Reproduction of the sandbar shark *Carcharhinus plumbeus* in the US Atlantic Ocean and Gulf of Mexico

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Abstract

A total of 1194 (701 females, 493 males) sandbar sharks *Carcharhinus plumbeus* were examined for reproductive assessment. Size and age at 50% maturity for males was 151.6 cm FL (13.1 years) and 154.9 cm FL (14.1 years) for females, while the size at which 50% of females were in reproductive condition was 162.6 cm FL (16.8 years). Males and females showed distinct seasonal reproduction patterns, with peak mating and parturition occurring from April through June. Female fecundity averaged 8.0 pups, and there was a weakly significant increase in fecundity with size and a significant increase in fecundity with age. Patterns of maximum ova diameter and gonadosomatic indices in females suggest that sandbar sharks may have a triennial reproductive cycle.

Introduction

The sandbar shark is a large Carcharhiniform shark that spends the majority of its life history offshore in U.S. waters (McEachran and Fechhelm, 2005). Several studies on the reproduction of the sandbar shark have been conducted by researchers throughout the range of the species (Cliff *et al.*, 1988; Joung and Chen, 1995; Saidi *et al.*, 2005; Daly-Engel *et al.*, 2007; Hazin *et al.*, 2007; McAuley *et al.*, 2007; Portnoy *et al.*, 2007; Diatta *et al.*, 2008). These studies have shown that sandbar sharks mature between 125-175 cm fork length (FL), average litter size ranges from 6.5-8.7 pups, gestation is 10-12 months in duration, and most that examined the relationship between maternal length and fecundity have found at least a weak relationship. Most published studies agree that reproduction in sandbar sharks is biennial, however (Merson, 1998) suggested that "females produce… pups possibly less than frequently as every other year." Very few studies have assessed the age-at-maturity through direct age estimation, therefore previous assessments have had to back-calculate ages using von Bertalanffy parameters to estimate age-at-maturity.

Methods

Sampling

Sandbar sharks were collected by one fishery-dependent source and two fishery-independent surveys. Fishery-dependent samples were collected by at-sea fishery observers aboard commercial longline fishing vessels. Samples obtained by at-sea observers from the bottom longline commercial shark fishery (including the sandbar shark research fishery) had the following gear characteristics: average length of the monofilament mainline of 15.1 km, average number of hooks of 513.6 hooks, and the most common size and type of hook utilized was 18.0 circle hooks. The majority of fishery-dependent samples were collected on the east coast of Florida and from the Florida Keys (Fig. 1). Fishery-independent samples were collected by the South Carolina

Department of Natural Resources (SCDNR) in the U.S. Atlantic Ocean and the Cooperative Gulf States Shark Pupping and Nursery (GULFSPAN) survey in the eastern Gulf of Mexico (Fig. 1). The SCDNR survey deployed a mixture of gillnets and longlines. The hydraulic longline was 275 m in length, with 40 gangions set with 15/0 offset circle hooks, the hand-deployed longline consisted of 306 m of mainline with 50 12/0 offset circle hooks, and the gillnet was 231 m long , 3 m deep, and had a stretch mesh of 10.3 cm. The GULFSPAN was strictly a gillnet survey with 6, 33 m panels of 7.6-13.9 cm stretch mesh. Two additional fishery-independent samples were collected by a survey using a hydraulic longline with 1.85 km of monofilament mainline set with 100 gangions with 20/0 offset circle hooks in the Gulf of Mexico.

Sandbar sharks collected by SCNDR and GULFSPAN were measured for FL (+/- 1 cm) in a straight line from the tip of the nose to the fork in the caudal fin and sexed, and then a 10 cm section of vertebrae was removed from the portion of the spinal column just below the first dorsal fin. Vertebral sections were then frozen whole at the NOAA Fisheries Panama City Laboratory at -5^{o} C until they were processed. At-sea observers aboard commercial longline vessels sampled sandbar sharks in an opportunistic fashion, when sea conditions were favorable and fishing operations allowed. Observers measured all sandbar sharks for FL (straight line), then removed reproductive organs and a 10 cm segment of vertebrae. For females, the right ovary, both nidamental glands, and both uteri (and contents) were sampled; for males, both testes, both epididymedes, the seminal vesicle, and at least one clasper were removed when possible. Because the carcasses were commercial products, the vertebrae were sampled from the discarded portion of the shark, in the cervical region of the spinal column. Vertebral and reproductive samples were either frozen on-board and then shipped, or were immediately shipped on ice to the NOAA Fisheries Panama City Laboratory. Vertebrae were frozen whole, and reproductive samples were immediately processed at the laboratory by fishery biologists. Vertebral sections were processed for ageing and ages were assigned according to methods described in Hale and Baremore (2010).

Reproductive analysis

Female reproductive organs were measured for ovary length, width (+/- 1 mm), and weight (+/- 1.0 g), maximum oocyte diameter (MOD) (or second largest if one was notably larger than the rest) nidamental gland width, and uterus width (mm). Uteri were cut open to determine whether sperm packets or placental scarring were present, or to remove pups if pregnant. Pups were enumerated by uterus, then sexed, weighed (g), and measured for FL and stretch total length (STL). All females were staged by reproductive condition: 1) juvenile, 2) juvenile, developing, 3) mature, non-gravid, 4) ovulatory, 5) gravid, 6) mating condition, and 7) post partum (Table 1). Stage 2 females had MOD < 10 mm, nidamental gland width < 30 mm, uterus width < 30 mm, and were not in reproductive condition (i.e. oocytes would not be ready for ovulation within the next season). Based on these classifications, females were considered mature when pregnant, ovulating, or post-partum (stages 4-7), or if the reproductive measurements met the following criteria: MOD >/= 10 mm, nidamental gland width > 30 mm, and uterus width > 30 mm (stage 3). Stage 4 females contained at least one fertilized egg in the uterus, along with mature yolked ova in the ovary > 30 mm in diameter, stage 6 females had visible sperm packets in the uterus but no ovulated ova, and stage 7 females had very distended and thin uteri with visible internal placental scarring. Additionally females were considered to be in maternal condition (Walker, 2005) if gravid (stage 5) or would most likely become gravid within the year (stage 3 with MOD>25 mm from January-March and >30 from April-June). Male reproductive organs were measured for length, width, and weight of the testes, length of the claspers, and width of the epididymis. Clasper calcification was noted, as was the presence and nature of semen in the seminal vesicle. Males were staged by reproductive condition: 1) juvenile, 2) mature, 3) mature, running ripe (Table 1). Stage 3 males possessed engorged seminal vesicles and ropy packets of spermatozoa. Males were mature when the claspers were fully calcified.

Scatter plots of MOD, ovary weight, and nidamental gland width (stage 3 females) and testis weight, testis width, and epididymis width (stages 2-3 males) were made by month to assess the seasonal mating pattern of sandbar sharks. Because fishery-dependent sharks were not weighed, gonadosomatic indices (GSI) were calculated as GSI=gonad weight/FL. Additionally, percentage of adult females in each stage (3-7) were plotted by month to calculate the proportion of mature females in maternal condition and to further elucidate the mating season.

A scatter plot of embryo length by month was used to find length of gestation, time of parturition, and size-at-birth. The litter size (number of pups per female) was regressed by maternal FL and age to test whether larger and older females produce more offspring than smaller and younger ones. The sex ratio of embryos and the number of embryos in each uterus per female were tested for significant difference from a 1:1 relationship with χ^2 tests.

Logistic curves were used to analyze size and age of maturity for males and females.

(y= (1/(1+exp(-(a+b*(FL))))))

using binomial maturity data (0=juvenile, 1=mature). The sizes and ages at which 50% of the individuals were mature were calculated (y=-a/b), as were standard errors (SE) of the estimates. An additional maternity ogive was plotted to assess the size and age of females in maternal condition, with binomial maternity data (0=juvenile or mature but not in maternal condition, 1=mature in maternal condition) (Walker, 2005). Stage 3 females were considered to be in maternal condition when MOD was > 20 mm in January-March and females with MOD > 25 mm in April through June. Logistic analysis was performed using the lrm procedure in Program R. Likelihood ratio tests were used to test for differences in size and age of maturity.

Results

Seasonal trends in reproduction

A total of 1194 sandbar sharks were sample for age, growth, and reproductive analysis, (701 females and 493 males) (Fig. 2). Both male and female sandbar sharks showed strong seasonal trends in reproduction, with a peak in all gonad measurements occurring from April through June (Figs. 3-6). Stage 3 (mature, non-gravid) females showed a maximum in GSI and MOD in June (Fig. 3a, b), with Stage 4 (ovulating) females occurring in June and July, and 7 (sperm present in uterus) females found from April through August (Fig. 4). The drastic decrease in MOD and GSI (Fig. 3a, b) indicated that mating ceased in July, which corresponds to the smallest embryos being found *in utero* in August (Fig. 5). Ovulation occurred at an MOD of 30-40 mm and GSI > 2.0. Male GSI peaked in April, while epididymis width peaked in June (Fig. 6). The lag in these trends corresponded to peak sperm production in the testes just prior to mating, with peak in epididymis width consistent with peak mating. Stage 3 males first appeared in April, and were present through June.

Female reproductive periodicity

Stage 5 females did not show any signs of vitellogenesis during or shortly after gestation, indicating that reproduction is at least biennial. The wide spread of MOD and GSI exhibited by females in the first half of the year (January-June), and especially the presence of stage 3 females with unyolked oocytes <25 mm from March-June provides evidence of a three-year cycle (Fig. 7). These observations indicate that, during the spring months, mature females can be categorized into three distinct years of vitellogenesis: year 1 females most likely pupped the previous year and had MOD < 25 mm during the peak of mating activity (April-June), year 2 females showed an increase in MOD from 25-35 mm in spring months prior to ovulation and would presumably be pregnant by June, and year 3 females were gravid and show no signs of vitellogenesis. Approximately 36% of stage 3 females were in this condition during this time period. Overall, 37% of all mature females collected were gravid.

Gestation period and pup characterization

A total of 123 stage 5 females were examined. The gestation period for sandbar sharks is approximately 12 months (Fig. 4), and pups are between 39 and 55 cm fork length (FL) at birth (Fig. 5), with an average FL of 46 cm (Hale and Baremore 2010). The relationship between maternal FL and number of offspring per cycle was weak but significant (R^2=0.06, p=0.01117, n=99 females, Fig. 8a). The relationship between maternal age and number of offspring was stronger and highly significant (R^2=0.3664, p=0.0002, n=99, Fig. 8b). The average number of pups per female was 8.0 (±2.39 SD), with a range of 3-12. The sex ratio of *in utero* pups was not significantly different from 1:1 among uterine branches or overall among females (χ^2=0.36, 0.25, respectively).

Of the 99 females with intact uteri that were examined for pup data, 34 (34%) contained at least one unfertilized egg in one uterus. When unfertilized eggs were present, females had on average 1.3 unfertilized eggs. Unfertilized eggs were characterized by a grayish color and chalky texture and were out of sync with other uterine contents (i.e. well developed embryos were also present), but otherwise appeared similar to newly ovulated eggs. There were three cases of fetal mummification, two of which were from the same litter. In this instance, the mummified fetuses and unfertilized ova were in the same uterus (left), while the right uterus of the same female contained three viable fetuses.

Maturity and maternity indicators and ogives

Sizes at which 50% of individuals were mature were 151.6 (±4.23 SE, n=449) and 154.9 (±2.83 SE, n=658) cm FL for males and females, respectively. Ages at 50% maturity were 12.1 (±1.18 SE, n=449) for males and 13.1 (±0.72 SE, n=656) years for females

(Figs 9a, b, Table 2, 3). Size of 50% of females in maternal condition was 162.0 (±2.01 SE, n=645) cm FL, or 15.5 (±0.51 SE, n=640) years of age (Fig. 10, Tables 2, 3). Likelihood ratio tests showed significant differences in the logistic regressions for both sizes and ages at maturity between sexes ($p<0.05$). Likewise, size at maternal condition was significantly different from size-at-maturity for all females ($p<0.05$).

Discussion

Results from this study are not outside the range of reproductive parameter estimates previously reported for sandbar sharks (Table 4), with size-at-maturity, fecundity, gestation period, and seasonality falling within expected limits. However, there is increasing evidence in this species for a three-year cycle for at least part of the population of females. During spring months, females exhibited two distinct phases of vitellogenesis at the same time as gravid females. Additionally, among mature females examined, only 37% were gravid, indicating that even if capable of reproducing biennially, females were not necessarily doing so. While it is possible that these results are due to sampling bias, females in both phases of vitellogenesis, along with gravid females, were observed on the same day and in the same location.

Two previous stock assessments for sandbar sharks were completed in 2002 and 2006 (NMFS, 2002; 2006). The 2006 assessment used different reproductive parameters from the 2002 assessment: female age-at-maturity was increased from 13 to 19 years, and fecundity was reduced from 12 to 8.4 pups per female. These parameters were based largely on a literature review of several studies conducted prior to 2000 (Romine and Musick, 2006), and the age at maturity was based on Merson;s (1998) study.

Direct age estimation of sandbar sharks in western Australia produced age at 50% maturity estimates of 13.8 and 16.2 years for males and females, respectively (McAuley *et al.*, 2007). Other age and growth studies have back-calculated ages using previously reported data (Merson, 1998; Romine and Musick, 2006) or back-transformed ages at maturity from the von Bertalanffy growth equation (Casey *et al.*, 1985; Casey and Natanson, 1992; Joung *et al.*, 2004; Romine *et al.*, 2006). These papers have provided age-at-maturity estimates ranging from 7.5 to 30 years. Maturity estimates provided by this paper of 12.1 (males) and 13.1 (females) are younger than reported for the western Atlantic of 15 for females and 18 for males(Merson, 1998), but are well within the range of ages in other regions. Age at maternity has not been reported for sandbar sharks, but is an important estimate for stock assessment purposes (Walker, 2005). The estimate of 16.8 years is 3.7 years older than the median age at maturity.

The relationship between maternal length and number of embryos was weakly significant, but this relationship seemed to be influenced by the largest female examined. However, when this point was removed, the significance level of the regression changed very little, from $p=0.03$ to $p=0.04$ ($y=0.0558x - 1.3458$, $R^2=0.04$). Using the original fecundity regression, female sandbar sharks appear to increase their fecundity by one pup with every 20 cm in growth. Therefore, a female sandbar shark can potentially increase its fecundity by approximately two pups over the course of its reproductive lifetime: at

50% size-at-maturity (155 cm FL) the average female will carry 7.3 pups, and at the maximum observed size (202 cm FL) the average female will carry 9.9 pups. Accordingly, female sharks at the oldest observed age in this study (27 years) would average 10.9 pups.

Teleost fishes are known to increase both number and quality of eggs as females increase in size and age (Berkeley *et al.*, 2004). Most Carcharhinid sharks do not dramatically increase fecundity with size, nor quality of offspring (i.e. size of pups at birth, (Carrier *et al.*, 2004)), but little else is known about potential differences in reproductive output and quality as sharks age. We found that the relationship between maternal age and fecundity was more significant than that of maternal length and fecundity. This indicates that, like many teleost fishes, older sharks may be more fit as mothers, possibly able to devote more energy into reproduction that younger sharks. In fact, the oldest observed pregnant female in this study (25 years) carried 12 pups, while the biggest (202 cm FL) carried only 10. Sample sizes in this study were not large enough to test whether older females had a higher frequency of reproduction than younger ones (biennial vs. triennial), however comparisons of the ages of sharks that were considered in “year one” of vitellogenesis (MOD < 25 mm March-June) were not notably different from those in “year two” (MOD > 25 mm), with year one females averaging 15 (n=27) and year two averaging 15.9 (n=73) years of age.

This study is among the first to produce direct age estimates of maturity for the sandbar shark in the northwest Atlantic Ocean and Gulf of Mexico. This was accomplished because of the establishment of the sandbar shark research fishery, which was partially designed for the purpose of collecting biological data on this species. Differences in ages and sizes of maturity seen among this and previous studies highlight the need for current and accurate life history information, especially for a species that has historically been subjected to high fishing mortality.

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Table 1. Stage and maturity classification for *Carcharhinus plumbeus*. Female reproductive parameters are maximum ova diameter (MOD), nidamental width (NW), and uterine width (UW).

	Stage	1	2	3	4	5	6	7
Male		Juvenile	Mature	Mature, running ripe	-	-	-	-
	Claspers calcified	N	Y	Y	-	-	-	-
Female		Juvenile	Juvenile, developing	Mature, non-gravid	Ovulatory	Gravid	Post-partum	Sperm in uterus
	MOD (mm)	<10	>10	>10	>30	-	-	-
	NW (mm)	<10	>10, <30	>30	-	-	-	-
	UW (mm)	<10	>10, <30	>30	-	-	>50	-

Table 2. Maturity schedule for sizes of *Carcharhinus plumbeus*. Avg pr mat is the average proportion mature for each size bin, and SE is standard error.

	Females			Males			Maternity		
FL	Avg pr mat	SE	n	Avg pr mat	SE	n	Avg pr mat	SE	n
30-40				1.0389E-14		1			
41-50	1.5037E-11	3.4786E-12	2	1.7404E-13	4.0777E-14	4	3.5828E-08	3.8121E-05	2
51-60	7.3380E-11	2.4812E-11	6	8.8924E-13	4.9749E-13	4	9.5236E-08	2.2009E-05	6
61-70	8.9339E-10	1.8065E-10	6	4.5624E-11	2.8004E-11	2	4.8931E-07	2.3517E-04	6
71-80	1.1830E-08	5.0363E-09	3	2.9142E-10	1.3255E-10	3	2.5422E-06	3.5923E-04	3
81-90	9.9445E-08	4.3673E-08	2	7.1511E-09		1	1.0191E-05	4.3997E-04	2
91-100	0.000001	1.8714E-07	6	1.4586E-07	7.5384E-08	2	5.2788E-05	2.5401E-04	6
101-110	0.000011	0.000005	4	0.000003	0.000002	2	0.000205	0.0002	4
111-120	0.000202	0.000034	3				0.001400	0.0005	3
121-130	0.001383	0.000253	13	0.000934	0.000152	18	0.004614	0.0006	13
131-140	0.014760	0.001058	56	0.014708	0.001286	59	0.021554	0.0011	62
141-150	0.121835	0.005625	153	0.187661	0.012249	89	0.083343	0.0029	150
151-160	0.529972	0.012594	155	0.742343	0.012935	132	0.278289	0.0072	153
161-170	0.905903	0.003798	153	0.967336	0.001923	103	0.609859	0.0073	152
171-180	0.987557	0.000668	70	0.997613	0.000205	29	0.855524	0.0050	70
181-190	0.998685	0.000175	14				0.960618	0.0039	11
191-200	0.999976		1				0.996877	0	1
201-210	0.999985		1				0.997693	0	1

Table 3. Maturity schedule (proportion mature) for ages of *Carcharhinus plumbeus*. SE a and SE b are standard errors from the logistic model for parameters a and b.

Age	Females	SE a	SE b	n	Males	SE a	SE b	n	Maternity	SE a	SE b	n
0	0.000095	0.716	0.509	11	0.000004	1.185	0.090	9	0.001570	0.507	0.035	11
1	0.000182			5	0.000011			5	0.002375			5
2	0.000349			2	0.000029			1	0.003593			2
3	0.000669			4				0	0.005431			4
4	0.001282			4	0.000189			2	0.008203			4
5	0.002455			4	0.000485			1	0.012372			4
6	0.004697			6	0.001242			3	0.018619			5
7	0.008968			10	0.003176			14	0.027931			9
8	0.017057			16	0.008100			17	0.041702			15
9	0.032205			49	0.020498			33	0.061832			48
10	0.059985			73	0.050902			55	0.090759			70
11	0.109029			67	0.120840			44	0.131324			66
12	0.190063			57	0.260494			38	0.186305			57
13	0.310346			58	0.474447			40	0.257481			57
14	0.463217			43	0.698212			44	0.344343			43
15	0.623328			63	0.855685			29	0.443024			60
16	0.760387			37	0.938254			26	0.546416			37
17	0.858866			38	0.974964			34	0.645954			38
18	0.921072			25	0.990080			22	0.734271			25
19	0.957226			27	0.996106			18	0.807135			26
20	0.977228			19	0.998477			5	0.863727			19
21	0.987994			17	0.999405			4	0.905655			16
22	0.993703			7	0.999768			5	0.935644			7
23	0.996706			3					0.956557			2
24	0.998280			7					0.970886			7
25	0.999532			2					0.980585			2
26	0.999532			1					0.987096			1
27	0.999756			1								

Table 4. Reproductive parameters reported for the sandbar shark, *Carcharhinus plumbeus*.

Study	Region	Periodicity	Fecundity	Increased fecundity with size?	Size-at-maturity (females)	N (females)	Gestation time (months)
Cliff et al. 1988	South Africa	-	7.2	Y	130 PCL	162	12
Joung and Chen 1995	Taiwan	-	7.5	-	170 TL	437	10-12
Saidi et al. 2005	Tunisia	Biennial	6.9	-	172 TL	596	12
Merson 2008	NW Atlantic	Biennial or triennial	8	N	156 FL	385	12
NMFS 2006	NW Atlantic	Biennial	8.4	-	141 PCL		12
Hazin et al. 2007	Brazil	-	8.7	-	-	17	12
McAuley et al. 2007	Western Australia	Biennial	6.5	Y	136 FL	773	12
Diatta et al. 2008	Senegal	Biennial	7.7	-	220 TL	62	12
Present study	NW Atlantic, Gulf of Mexico	Triennial	8	Y	155 FL	658	12

Figure legend

Figure 1. Capture locations for all *Carcharhinus plumbeus* assigned ages in this study. Grid colors indicate number of sandbar sharks sampled.

Figure 2. Length-frequency distribution of all sandbar sharks assessed for maturity state (n=701 females, 493 males).

Figure 3. Mean A) gonadosomatic indices (GSI) and B) maximum ovum diameters (MOD) for stage 3 ● and stage 5 ○ female *Carcharhinus plumbeus*, plotted by month. Error bars represent standard deviation.

Figure 4. Cumulative frequency of mature female *Carcharhinus plumbeus* stages by month. Stage 3 mature, non-gravid, Stage 4 ovulatory, Stage 5 gravid, Stage 6 post-partum, Stage 7 sperm present in uterus.

Figure 5 Mean length of *in utero Carcharhinus plumbeus* embryos plotted by month. Error bars are ±1 standard deviation.

Figure 6. Mean A) gonadosomatic indices (GSI) and B) epididymis width values for male *Carcharhinus plumbeus* plotted by month. Error bars are ±1 standard deviation.

Figure 7. Scatter plot of maximum ovum diameter (MOD) values for stage 3 female *Carcharhinus plumbeus* plotted for spring months (January-June), indicating a three year reproductive cycle.

Figure 8. Scatter plot and regression analysis of number of pups with A) increasing fork length (FL) and B) increasing age.

Figure 9. Logistic curve plots for A) size and B) age of maturity for male and female *Carcharhinus plumbeus*

Figure 10. Logistic curve plots for A) size and B) age at maternal condition for female *Carcharhinus plumbeus*

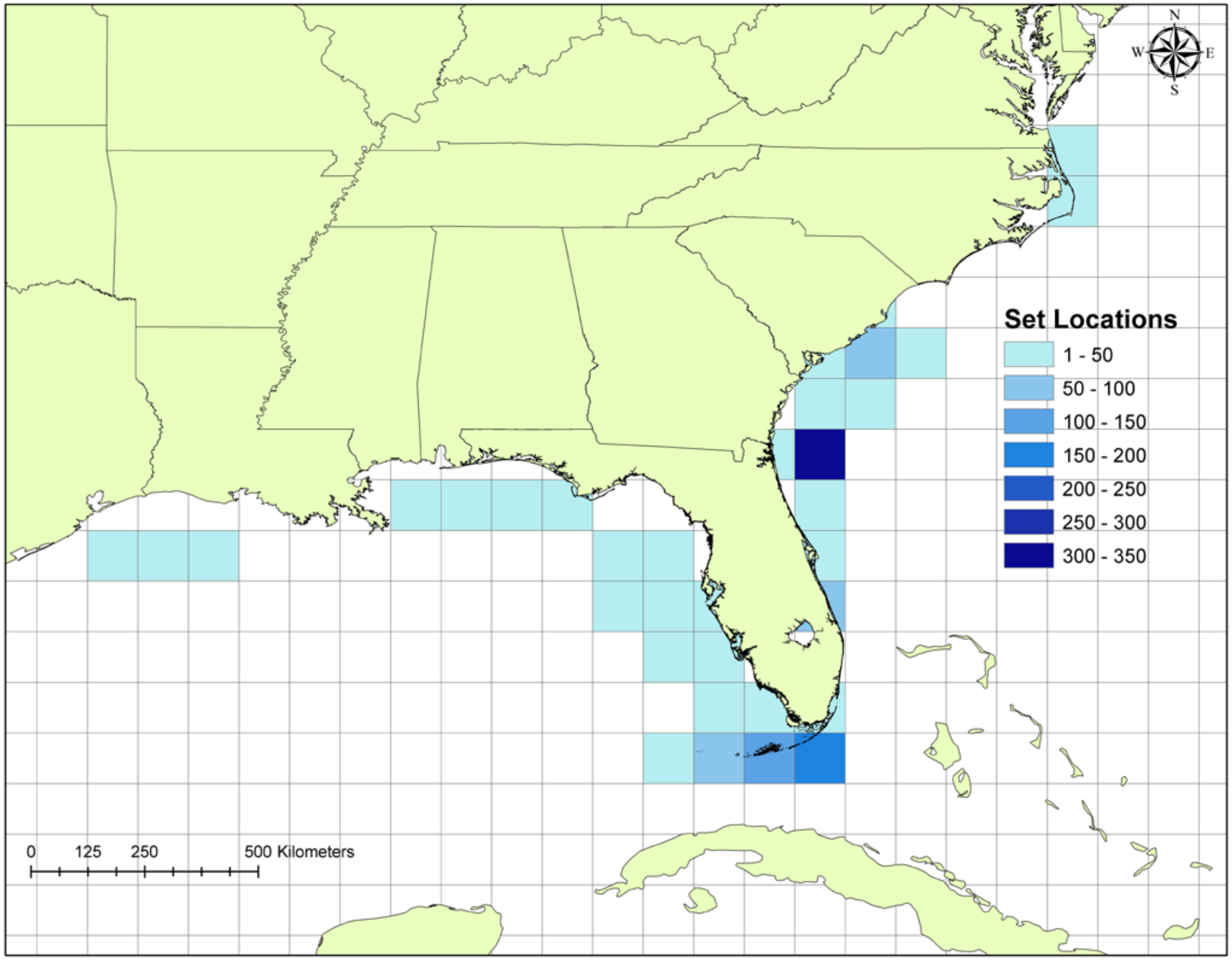

N
W
E
S
Set Locations
1 - 50
50 - 100
100 - 150
150 - 200
200 - 250
250 - 300
300 - 350
0
125
250
500 Kilometers

Figure 1

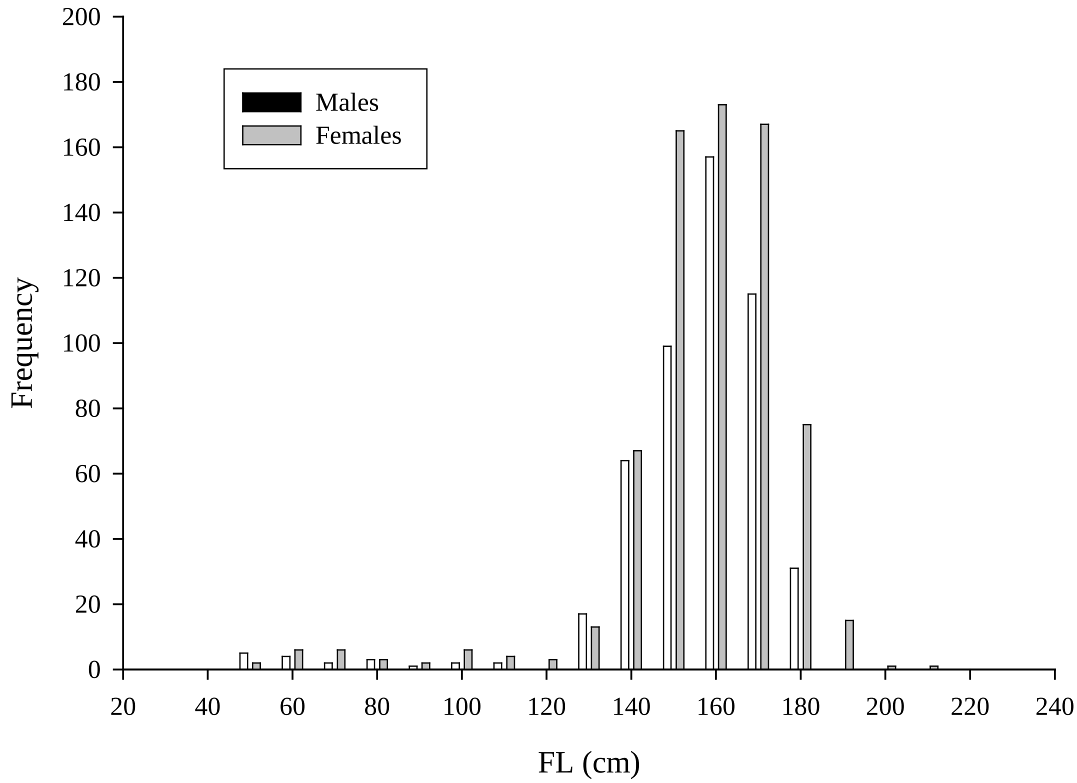

Males
Females
Frequency
200
180
160
140
120
100
80
60
40
20
0
20
40
60
80
100
120
140
160
180
200
220
240
FL (cm)

Figure 2

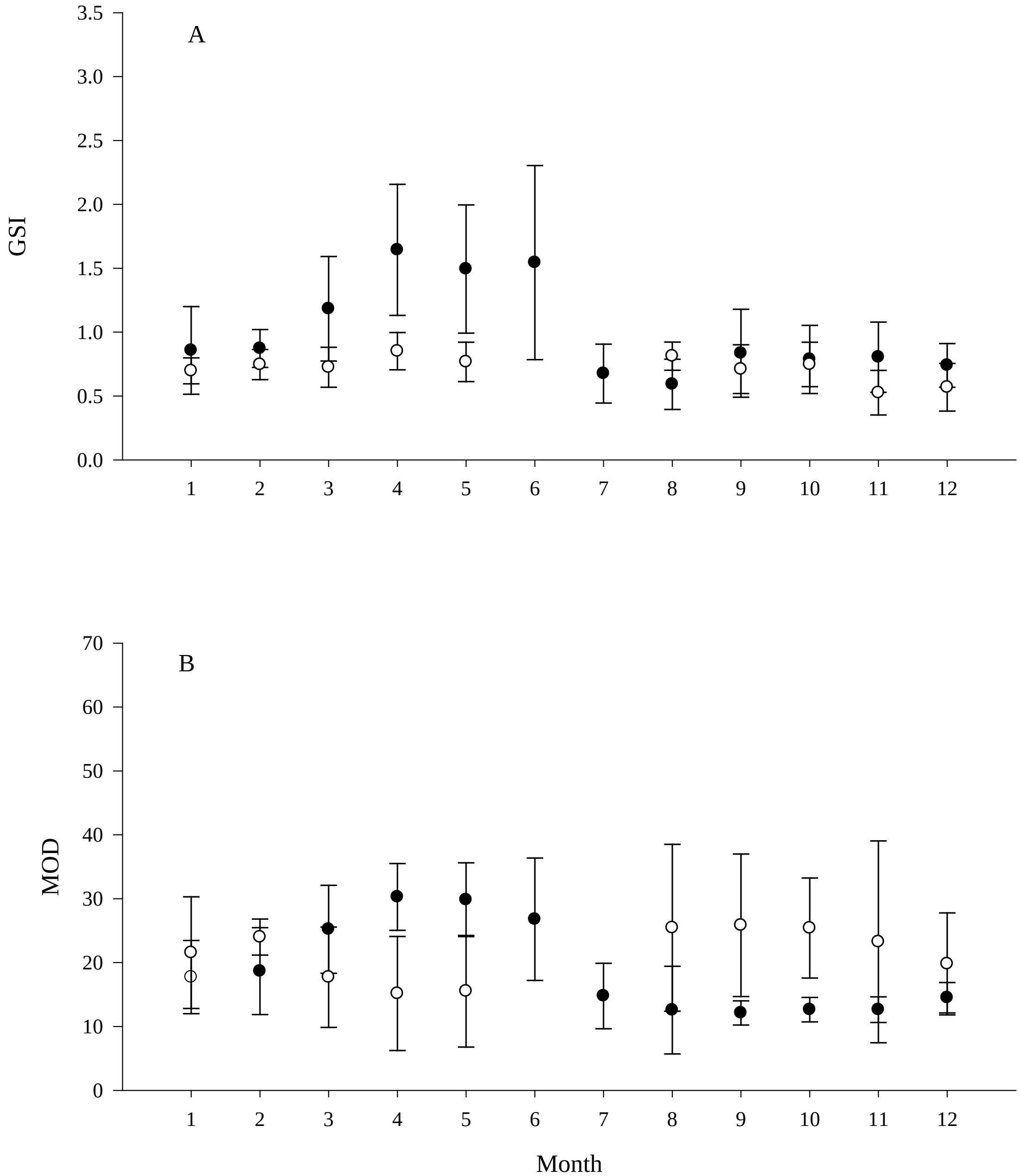

A
GSI
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1
2
3
4
5
6
7
8
9
10
11
12
B
MOD
70
60
50
40
30
20
10
0
Month

Figure 3

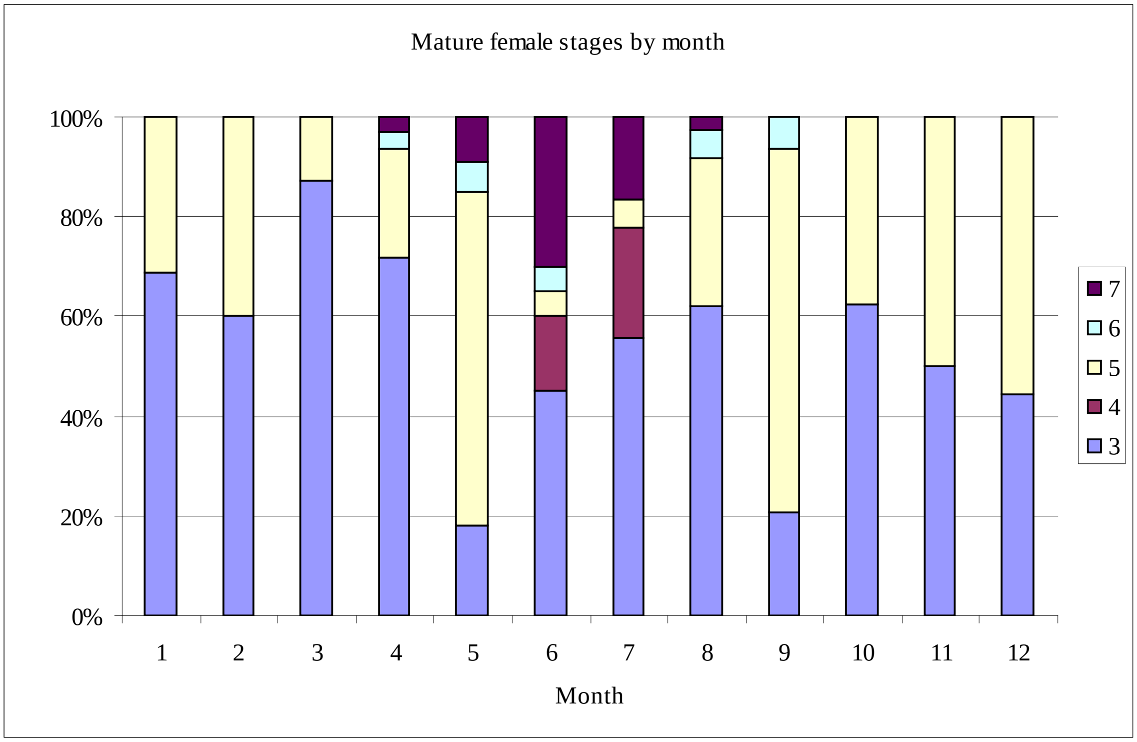

Mature female stages by month
100%
80%
60%
40%
20%
0%
1
2
3
4
5
6
7
8
9
10
11
12
Month
7
6
5
4
3

Figure 4

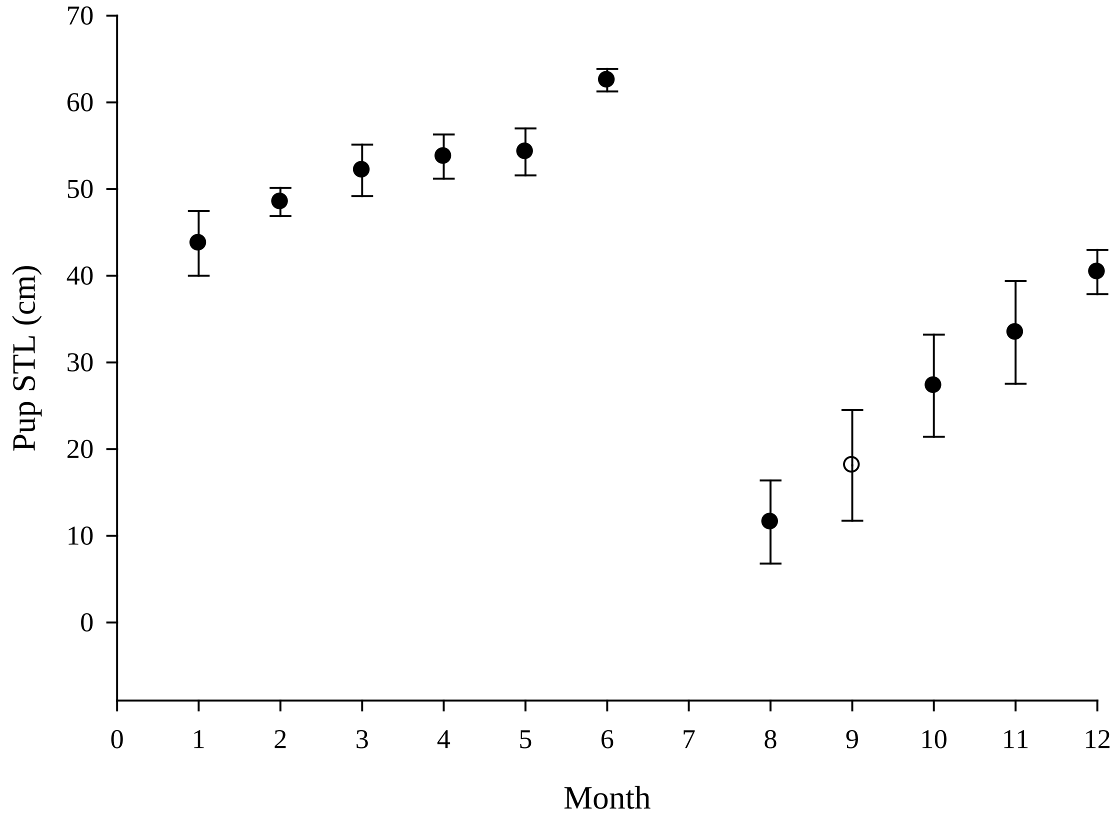


Figure 5

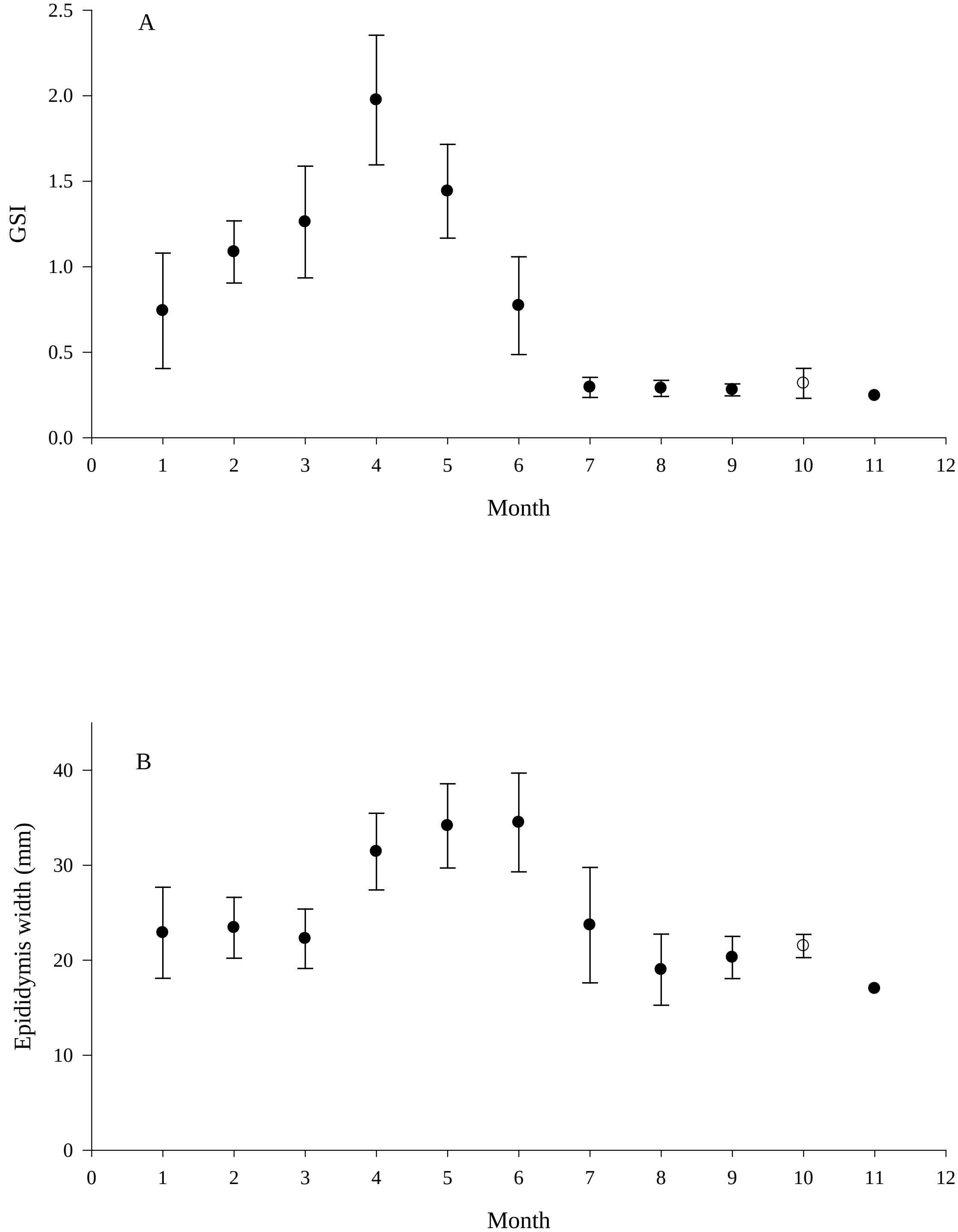

A
GSI
2.5
2.0
1.5
1.0
0.5
0.0
0 1 2 3 4 5 6 7 8 9 10 11 12
Month
B
Epididymis width (mm)
40
30
20
10
0
0 1 2 3 4 5 6 7 8 9 10 11 12
Month

Figure 6

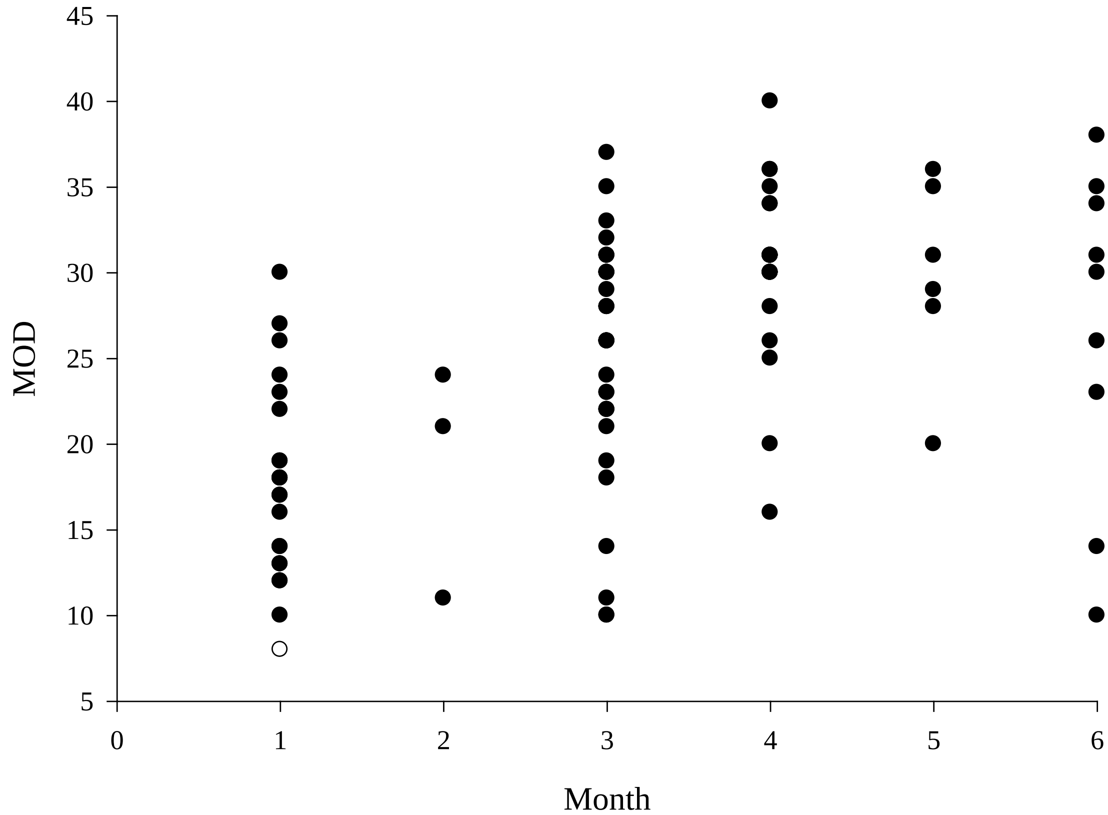
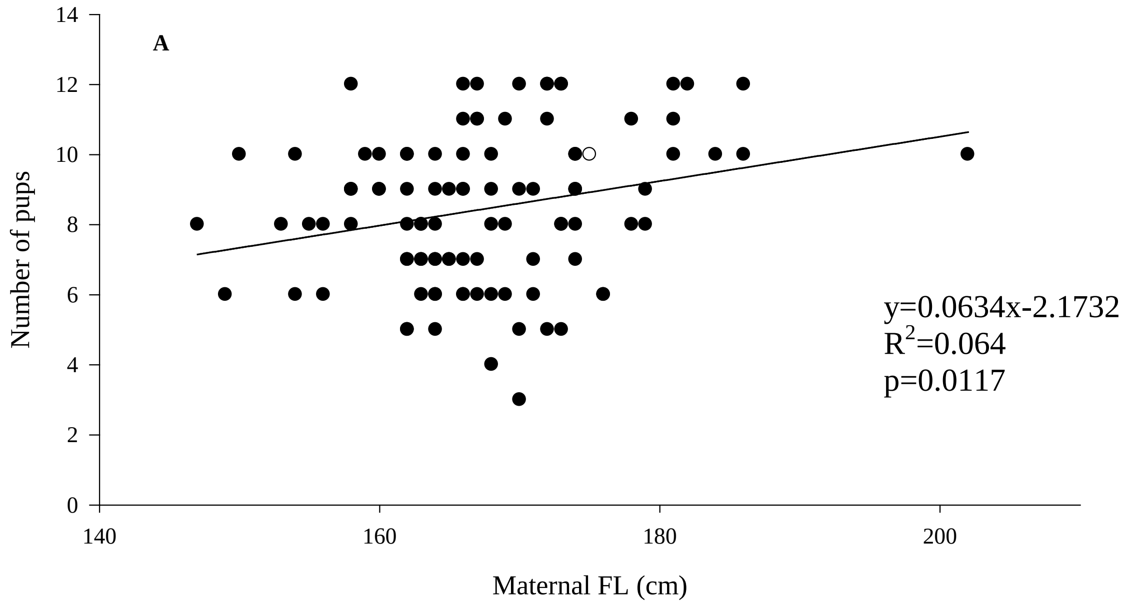


Figure 7


A
Number of pups
Maternal FL (cm)
y=0.0634x-2.1732
R2=0.064
p=0.0117

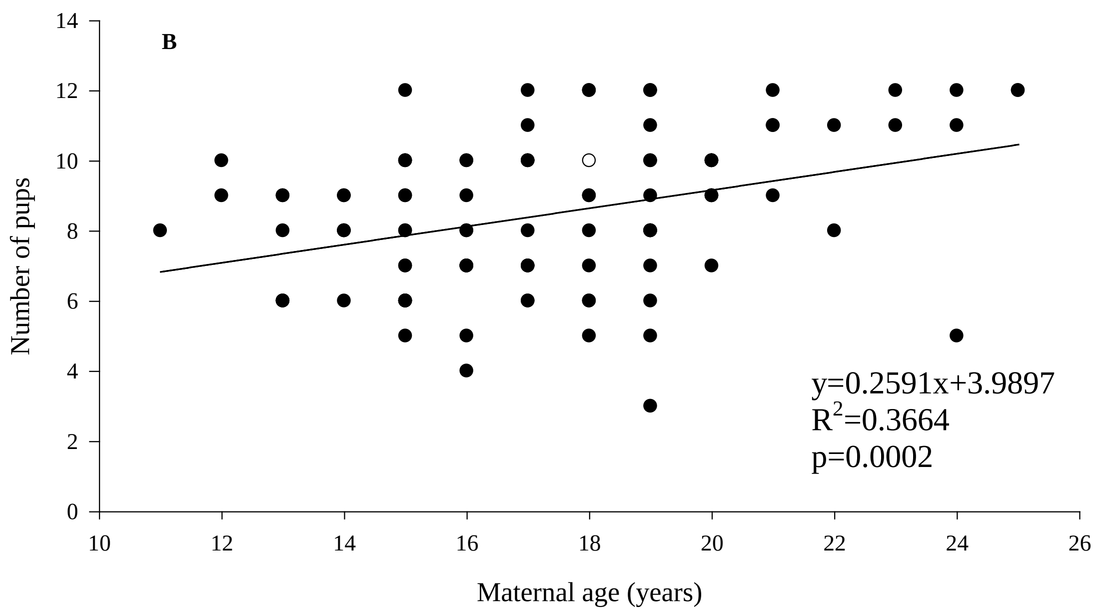

B
Number of pups
Maternal age (years)
y=0.2591x+3.9897
R2=0.3664
p=0.0002

Figure 8

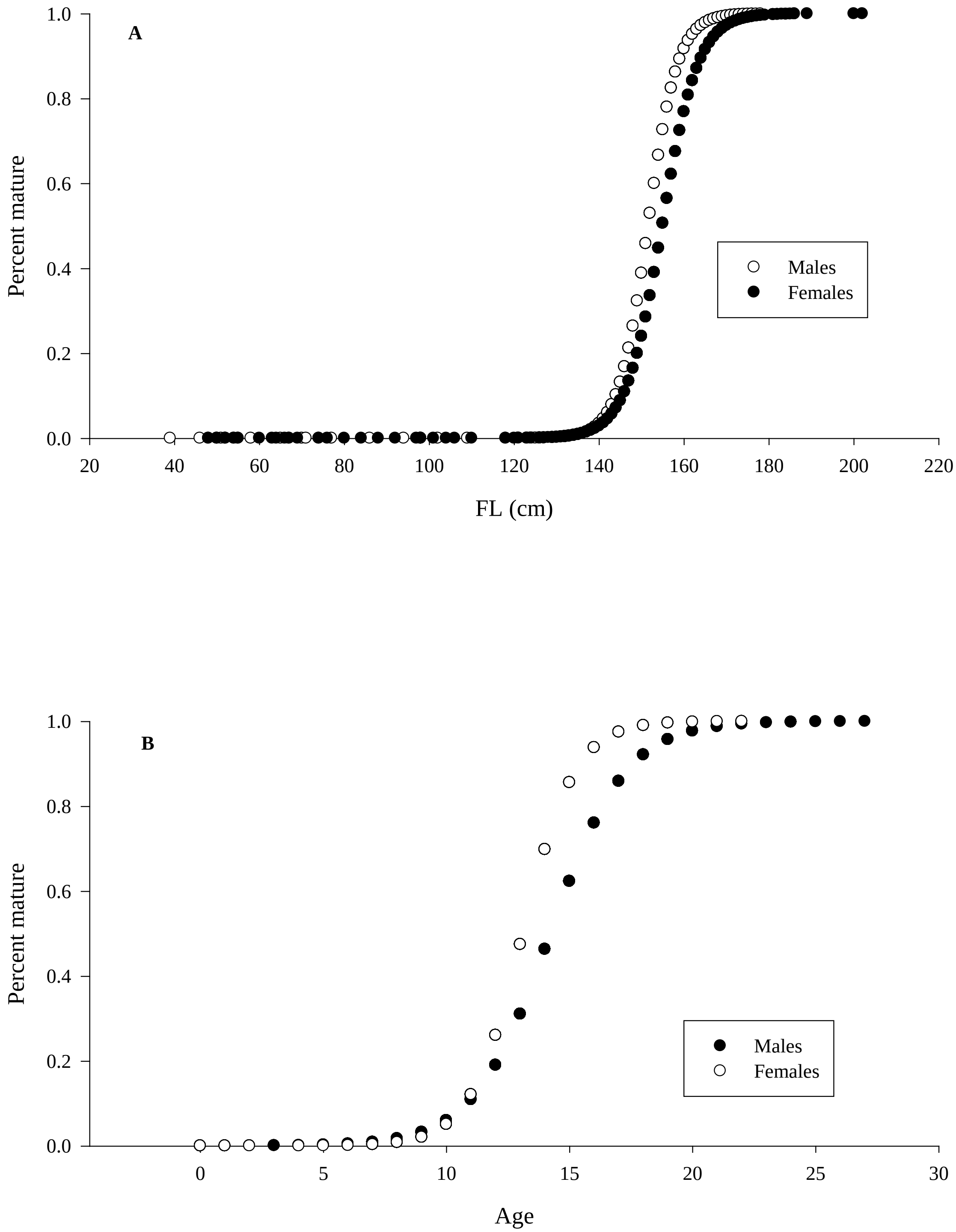

A
Percent mature
FL (cm)
Males
Females
0.0
0.2
0.4
0.6
0.8
1.0
20
40
60
80
100
120
140
160
180
200
220
B
Percent mature
Age
Males
Females
0.0
0.2
0.4
0.6
0.8
1.0
0
5
10
15
20
25
30

Figure 9

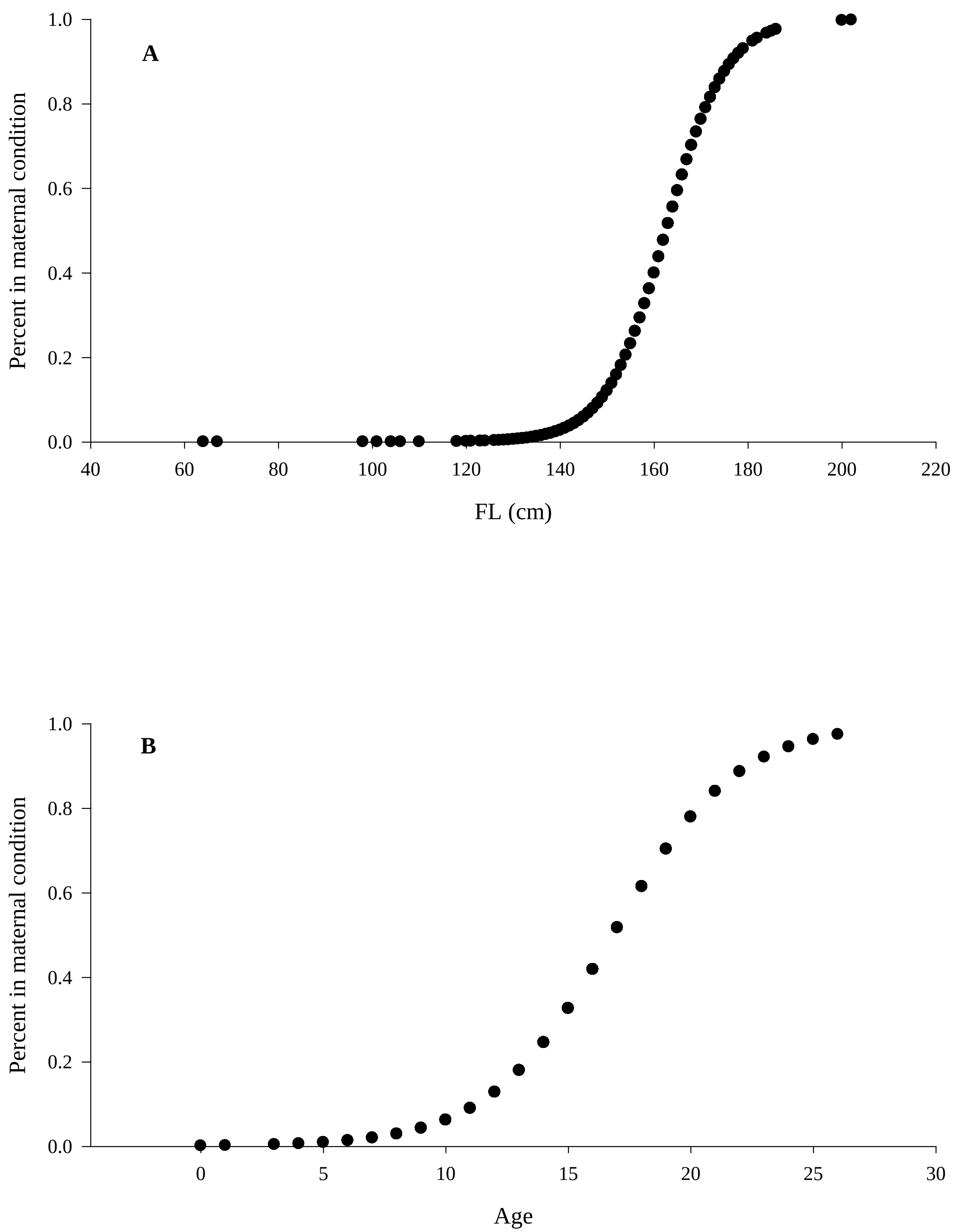

A
Percent in maternal condition
1.0
0.8
0.6
0.4
0.2
0.0
40
60
80
100
120
140
160
180
200
220
FL (cm)
B
Percent in maternal condition
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
25
30
Age

Figure 10