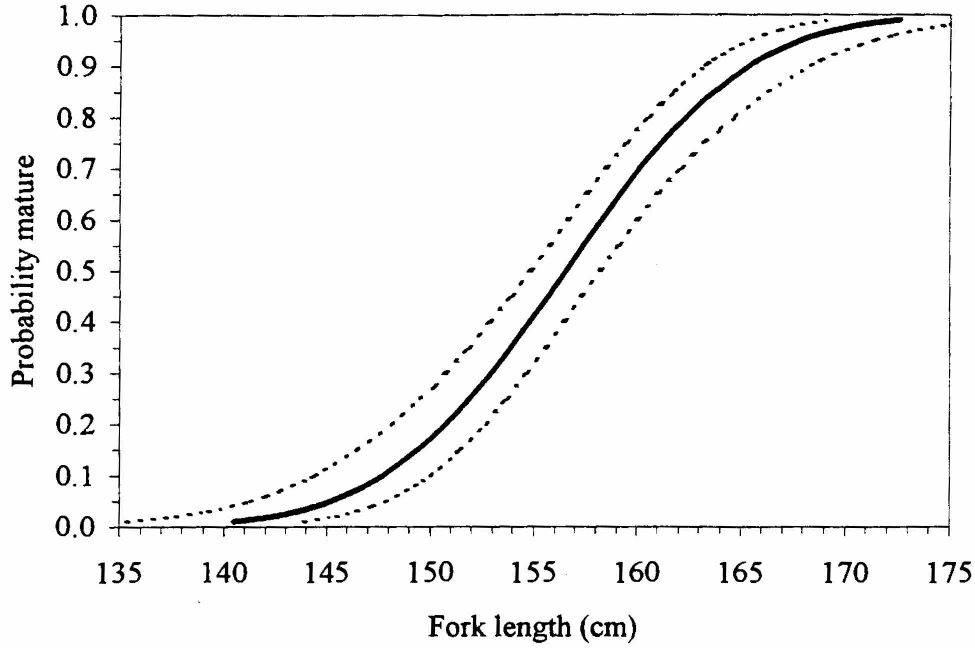
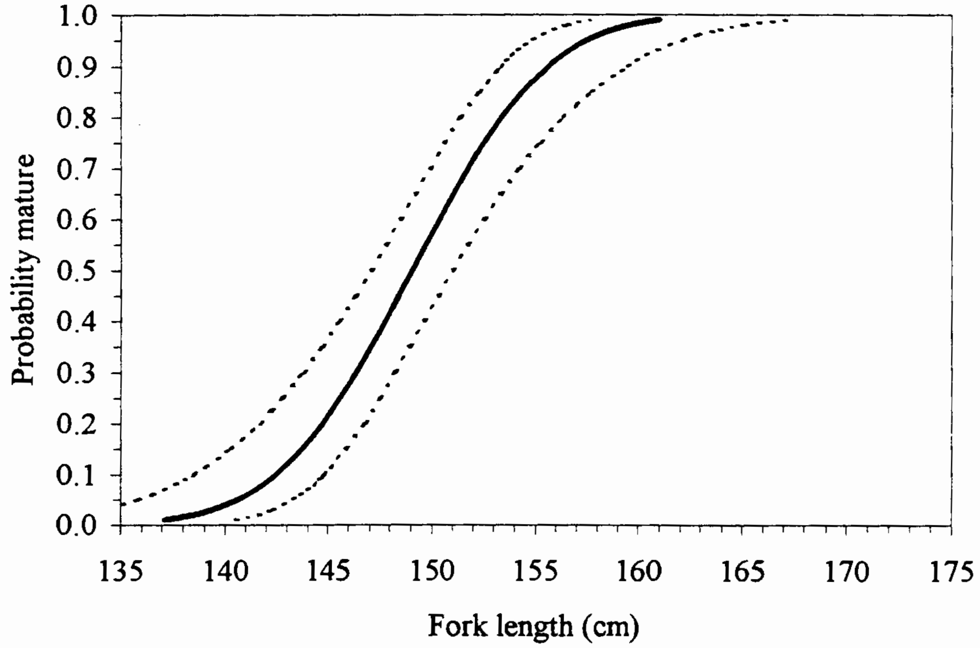

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Probability mature
135
140
145
150
155
160
165
170
175
Fork length (cm)

Figure 7. Probability of maturity-at-length from probit analyses of female (upper panel) and male sandbar sharks (lower panel) from combined data (sharks examined during this study and the National Marine Fisheries Service reproduction database). Solid lines are values, dashed lines are 95% lower and 95% upper fiducial limits. All probit analyses have Chi-square goodness-of-fit probability>0.99. Fiducial limits were calculated using a t-value of 1.96.



1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Probability mature
135
140
145
150
155
160
165
170
175
Fork length (cm)



1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Probability mature
135
140
145
150
155
160
165
170
175
Fork length (cm)