Marine and Coastal Fisheries, 2025, **17**, vtaf006
https://doi.org/10.1093/mcfafs/vtaf006
Advance access publication: April 30, 2025
Article

American Fisheries Society

Regional differences in reproduction of Blacktip Shark in the northern Gulf of Mexico

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ABSTRACT

Objective: Blacktip Sharks *Carcharhinus limbatus* are common in the U.S. Gulf of Mexico and are targeted in both recreational and commercial fisheries. Recent studies have supported biological separation between the eastern and western Gulf of Mexico for Blacktip Sharks, which are currently managed through separate quotas. However, comprehensive reproductive information throughout these areas is lacking. To further investigate the potential for separate stocks in the Gulf of Mexico, reproductive data were examined for Blacktip Sharks collected from the eastern and western regions.

Methods: A total of 236 Blacktip Sharks (146 females, 90 males) were collected from July 2020 to October 2021 using both fishery-independent and fishery-dependent methods. Additional length, age, and maturity data from 2006 to 2021 were incorporated into the analysis for a total of 1,308 Blacktip Sharks (726 females, 382 males).

Results: Results confirmed a seasonal and synchronous reproductive cycle for Gulf of Mexico Blacktip Sharks. Females exhibited a biennial ovarian cycle, and peak mating activity occurred in March–May followed by a 12-month gestational period. Some variability was observed within the reproductive cycle compared with past studies, indicating that some Blacktip Sharks may demonstrate a more protracted mating and ovulation period than previously described. Median size and age at maturity differed significantly by sex and region. Median length at maturity was 94.7 cm FL for males and 100.6 cm FL for females in the western Gulf of Mexico ($n = 452$) and 105.7 cm FL for males and 116.1 cm FL for females in the eastern Gulf of Mexico ($n = 856$). Median age at maturity was 3.1 years for males and 3.5 years for females in the western Gulf of Mexico and 4.7 years for males and 6.4 years for females in the eastern Gulf of Mexico.

Conclusions: These results suggest that there are significant Blacktip Shark life history differences between the eastern and western Gulf of Mexico and that separate quotas may need to be implemented for effective fisheries management.

KEYWORDS: elasmobranchs, Gulf of Mexico, life history, stock assessment

LAY SUMMARY

A comprehensive evaluation of Blacktip Shark reproductive biology in the Gulf of Mexico indicates significant life history differences between the eastern and western gulf, thus providing better reproductive parameters for stock assessment.

INTRODUCTION

The Blacktip Shark *Carcharhinus limbatus* inhabits coastal tropical and subtropical waters worldwide and is abundant in the U.S. Atlantic Ocean and the Gulf of Mexico (Castro, 1996). Commonly occurring on continental shelves and shallow inshore areas, Blacktip Sharks are targeted in both commercial and recreational fisheries for their valuable meat and fins (Southeast Data, Assessment, and Review [SEDAR], 2012, 2020). They are the most frequently harvested species in the U.S. Atlantic and Gulf of Mexico large coastal shark fishery (SEDAR, 2012) and account

Received: June 25, 2024. **Revised:** January 21, 2024. **Editorial decision:** January 27, 2025

for approximately 60% of the commercial and recreational catch of large coastal shark species (National Marine Fisheries Service [NMFS], 2023). In 2021, commercial landings of U.S. Atlantic and Gulf of Mexico Blacktip Sharks totaled 64,410 kg while recreational landings totaled 443,160 kg, with most recreational landings coming from the Gulf of Mexico (NMFS, 2023). Current assessments indicate that neither the Gulf of Mexico nor the U.S. Atlantic Blacktip Shark stocks are overfished, and overfishing is not occurring (SEDAR, 2012, 2020).

Despite successful management of this fishery, uncertainty regarding stock structure and life history parameters remains. Genetic studies support separate Blacktip Shark stocks in the U.S. Atlantic Ocean and Gulf of Mexico (Swift et al., 2023), and tagging data show little exchange between these two regions (Bethea et al., 2012; Kohler & Turner, 2019). Carlson et al. (2006) determined that median age at maturity was 4.5 years and 5.7 years for males and females in the eastern Gulf of Mexico, respectively, while age at maturity was 5.0 years for males and 6.7 years for females for those from the U.S. Atlantic. Updated analyses for the Gulf of Mexico and U.S. Atlantic determined median age at maturity of 4.8 and 6.3 years (Gulf of Mexico) and 5.3 and 6.7 years for males and females, respectively (Baremore & Passerotti, 2013; Natanson et al., 2019). However, due to varying statistics and the potential for temporal sampling bias, it could not be definitively concluded that differences in life history characteristics exist between these areas. Regardless of the lack of conclusive evidence for life history differences in Gulf of Mexico Blacktip Sharks, SEDAR 29 recommended a benchmark assessment be undertaken to evaluate treating Blacktip Sharks as separate stocks within the Gulf of Mexico (SEDAR, 2012), thus comprising a potential eastern and western stock separated at 88°W. Previous studies assessing Blacktip Shark life history have only been conducted in the eastern Gulf of Mexico (Baremore & Passerotti, 2013) and off the East Coast of the United States (Carlson et al., 2006; Castro, 1996). However, no studies have examined the reproductive biology of the species in the western Gulf of Mexico.

Stock assessment models rely on accurate reproductive measurements, such as fecundity, size and age at maturity, and reproductive seasonality and synchrony. Thus, the objectives of this study were to examine the reproductive biology of Blacktip Sharks and determine if reproductive parameters varied between the eastern and western Gulf of Mexico.

METHODS

Data collection and sampling

Archived Blacktip Shark reproductive data collected by researchers at the NMFS Southeast Fisheries Science Center (Baremore & Passerotti, 2013; Passerotti & Baremore, 2012), Texas A&M University at Galveston (R. J. D. Wells, unpublished data), and Mississippi State University (J. M. Drymon, unpublished data) from 2006 to 2021 were used to supplement sample sizes in this study (Figure 1). Most archived samples from NMFS were collected by NMFS fisheries observers aboard commercial longline vessels and fishery-independent gill-net surveys in the eastern Gulf of Mexico (Baremore & Passerotti, 2013; Passerotti & Baremore, 2012). Archived NMFS data included detailed measurements of reproductive organs, maturity stage, and estimated age for each Blacktip Shark (Baremore & Passerotti, 2013; Passerotti & Baremore, 2012). Most archived samples from Texas A&M University at Galveston and Mississippi State University were collected through fishery-independent bottom longline surveys (e.g., Drymon et al., 2020).

For this study, Blacktip Sharks were sampled off Texas, Louisiana, Alabama, and Florida from July 2020 through October 2021. Sampling occurred throughout the year in coastal waters. Most samples were obtained by bottom longline as part of fishery-independent sampling efforts, but some samples were collected from fishery-dependent gill nets and trawls. Following capture, individuals were given a unique ID and capture date, and precaudal length (PCL; tip of the rostrum to precaudal pit), fork length (FL; tip of the rostrum to the fork on the caudal fin), and stretched total length (STL; tip of the rostrum to the posterior end of the extended caudal fin) were measured in centimeters. Fork length was the primary length measurement used in this study because it is preferred in cases when a fish species exhibits a deeply forked caudal fin (Holden & Raitt, 1974), is known to be less variable than total length (Francis, 2006), and was used in the most recent Blacktip Shark stock assessments (SEDAR, 2012, 2018, 2020). Reproductive measurements were recorded in the field and followed standard protocols used in previous elasmobranch reproduction studies (e.g., Driggers et al., 2004; Hoffmayer et al., 2013; Sulikowski et al., 2007). Samples were divided based on the location of capture to evaluate reproductive differences between the eastern and western Gulf of Mexico. Sharks collected west of 88°W were assigned a western Gulf of Mexico designation, while sharks collected east of 88°W were assigned an eastern Gulf of Mexico designation.

For males, maturity was assessed macroscopically following Clark and von Schmidt (1965). Mature males were defined based on the following three criteria: (1) having fully calcified claspers, (2) having claspers that rotated 180 degrees anteriorly, and (3) the presence of a rhipidion that flares open completely. Outer clasper (from the pelvic fin insertion to the clasper tip) measurements were recorded, along with right testis length (mm), maximum width (mm), and weight (g). The presence or absence of sperm in the seminal vesicle, epididymis, or ductus deferens was also recorded.

For females, ovary length (mm), width (mm), and weight (g) were measured and the approximate total number of visible follicles was estimated. If present, the number of vitellogenic ova was recorded along with the diameter of the five largest, nonatretic follicles. The width of the right oviducal gland and the right uterus were also measured (mm), and uterus condition was recorded as follows: thick walled, thin walled, cut/damaged, never pupped, distended/recently pupped, pregnant, or juvenile. If present, the number of pups was recorded for each uterus. Examples of reproductive organs are shown in Castro (2010).

All Blacktip Sharks were assigned a reproductive stage following protocols from the NMFS Southeast Fisheries Science Center (Baremore & Passerotti, 2013). Males were assigned a stage from 1 to 4 as follows: (1) juvenile (no clasper calcification, rhipidion does not easily open, no clasper rotation); (2) juvenile, maturing (partial clasper calcification, rhipidion cannot be easily opened, poor clasper rotation); (3) mature (fully

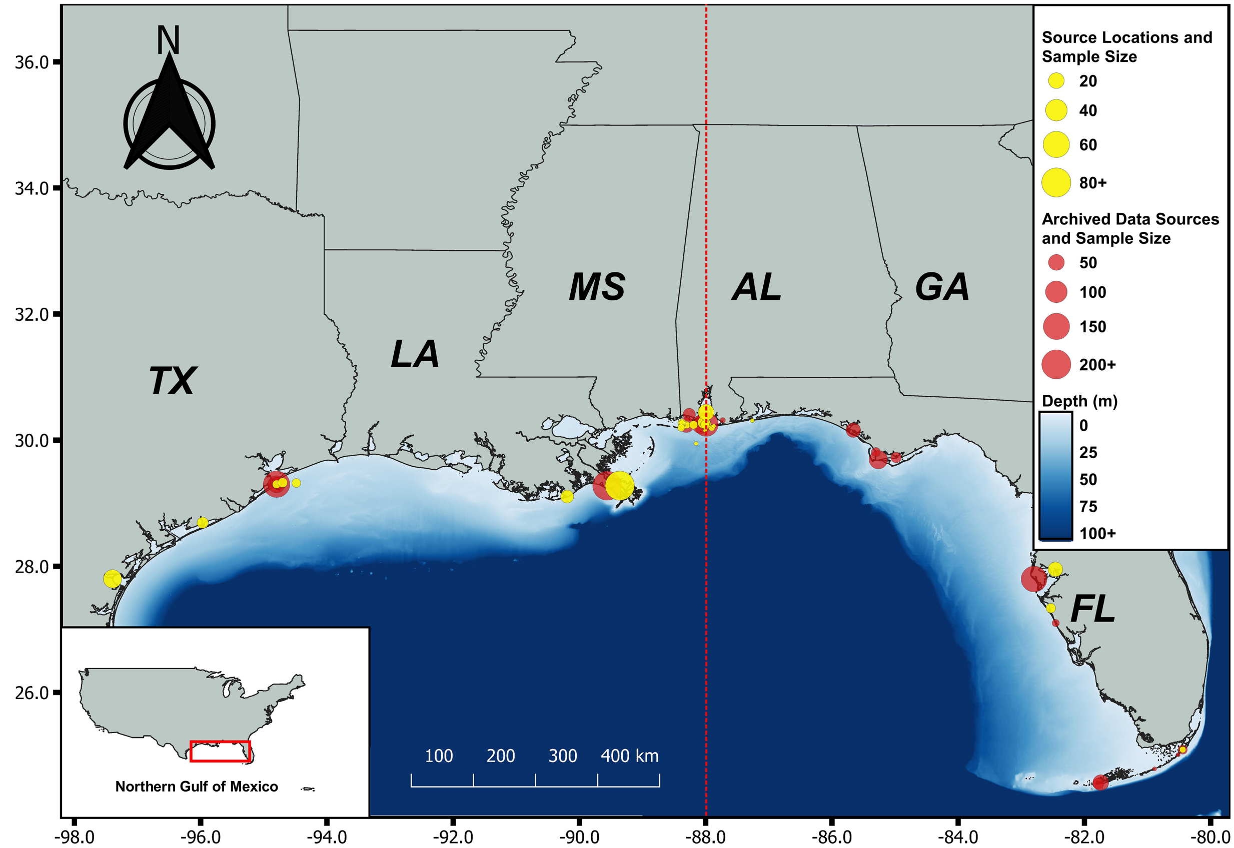

Figure 1. Map showing locations of data acquisition in the present study. Blacktip Sharks sampled during 2020–2021 fishery-independent and fishery-dependent sampling efforts are shown in yellow. Additional archived data sources collected from 2006 to 2021 are shown in red. The vertical dotted red line separates western versus eastern samples at 88°W. State abbreviations are as follows: TX = Texas, LA = Louisiana, MS = Mississippi, AL = Alabama, GA = Georgia, and FL = Florida.

calcified claspers, rhipidion completely and opens easily, full clasper rotation); or (4) mature with sperm present. Females were assigned a stage from 1 to 7 as follows: (1) very juvenile; (2) juvenile, maturing (never pupped); (3) mature (not gravid); (4) ovulatory (yolk present in uterus); (5) gravid; (6) postpartum (distended uterus); or (7) sperm present in uterus (Table 1). For sharks that were not initially assigned a maturity state, reproductive stage was used to determine a maturity state when possible.

Analysis

Plots of gonad measurements were constructed to assess the reproductive seasonality and synchrony of Gulf of Mexico Blacktip Sharks. For males, differences among mean testis width, testis weight, testis length, and epididymis width values by stage were tested using an ANOVA with post hoc pairwise comparisons using Tukey's least-square difference test. If observations failed to meet the assumptions of normality and homoscedasticity, a Kruskal–Wallis test was used to determine differences among stages followed by pairwise comparisons performed with a Wilcoxon rank-sum test with the Holm–Sidak correction. For females, differences among mean maximum follicle diameter (MFD), ovary weight (OW), uterus width (UW), and oviducal gland width (OGW) values by stage were tested using the same methodology. Differences in these reproductive measurements were also analyzed by region for each reproductive stage using Welch's two-sample *t*-test. Mean reproductive values for stage-3 and stage-4 males and stage-3 females were plotted by month and region to visualize reproductive patterns and potential differences between the eastern and western Gulf of Mexico. The relative frequency of reproductive stages for both male and female Blacktip Sharks by month were also plotted to visually assess differences in reproductive seasonality.

Because many adult Blacktip Sharks were not weighed, weights for mature individuals were estimated using a length–weight regression (SEDAR, 2020). With these data, a gonadosomatic index (GSI) was calculated to estimate the timing of vitellogenesis and ovulation in females and spermatogenesis in males. Significant differences in male and female GSI by month and region were tested with a Kruskal–Wallis test followed by Dunn's post hoc test since observations did not satisfy the assumption of normality. The GSI for each individual was calculated using the following modified formula (Nikolsky, 1963):

$$\text{GSI} = 100 \times \{\text{gonad mass (g)} / [\text{total mass (g)} - \text{gonad mass (g)}]\},$$

where testis or ovary mass were used for male or female Blacktip Shark gonad mass, respectively.

Table 1. Reproductive stage classifications for female Blacktip Sharks used in the present study. Descriptions follow Walker (2005) and Baremore and Hale (2012).

Stage	Classification	Description
1	Very juvenile	Thin, white uteri; oviducal glands similar size as uteri; granular/clear ovarian follicles
2	Juvenile, maturing	Uteri and oviducal glands distinct; yellow follicles present in ovary
3	Mature	Enlarged ovarian follicles and evidence of vitellogenesis
4	Ovulatory	Yolk present in uterus
5	Gravid	Pup(s) present in uterus
6	Postpartum	Visible umbilical scars present
7	Sperm present in the uterus	Sperm packs observed in uterine lining

The relationship between maternal FL, age, and weight and brood size was compared using linear regression to determine if fecundity increased with female age or size. Brood size was compared by region using a Kruskal–Wallis test, and the number of pups found in the left and right uteri were compared using a Mann–Whitney *U*-test since observations did not satisfy the assumption of normality (Kruskal & Wallis, 1952).

Differences in FL between sex and region were evaluated using a Kruskal–Wallis test since the assumptions of normality and equal variance were not met. A Welch two-sample *t*-test was used to test for differences between regions by sex. Median size and age at maturity were estimated with a logistic regression

$$y = \frac{1}{\left(1 + e^{-(a+bx)}\right)}$$

fit to binomial maturity data (0 = juvenile, 1 = mature) using the R packages "FSA" and "car" (Fox & Weisberg, 2019; Ogle et al., 2021), where x = FL or age (Carlson et al., 2006). All samples were aged independently by two readers who counted band pairs (one opaque and one translucent) distal to the birth mark, which was denoted by a pronounced change in the angle of the intermedialia. Archived data from Passerotti and Baremore (2012) supplemented age data for Blacktip Sharks from the eastern Gulf of Mexico. Band pair counts were based on the assumption that Blacktip Sharks deposit one band pair per year (Carlson et al., 2006). Age assignments for this study were based on a putative May 1 birthdate following Carlson et al. (2006) (R. J. D. Wells, Texas A&M University, unpublished data). Reproductive data were paired with age data to determine median age at maturity. Logistic regressions of median length and age at maturity were then compared between region and sex with logistic regressions and likelihood-ratio chi-square tests. Median length and age at maturity were also plotted to visualize potential differences between regions and sex.

RESULTS

Archived length, age, and maturity data were obtained from 1,072 Blacktip Sharks (580 females, 492 males) sampled from 2006 to 2021 (Wells, unpublished data; J. M. Drymon, unpublished data; NMFS, unpublished data; Baremore & Passerotti, 2013; Passerotti & Baremore, 2012). A total of 236 Blacktip Sharks (146 females, 90 males) were sampled off Texas (n = 52), Louisiana (n = 87), Alabama (n = 71), and Florida (n = 26) for reproductive analysis in the present study. Of these, 153 Blacktip Sharks were sampled from the western gulf, and 83 Blacktip Sharks were sampled from the eastern gulf. The combined data set encompassed a total of 1,308 Blacktip Sharks (726 females and 582 males); of these, 452 Blacktip Sharks were sampled from the western gulf and 856 Blacktip Sharks were sampled from the eastern gulf (Table 2).

Of the 1,308 Blacktip Sharks that could be examined, 370 males (63.6%) and 464 females (63.9%) were mature. In contrast, 212 males (36.4%) and 262 females (36.1%) were immature. The size of male Blacktip Sharks ranged from 43.5 to 155.0 cm FL, and the size of female Blacktip Sharks ranged from 40.0 to 164.0 cm FL (Figure 2). Females were significantly larger than males (H = 71.01, df = 1, P < 0.005), and both males and females were significantly larger in the western area than the eastern area (Welch's t-test: P < 0.05).

For male Blacktip Sharks, median length at maturity was 100.8 cm FL (95% CI = 98.9–102.6), and for female Blacktip Sharks, median length at maturity was 108.3 cm FL (95% CI = 106.4–110.5; Table 2). The smallest fully mature male Blacktip Shark was 87.6 cm FL, and the largest immature male examined was 130.0 cm FL. The smallest fully mature Blacktip female measured 87.9 cm FL (maturity stage = 3), and the largest immature Blacktip female measured 142.0 cm FL (maturity stage = 2).

For the western Gulf of Mexico, median length at maturity was 94.7 cm FL (95% CI = 89.4–98.6) for Blacktip Shark males and 100.6 cm FL (95% CI = 97.2–103.7) for females. For the eastern Gulf of Mexico, median length at maturity was 105.7 cm FL (95% CI = 103.5–107.8) for males and 116.1 cm FL (95% CI = 113.6–118.3) for females (Figure 3). Significant differences in median length at maturity were found between sexes (chi-square likelihood ratio = 36.86, P < 0.0005) and regions for Blacktip Shark males (chi-square likelihood ratio = 18.85, P < 0.005) and females (chi-square likelihood ratio = 61.42, P < 0.005).

Age and maturity information was available for 853 Blacktip Sharks (462 female, 391 males; Table 2). For the entire Gulf of Mexico, median age at maturity was 4.0 years for male Blacktip Sharks (95% CI = 3.7–4.4) and 5.2 years for female Blacktip Sharks (95% CI = 4.7–5.6). Significant differences were found between sexes for median age at maturity (chi-square likelihood ratio = 15.89, P < 0.005).

For the western Gulf of Mexico, median age at maturity for Blacktip Shark males was 3.1 years (95% CI = 2.1–3.8) and 3.5 years (95% CI = 2.7–4.2) for females. For the eastern Gulf of Mexico, median age at maturity for males was 4.7 years (95% CI = 4.2–5.2) and 6.4 years (95% CI = 5.8–6.9) for females. Regional differences for males (chi-square likelihood ratio = 15.69, P < 0.005) and females (chi-square likelihood ratio = 44.27, P < 0.005) were observed (Figure 4). Parameters for each logistic model are presented in Table 2.

Table 2. Length and age at maturity for Blacktip Sharks collected from the Gulf of Mexico from 2006 to 2021. The parameters *a* (intercept) and *b* (slope) were estimated by the logistic model and are presented with their standard errors. Data are separated by region. Abbreviations are as follows: LCI = lower limit of the confidence interval and UCI = upper limit of the confidence interval.

	Length at maturity (cm FL)								Age at maturity (years)							
Sex	**Value**	***a***	**SE**	***b***	**SE**	**LCI**	**UCI**	***n***	**Value**	***a***	**SE**	***b***	**SE**	**LCI**	**UCI**	***n***
Gulf of Mexico																
Female	108.3	−14.00	1.16	0.13	0.01	106.2	110.2	726	5.2	−3.46	0.34	0.67	0.06	4.74	5.62	462
Male	100.8	−15.57	1.52	0.15	0.01	98.91	102.6	582	4.0	−3.47	0.39	0.86	0.08	3.70	4.39	391
Western Gulf of Mexico																
Female	100.6	−14.81	2.32	0.15	0.02	97.30	103.7	250	3.5	−2.73	0.74	0.79	0.15	2.68	4.16	157
Male	94.7	−11.00	2.19	0.12	0.02	89.39	98.59	202	3.1	−2.59	0.85	0.84	0.19	2.02	3.84	126
Eastern Gulf of Mexico																
Female	116.1	−19.4	2.16	0.17	0.02	113.7	118.4	476	6.4	−4.38	0.51	0.69	0.07	5.80	6.92	305
Male	105.7	−22.32	2.97	0.21	0.03	103.5	107.8	380	4.7	−4.03	0.51	0.85	0.10	4.23	5.19	265

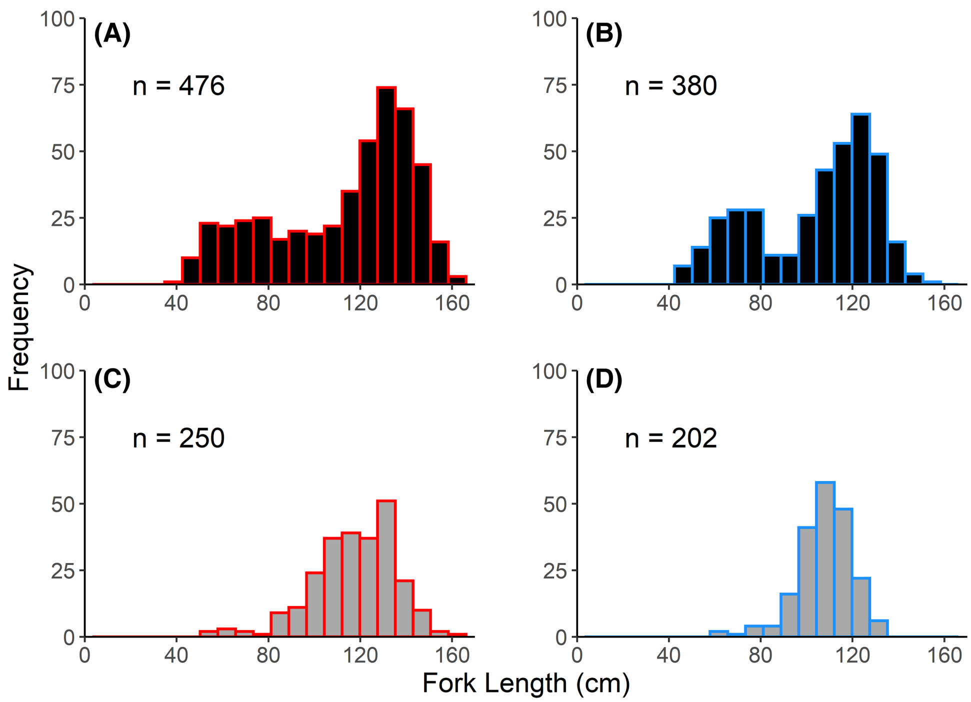

Figure 2. Length-frequency distributions of Blacktip Sharks collected from the Gulf of Mexico from 2006 to 2021. Panels show the length distribution of (A) female and (B) male Blacktip Sharks in the eastern Gulf of Mexico and the length distribution of (C) female and (D) male Blacktip Sharks in the western Gulf of Mexico.

Male reproductive analysis

Male Blacktip Shark reproductive stages were modified due to low sample sizes of stage-2 individuals ($n = 7$); thus, stage 1 and stage 2 (juvenile and juvenile, maturing, respectively) were combined for analysis. A total of 552 Blacktip Shark males were assigned a reproductive stage. Revised male reproductive stages were as follows: stage 1/2 = juvenile and juvenile, maturing ($n = 212$); stage 3 = mature ($n = 226$); and stage 4 = mature with sperm present ($n = 114$). Sample sizes for reproductive analysis varied by reproductive measurement (Table 3; see Supplementary Material).

Outer clasper length increased gradually in male Blacktip Sharks <90 cm FL, followed by rapid growth until ~110 cm FL (Figure 5), falling just below the onset of maturity estimated in the present study. Mean ± SD outer clasper length of immature males was 61.0 ± 36.4 mm, while mature males had a mean ± SD outer clasper length of 115.5 ± 10.4 mm. Outer clasper length values were not significantly different by region ($t = -0.65$, df = 111.44, $P = 0.514$). Mature males were collected during each month of the study, and stage-4 males were collected in all months except November (Figure 6). While significant differences in relative monthly frequencies of mature males by region were detected ($X^2 = 45.49$, df = 11, $P < 0.005$), sample sizes were limited from the western Gulf of Mexico.

The values for testis weight, testis width, testis length, and epididymis width were well defined for stage 1/2 and stage 3 but were less defined for stage-4 Blacktip Shark males (Table 2; Supplementary Material). Only testis length values were not heteroscedastic and satisfied the assumptions of normality. Significant differences were found in testis width ($H = 83.34$, df = 2, $P < 0.001$), testis weight ($H = 0.53$, df = 2, $P < 0.001$), testis length ($F_{2,403} = 87.88$, $P < 0.001$), and epididymis width

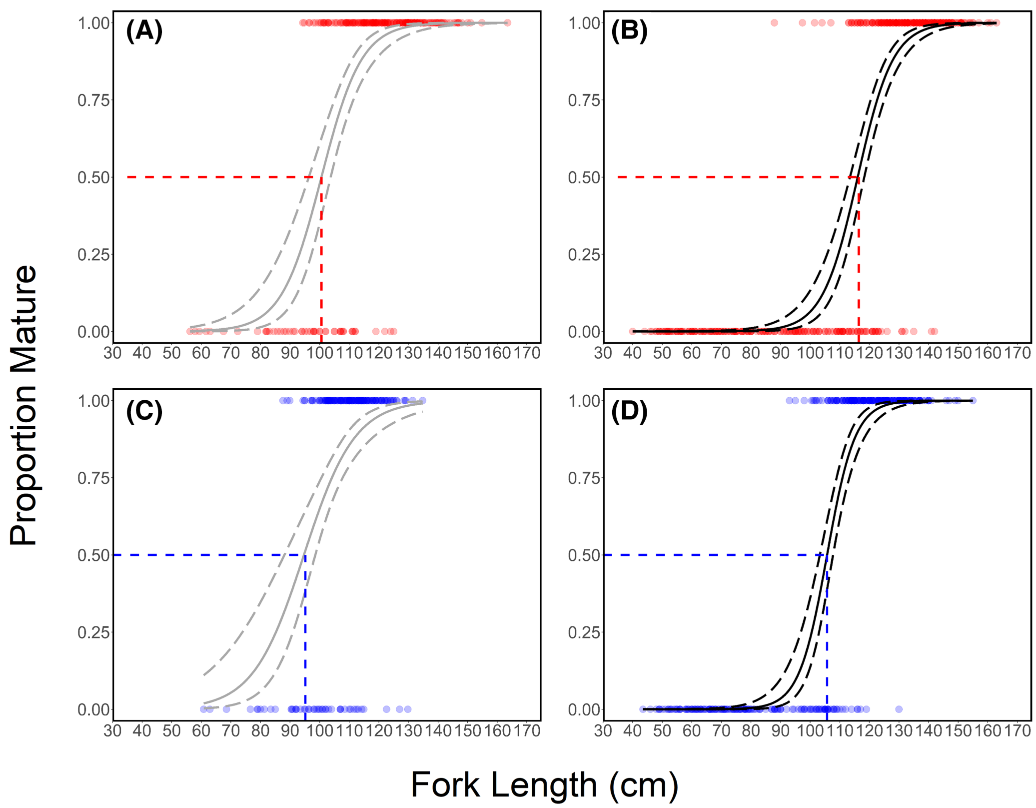

Figure 3. Logistic models fitted to predicted length at maturity for female and male Blacktip Sharks collected from the Gulf of Mexico from 2006 to 2021. Panels (A) and (B) represent predicted length at maturity for female Blacktip Sharks, while panels (C) and (D) represent predicted length at maturity for male Blacktip Sharks. Gray lines indicate Blacktip Sharks collected from the western Gulf of Mexico (females: $n=250$, males: $n=202$), and black lines indicate samples collected from the eastern Gulf of Mexico (females: $n=476$, males: $n=380$). Dashed lines represent 95% confidence intervals of the logistic curve of the same color. Darker points represent more Blacktip Sharks in a given size-class.

($H=70.13$, df $=2$, $P<0.001$) between stage 1/2 and stage 3 and between stage 1/2 and stage 4, but no differences between stage 3 and stage 4 were detected for any of the four measurements (Supplementary Material). Differences between stages by region varied by measurement (Supplementary Material).

Stage-3 and stage-4 Blacktip Shark males had the highest testis weight, length, and width values from February to May, while epididymis width peaked in April–June (Figure 7). Testis weight ($H=8.83$, df $=1$, $P=0.003$), length ($H=15.07$, df $=1$, $P<0.0005$), and width ($H=13.14$, df $=1$, $P<0.0005$) were significantly different by region, but epididymis width was similar between regions. There were significant differences by month for testis weight ($H=183.29$, df $=11$, $P<0.005$), testis length ($H=103.04$, df $=11$, $P<0.001$), testis width ($H=182.76$, df $=11$, $P<0.005$), and epididymis width ($F_{11,\ 220}=11.43$, $P<0.005$), with testis weight, length, and width having significantly higher values in spring months (February–May) compared with summer, fall, and winter months. Post hoc tests also showed epididymis width values to be significantly higher between February and June, with a sharp decline observed in August (Figure 7).

The monthly male GSI exhibited prominent peaks in spring (March–May; Figure 8) and was significantly higher ($H=170.5$, df $=11$, $P<0.005$) in March and April (0.58–0.62) compared with summer, fall, and winter months (June–December; 0.04–0.27). While significant differences in GSI by region were found ($H=39.70$, df $=1$, $P<0.005$), GSI values for the western Gulf of Mexico could only be calculated for February–May. Semen was observed in the lower reproductive tract of males in all months ($n=132$), with the highest frequency occurring in February, April, and May and the lowest frequency observed from October to January.

Female reproductive analysis

A total of 581 female Blacktip Sharks were assigned a reproductive stage, but sample sizes for reproductive analysis varied by reproductive measurement (Table 4; Supplementary Material). At approximately 110 cm FL, the oviducal gland began to rapidly increase in size from a mean $\pm$ SD of 16.9 ± 8.2 mm for immature females to 27.4 ± 5.9 mm for newly mature females (Figure 9), which aligns with the estimated median length at maturity for female Blacktip Sharks in this study. Oviducal gland width values were marginally significantly different by region ($t=2.04$, df $=133.71$, $P=0.043$). Mature females were captured every month, and significant differences in relative monthly frequencies of mature females by region were detected ($X^2=155.0$, df $=11$, $P<0.005$, Figure 10). Ovulation most frequently occurred in June for females collected from both regions. Pupping most likely occurred in May since no gravid females were observed in June and pregnant females were first

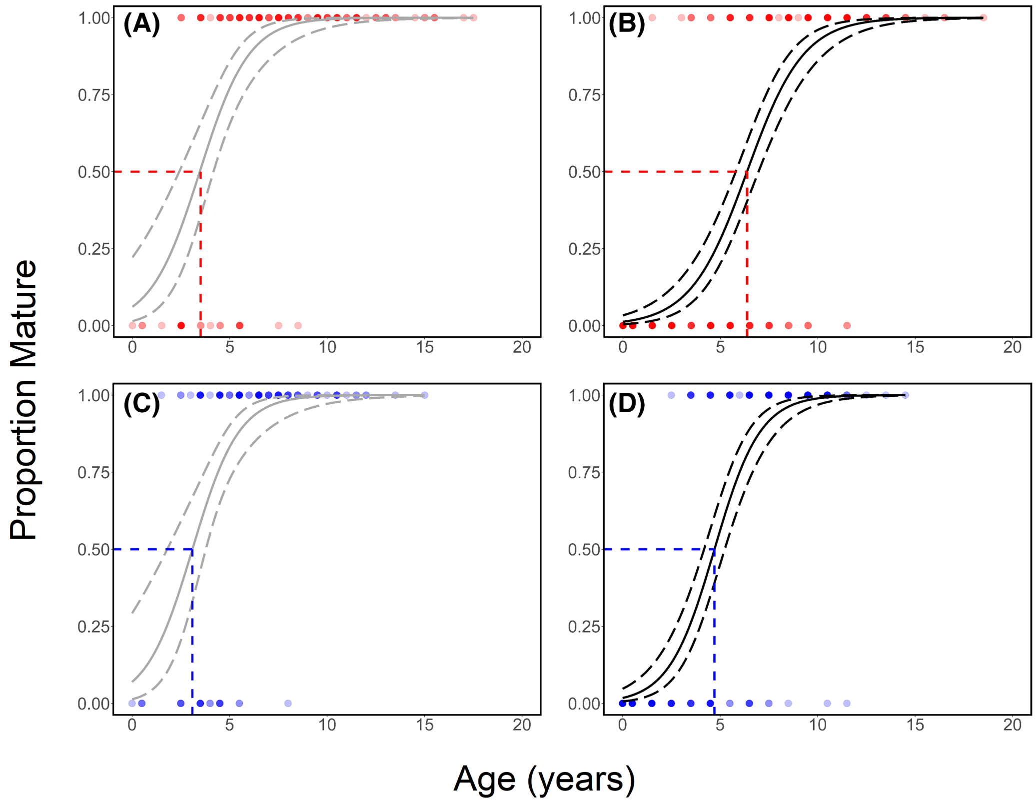

Figure 4. Logistic models fitted to predicted age at maturity for female and male Blacktip Sharks collected from the Gulf of Mexico from 2006 to 2021. Panels (A) and (B) represent predicted age at maturity for female Blacktip Sharks, while panels (C) and (D) represent predicted age at maturity for male Blacktip Sharks. Gray lines indicate samples collected from the western Gulf of Mexico (females: $n=157$, males: $n=126$), and black lines indicate samples collected from the eastern Gulf of Mexico (females: $n=305$, males: $n=265$). Dashed lines represent 95% confidence intervals of the logistic curve of the same color. Darker points represent more Blacktip Sharks in a given size-class.

Table 3. Mean ± SD values for testis width, testis weight, testis length, and epididymis width for each reproductive stage for male Blacktip Sharks collected from the Gulf of Mexico from 2006 to 2021. Stages are as follows: 1/2 = juvenile and juvenile, maturing; 3 = mature; and 4 = mature, sperm present. Values that were not available are indicated as "NA."

		Testis width (mm)			Testis weight (g)			Testis length (mm)			Epididymis width (mm)		
Stage	**Region**	**Mean**	**SD**	***n***	**Mean**	**SD**	***n***	**Mean**	**SD**	***n***	**Mean**	**SD**	***n***
1/2	All	20.8	20.7	77	23.9	26.9	57	106.0	32.4	76	14.7	5.02	52
1/2	Western	21.6	11.1	27	50.2	27.5	9	109.0	33.9	27	16.8	2.80	8
1/2	Eastern	20.1	26.1	51	18.9	24.0	48	105.0	31.3	50	14.3	5.25	44
3	All	32.5	13.4	197	83.2	55.9	185	161.0	32.6	194	23.5	5.80	185
3	Western	36.0	9.46	52	108.0	37.7	44	151.0	29.2	52	23.7	5.04	42
3	Eastern	31.0	14.4	145	75.5	58.4	141	165.0	33.1	142	23.5	6.02	143
4	All	33.8	10.5	81	80.2	57.5	44	156.0	36.6	81	23.3	7.06	46
4	Western	35.6	9.33	37	NA	NA	NA	152.0	31.3	37	13.0	4.24	2
4	Eastern	31.2	11.7	45	80.2	57.5	44	162.0	42.9	45	23.8	6.82	44

observed in July, with the highest frequencies of gravid females observed in September.

The values for ovary weight (OWT), uterus width (UW), and oviducal gland width (OGW) were well defined by reproductive stage (Supplementary Material). While a Kruskal–Wallis test indicated significant differences by stage for maximum follicle diameter (MFD) ($H=31.71$, df = 6, $P<0.005$), sample sizes were too low to compute pairwise comparisons. Mean OWT and OGW values were significantly different between stage-1, stage-2, and stage-3 females, while mean UW values were significantly different between all female stages except stage 6 and stage 7 (Kruskal–Wallis test: $P<0.05$; Supplementary Material).

Overall, reproductive measurements were highest in March–May and declined in June (Figure 11). Maximum follicle diameter values for stage-3 females were not compared by month or region due to low sample sizes. Uterus width, OWT, and OGW values for stage-3 females were significantly different by month (UW: $H=22.967$, df = 11, $P<0.005$, OWT: $H=34.669$, df = 11, $P<0.005$, OWG: $F_{11,\ 92}=6.683$, $P<0.005$) but not between regions. Uterus width measurements increased from

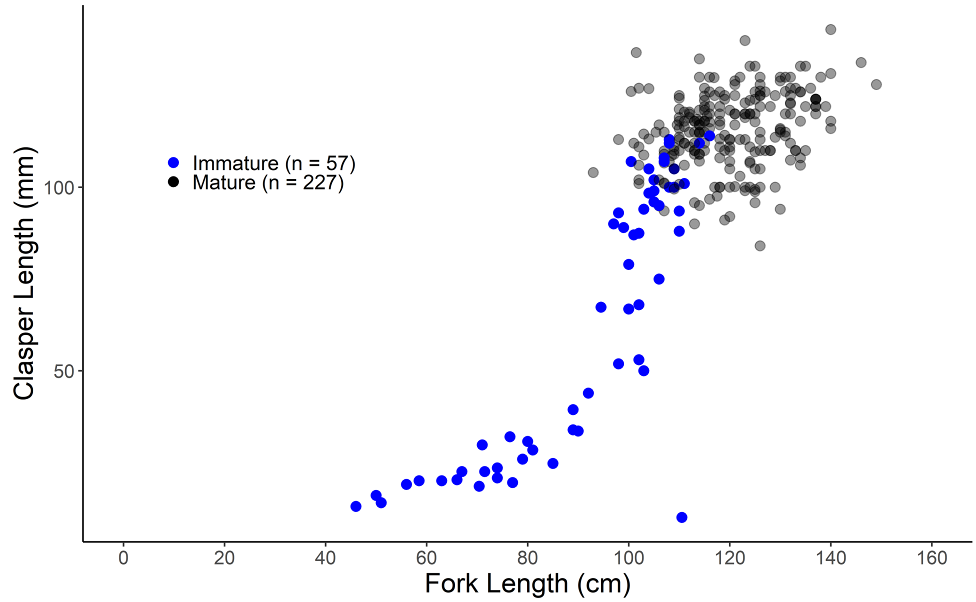

Figure 5. Relationship between fork length and outer clasper length for immature and mature male Blacktip Sharks collected from the Gulf of Mexico from 2006 to 2021.

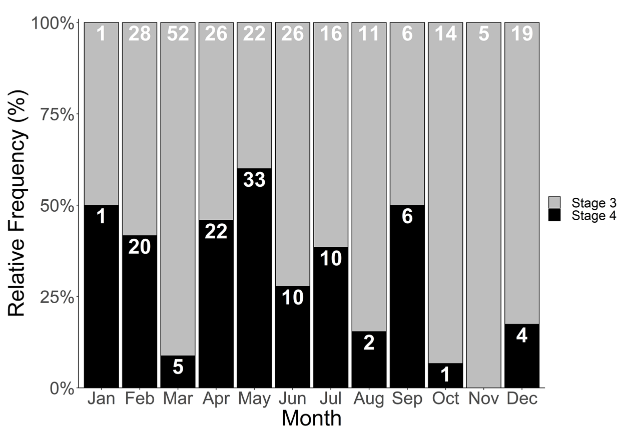

Figure 6. Relative frequencies of mature male Blacktip Sharks collected from the Gulf of Mexico from 2006 to 2021 by month. Stages are 3 = mature and 4 = mature, sperm present. Sample sizes are given at the top of each bar for each stage.

February to June followed by a sharp decline in August. Ovary weight was highest between February and May and declined sharply in June, and pairwise comparisons showed that OWT values for April were significantly different from OWT values in July and December (Kruskal–Wallis test: $P < 0.05$). Similarly, pairwise comparisons showed OGW values for stage-3 females to be significantly higher in March–May (Kruskal–Wallis test: $P < 0.05$). Differences between reproductive stages by region also varied for each measurement and are reported in Table 4 and the Supplementary Material.

The monthly female GSI varied significantly throughout the reproductive cycle ($H = 92.8$, df = 11, $P < 0.005$) but exhibited prominent peaks in April and June (0.28–0.34: Figure 12) compared with summer, fall, and winter months (July–February; 0.11–0.20). While significant differences in GSI by region were found ($H = 10.8$, df = 1, $P = 0.001$), GSI values for the western Gulf of Mexico could only be calculated for February–May and July.

A total of 205 females (28.2%) examined had pups, and approximately 44.2% of mature females collected were gravid. Brood size ranged from one to eight individuals, with a mean ± SD of 4.4 ± 1.6 pups. The number of pups was not significantly different by region (Kruskal–Wallis test: $H = 0.37$, df = 1, $P = 0.54$), and no significant difference between the mean ± SD number of pups in the left uterus (2.1 ± 0.9 pups) and right uterus (2.2 ± 0.9 pups) was found (Mann–Whitney test: $U = 12{,}591$, $P = 0.38$). The number of pups in the left and right uterus also did not differ by region (Kruskal–Wallis test: $P > 0.05$). While female fecundity (average number of pups per female) significantly increased with maternal FL, age, and weight ($P < 0.05$), correlations were weak (Supplementary Material). Maternal length and weight were the best predictors for female fecundity.

DISCUSSION

This study represents the most comprehensive reproductive analysis to date for Blacktip Sharks in the Gulf of Mexico and is the first to incorporate the reproductive biology of Blacktip Sharks in the western gulf. Most population reproductive parameters fell within expected ranges compared with previous studies (Baremore & Passerotti, 2013; Castro, 1996; Clark & von Schmidt, 1965). For example, analyses of male and female reproductive tissues support synchronous and seasonal reproduction, with peak mating activity occurring in March–May followed by a 12-month gestational period. Brood size averaged 4.4 pups per litter, with maternal length and weight being the best predictors for female fecundity. The absence of females exhibiting simultaneous formation of near-term pups and preovulatory follicles supports previous studies describing a biennial ovarian cycle for Blacktip Sharks in this region (Baremore & Passerotti, 2013; Castro, 1996).

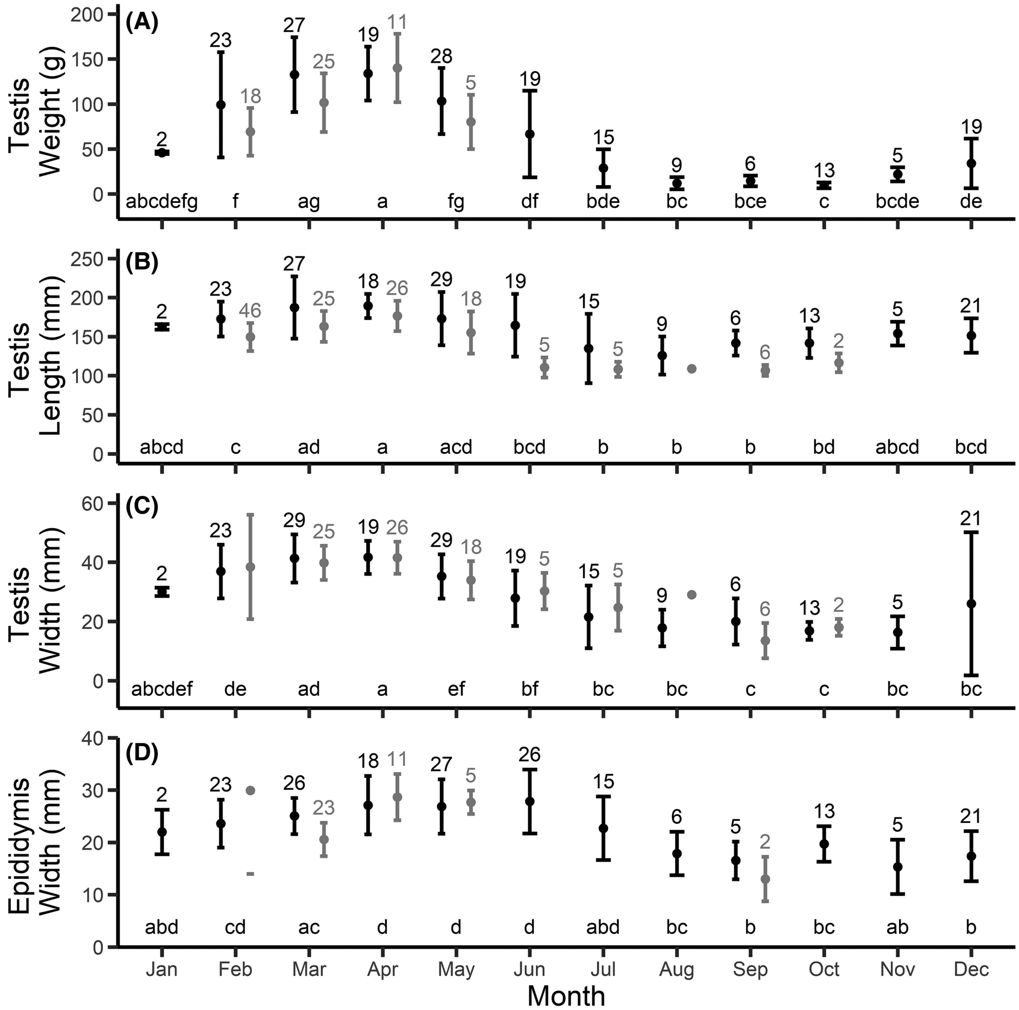

Figure 7. Mean (A) testis weight, (B) testis length, (C) testis width, and (D) epididymis width by month for stage-3 and stage-4 male Blacktip Sharks collected from the Gulf of Mexico from 2006 to 2021. Sample sizes are given above standard deviation bars for sample sizes >1. Gray represents samples collected from the western gulf, while black represents samples collected from the eastern gulf. Letters of significance are given above each month, and months with the same letters are not significantly different (Wilcoxon rank-sum test: $P > 0.05$, Tukey's least-square difference test: $P > 0.05$).

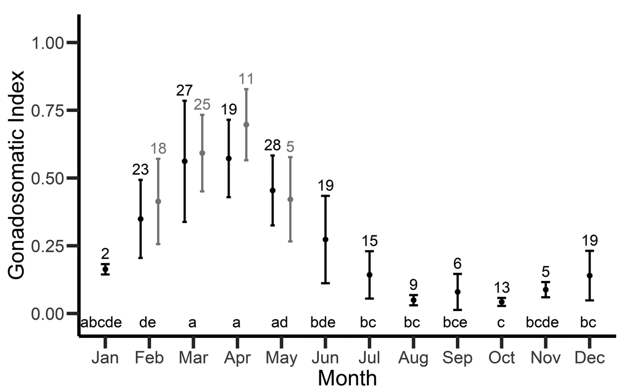

Figure 8. Gonadosomatic index for male Blacktip Sharks collected from the Gulf of Mexico from 2006 to 2021. Sample sizes are given above standard deviation bars for sample sizes >1. Gray represents samples collected from the western gulf, while black represents samples collected from the eastern gulf. Letters of significance are given above each month, and months with the same letters are not significantly different (Dunn post hoc test: $P > 0.05$).

Despite these population-wide similarities, some individuals showed unexpected variability within the reproductive cycle compared with previous studies. For example, postpartum and ovulatory females (stage 6 and stage 4, respectively) would be expected to occur only during certain months of the year corresponding to mating and parturition in synchronous populations. However, ovulatory females were observed in all months except June, and most postpartum females were seen outside the previously documented timing for mating for this species (Baremore & Passerotti, 2013; Castro, 1996; Clark & von Schmidt, 1965). Additionally, stage-4 males (mature with sperm present) were collected in all months except November, and stage-7 females (sperm present in uterus) were encountered most months of the year. These observations indicate that some Blacktip Sharks may demonstrate a more protracted mating and ovulation period than previously documented in the Gulf of Mexico (Baremore & Passerotti, 2013; Castro, 1996; Clark & von Schmidt, 1965). Further investigation of possible variations in embryo development and histological analysis of mature spermatozoa is needed to confirm these observations.

Table 4. Mean ± SD values for maximum follicle diameter (MFD), ovary weight (OWT), uterus width (UW), and oviducal gland width (OGW) for each reproductive stage for female Blacktip Sharks collected from the Gulf of Mexico from 2006 to 2021. Stages are as follows: 1 = very juvenile; 2 = juvenile, maturing; 3 = mature, not gravid; 4 = ovulatory (yolk present in uterus); 5 = gravid; 6 = postpartum (distended); and 7 = sperm present in uterus. Values that were not available are indicated as "NA."

		MFD (mm)			OWT (g)			UW (mm)			OGW (mm)		
Stage	Region	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
1	All	4.8	3.33	8	10.6	13.3	19	4.9	5.35	34	8.7	4.93	32
1	Western	NA	NA	NA	25.4	24.2	4	9.7	6.64	7	12.2	7.18	7
1	Eastern	4.8	3.33	8	6.67	4.75	15	3.6	4.26	27	7.8	3.74	25
2	All	9.7	5.08	36	22.4	9.89	49	17.0	8.22	60	20.6	6.50	58
2	Western	8.7	1.71	5	19.1	8.40	10	15.9	6.37	11	18.0	6.45	11
2	Eastern	9.9	5.43	31	23.2	10.2	39	17.3	8.62	49	21.1	6.43	47
3	All	16.9	13.0	50	60.6	39.7	83	31.3	12.8	105	27.6	5.50	104
3	Western	20.6	20.6	14	58.4	40.4	21	32.2	13.9	28	26.8	5.00	27
3	Eastern	15.4	8.53	36	61.3	39.8	62	31.0	12.4	77	27.8	5.67	77
4	All	17.1	11.4	3	88.1	62.9	9	53.9	16.9	13	33.4	11.6	13
4	Western	10.7	3.39	2	24.8	5.05	3	41.1	12.1	5	21.8	2.11	5
4	Eastern	30.0	NA	1	120.0	52.0	6	61.9	14.7	8	40.6	8.58	8
5	All	12.0	6.61	55	56.9	30.7	106	127.0	37.3	147	27.0	5.30	153
5	Western	8.6	4.57	13	71.0	34.8	21	133.0	41.1	27	25.2	6.06	27
5	Eastern	13.0	6.83	42	53.5	28.8	85	126.0	36.4	120	27.4	5.07	126
6	All	14.6	7.40	7	58.2	28.0	20	40.5	22.5	26	25.2	5.55	25
6	Western	16.0	5.17	3	49.0	16.6	2	27.9	5.9	3	25.8	5.86	3
6	Eastern	13.6	9.42	4	59.2	29.2	18	42.1	23.4	23	25.1	5.64	22
7	All	40.0	NA	1	71.5	29.8	19	36.8	9.97	23	28.0	4.91	23
7	Western	NA	NA	NA	127.0	NA	1	37.3	NA	1	28.3	NA	1
7	Eastern	40.0	NA	1	68.4	27.3	18	36.7	10.2	22	27.9	5.03	22

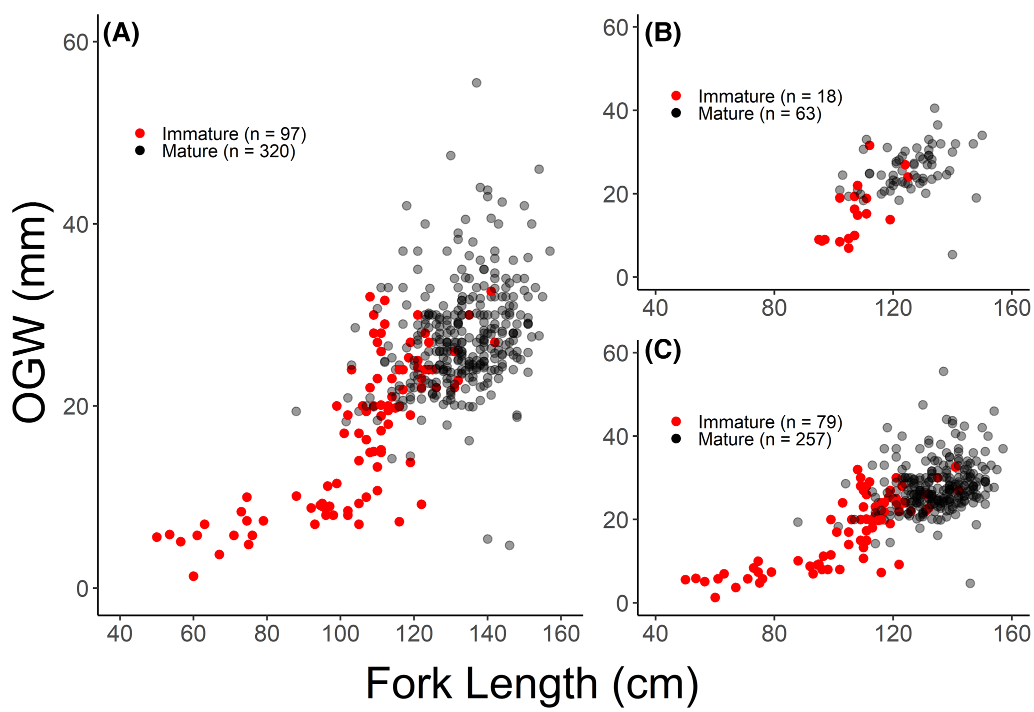

Figure 9. Relationship between fork length and oviducal gland width (OGW) for immature and mature female Blacktip Sharks collected from the Gulf of Mexico from 2006 to 2021. Panel (A) shows all female Blacktip Sharks, panel (B) shows females collected from the western Gulf of Mexico, and panel (C) shows females collected from the eastern Gulf of Mexico.

Results from the current study support growing evidence indicating that elasmobranch reproductive variability may be the norm rather than the exception. For instance, Walker (2007) observed that most female Gummy Sharks *Mustelus antarcticus* off southern Australia showed highly synchronous reproductive cycles; however, some females were out of phase by 3 months. Similarly, Great Hammerheads *Sphyrna mokarran* in northern Australian waters showed mostly

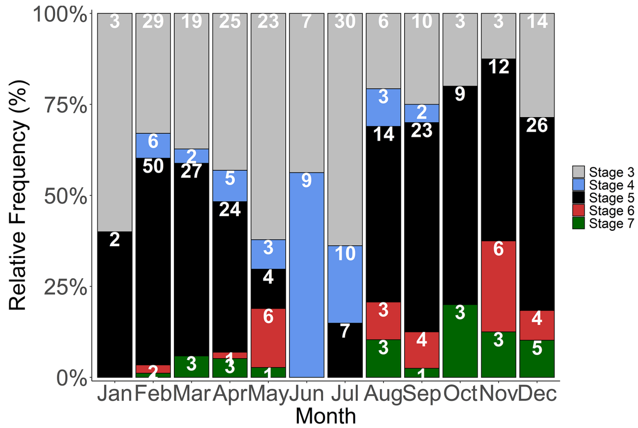

Figure 10. Monthly relative frequencies of mature female Blacktip Sharks collected from the Gulf of Mexico from 2006 to 2021. Stages are as follows: 3 = mature (not gravid), 4 = ovulatory (yolk present in uterus), 5 = gravid, 6 = postpartum (distended uterus), and 7 = sperm present in uterus. Sample sizes are given at the top of each bar for each reproductive stage.

synchronous reproductive cycles, with mating occurring in October–November. Even so, some females with ova in their uteri were found in February, April, and even as late as July, suggesting that mating and ovulation occurred over extended periods of time for some individuals (Stevens & Lyle, 1989). Baremore and Hale (2012) also reported postpartum Sandbar Shark *Carcharhinus plumbeus* females and females with sperm present occurring outside peak mating and parturition periods for the species in the U.S. South Atlantic and eastern Gulf of Mexico. In addition, Atlantic Sharpnose Sharks *Rhizoprionodon terraenovae* in the Gulf of Mexico exhibited reproductive asynchrony with a significantly protracted reproductive cycle (Hoffmayer et al., 2013). While peak mating and ovulation was previously thought to occur from May to July, postpartum females were observed from April to September and mature spermatozoa were found in males from March to November (Hoffmayer et al., 2013). While the cause of reproductive variability in carcharhinids warrants further investigation, variability in reproduction may be more common than previously reported.

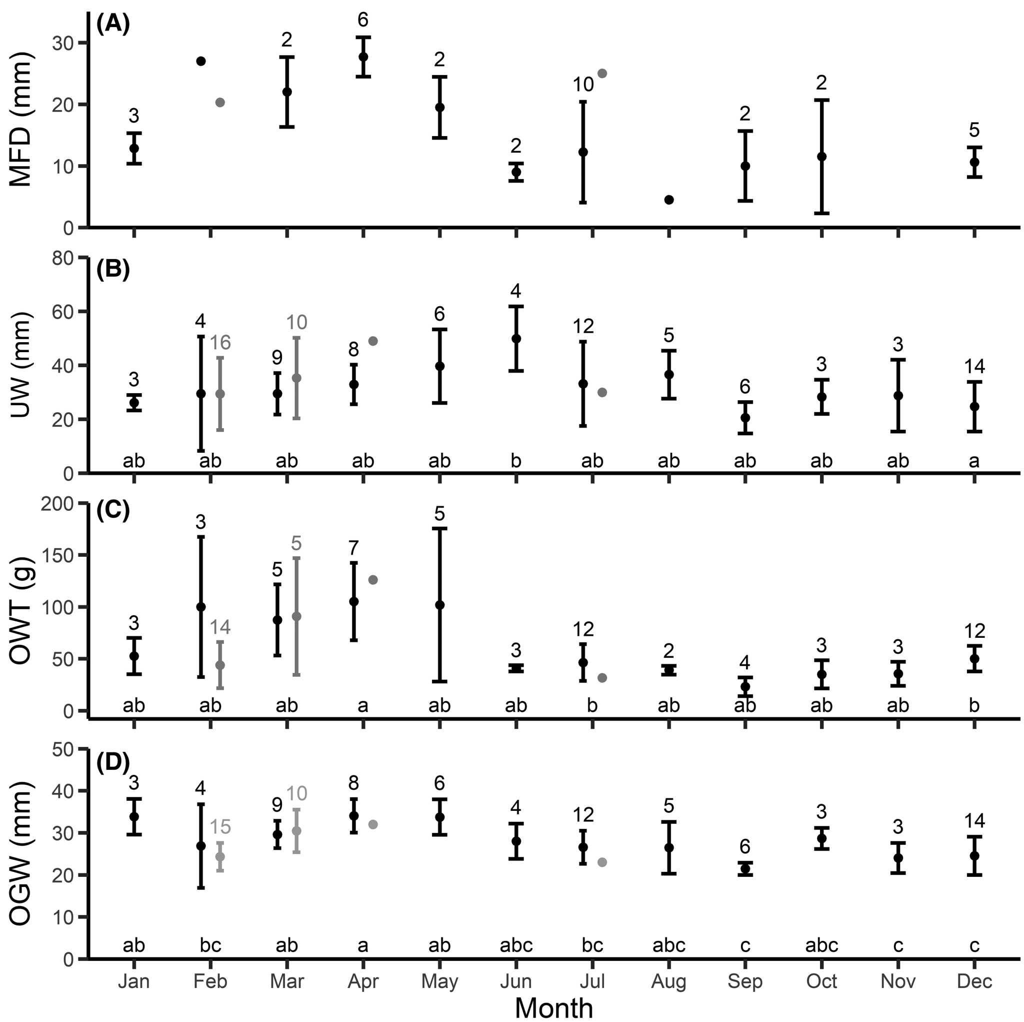

Figure 11. Mean (A) maximum follicle diameter (MFD), (B) uterus width (UW), (C) ovary weight (OWT), and (D) oviducal gland width (OGW) by month for stage-3 female Blacktip Sharks collected from the Gulf of Mexico from 2006 to 2021. Sample sizes are given above standard deviation bars for sample sizes >1. Gray represents samples collected from the western Gulf of Mexico, while black represents samples collected from the eastern Gulf of Mexico. Letters of significance are given above each month, and months with the same lowercase letters are not significantly different (Wilcoxon rank-sum test: $P > 0.05$, Tukey's least-square difference test: $P > 0.05$).

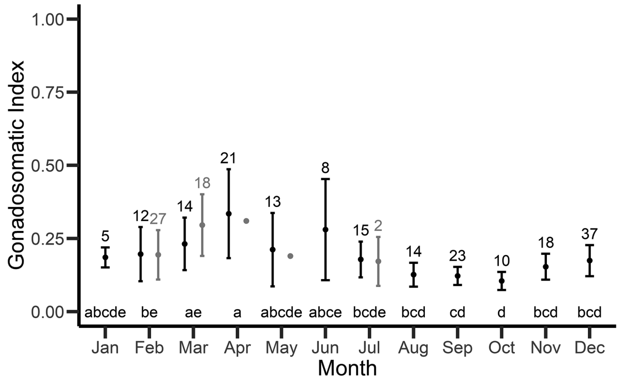

Figure 12. Gonadosomatic index for female Blacktip Sharks collected from the Gulf of Mexico from 2006 to 2021. Sample sizes are given above standard deviation bars for sample sizes >1. Gray represents samples collected from the western gulf, while black represents samples collected from the eastern gulf. Letters of significance are given above each month, and months with the same letters are not significantly (Dunn post hoc test: $P > 0.05$).

Size and age at maturity of Blacktip Sharks in the present study showed significant differences between regions in the Gulf of Mexico. Carlson et al. (2006) reported a length at maturity of 103.4 cm FL for Blacktip Shark males and 117.3 cm FL for females in the eastern gulf, while Baremore and Passerotti (2013) calculated length at maturity as 105.8 cm FL for males and 119.2 cm FL for females. These closely align with the eastern gulf estimates of length at maturity for both sexes in the present study (105.7 and 116.1 cm FL for males and females, respectively) but are over 10 cm higher than those calculated for the western gulf (94.7 and 100.6 cm FL for males and females, respectively). In the western Gulf of Mexico, Branstetter (1987) reported length at maturity as 103.6 cm FL for male Blacktip Sharks and 120.7–124.0 cm FL for female Blacktip Sharks (SEDAR, 2020). Although these values are higher than estimates presented here, the current study significantly increased sample sizes in the western gulf compared to Branstetter (1987) ($n = 54$). Similarly, in the eastern gulf Carlson et al. (2006) reported age at maturity as 4.5 years for Blacktip Shark males and 5.7 years for females, and Baremore and Passerotti (2013) reported age at maturity as 4.8 and 6.3 years for male and female Blacktip Sharks, respectively. These age-at-maturity estimates are higher than the gulfwide estimates of age at maturity presented here. Like with size at maturity, our eastern Gulf of Mexico estimates align with those studies (4.7 years and 6.4 years for males and females, respectively), but our estimates for the western Gulf of Mexico were much younger (3.1 years and 3.5 years for males and females, respectively).

Differences in estimated length and age at maturity between Blacktip Sharks collected from the eastern and western Gulf of Mexico suggest that these stocks may be different and support separate quotas in this region. Recent evaluations of tagging, genetic, and diet information further support the biological separation of Blacktip Sharks between these areas. For example, an analysis of long-term mark–recapture tagging data suggests minimal exchange between eastern and western Gulf of Mexico Blacktip Sharks (Kohler & Turner, 2019), and recent investigations have confirmed genetically distinct units of Blacktip Sharks in the eastern and western Gulf of Mexico (Swift et al., 2023). Differences in diet and habitat use for Blacktip Sharks occupying different areas within the Gulf of Mexico further supports evidence presented here that stock separation between the eastern and western Gulf of Mexico is appropriate (Binstock et al., 2023; Kohler & Turner, 2019; Matich et al., 2020).

Previous studies on other carcharhinid species have attributed life history differences to geographic variation and abiotic or biotic environmental factors. For example, latitudinal variation in Bonnethead *Sphyrna tiburo* life history traits has been documented in the eastern Gulf of Mexico (Lombardi-Carlson et al., 2003), with larger and older individuals found at higher latitudes. This observation is thought to be the result of adaptive responses of Bonnetheads to environmental variability; specifically, cooler water temperatures at northern latitudes necessitate larger body sizes and faster growth rates to maximize offspring survivorship, thus resulting in larger and older median size and age at maturity estimates, respectively (Lombardi-Carlson et al., 2003). Differences in increased size at maturity estimates with increasing latitude have also been reported for other elasmobranch species. For example, Horie and Tanaka (2002) reported Cloudy Catshark *Scyliorhinus torazame* size at maturity to be larger in cooler waters in Japan, while the Shortspine Spurdog *Squalus mitsukurii* in the North Pacific Ocean demonstrated large differences in size at maturity and reproductive variation that was likely influenced by local environmental conditions (Taniuchi et al., 1993). Yamaguchi et al. (1998) reported significant differences in growth, maximum lengths, and maximum ages for the Starspotted Dogfish *Mustelus manazo* but attributed these differences to biotic factors rather than abiotic environmental conditions. Longitudinal differences in elasmobranch life history traits have also been observed. For instance, Gummy Shark populations sampled in Australian waters showed significantly different reproductive cyclicity east and west of 138°E (Walker, 2007), and genetic analysis confirmed the occurrence of two genetically separate populations of Blacknose Sharks *Carcharhinus acronotus* located in the eastern and western Gulf of Mexico (Portnoy et al., 2014). Accordingly, these findings support a growing body of literature demonstrating discrete stock structure for many shark populations.

Longitudinal differences in Blacktip Shark life history found in the current study correspond to the unique zoogeography of Mobile Bay, Alabama, and align with current commercial quota allocations for this species. High nutrient output from the Mississippi River and Mobile Bay characterizes eutrophic waters off the western Gulf of Mexico shelf; in contrast, the eastern Gulf of Mexico shelf is distinguished by oligotrophic waters with less nutrient output. This separation between eutrophic and oligotrophic waters also corresponds to a geomorphic division in the northern Gulf of Mexico, where terrigenous sediments are found in the west, while carbonate sediments are found in the east (McClure & McEachran, 1992). These biogeographic differences between the western and eastern Gulf of Mexico have been posited as drivers of the gradient in habitat suitability for Blacktip Sharks in the area (Drymon et al., 2020). Specifically, large areas of highly suitable Blacktip Shark habitat were predicted for the western Gulf of Mexico, while little suitable habitat was predicted for the eastern Gulf of Mexico

(Drymon et al., 2020). Additionally, large freshwater influxes from the Mississippi River and Mobile Bay may also prevent movement between the western and eastern Gulf of Mexico for migratory species like the Blacktip Shark (Portnoy et al., 2014; Swift et al., 2023). Highly suitable Blacktip Shark habitat in the western Gulf of Mexico and limited movement across the Gulf of Mexico could explain differences in size and age at maturity reported here. Specifically, highly suitable Blacktip Shark habitat in the western gulf may encourage higher numbers and lower age and length at maturity if resources for growth and reproduction are abundant. Biogeographic barriers to movement would also prevent gene flow between these two areas, further contributing to the observed life history differences reported in the present study. These longitudinal differences align with the disproportional quota allocation for Blacktip Sharks in the Gulf of Mexico, where the 2023 quota for the western Gulf of Mexico is nine times greater than the quota for the eastern Gulf of Mexico. While this disparate allocation represents an outcome of successful fisheries management based on recent stock assessments for Gulf of Mexico Blacktip Sharks (SEDAR, 2018), it is unclear if western Gulf of Mexico Blacktip Sharks can support higher quotas due to their life history, or if their life history has been altered due to increased fishing pressure.

Alternative mechanisms may also explain the observed differences in Blacktip Shark reproduction across the Gulf of Mexico. In particular, potential biases exist given the current study design. For example, most of the archived samples were from the eastern Gulf of Mexico and were aged by different readers, which could explain differences in age at maturity between regions; however, symmetry tests and age bias plots suggested no systematic bias (R. J. D. Wells, unpublished data). Also, differences in gear selectivity between regions could explain the differences reported in this study. Specifically, regional differences presented here could be the result of fewer immature sharks sampled in the western Gulf of Mexico. In addition, the samples examined spanned a large temporal window, which could potentially confound the interpretation of the results presented here. Seasonal residency and regional philopatry could also explain observed differences in Blacktip Shark reproductive parameters across the Gulf of Mexico. Previous tagging studies have supported philopatry in juvenile Blacktip Sharks, where they are seasonal residents of their natal sites for the first year of life (Hueter et al., 2004) and exhibit natal site fidelity across consecutive seasons (Chapman et al., 2015). Genetic studies have also demonstrated that Blacktip Shark females repeatedly use the same nursery grounds for parturition (Keeney et al., 2005; Swift et al., 2023), and stable isotope analysis confirmed regional residency, relatively high site fidelity, and low ecological connectivity between Blacktip Sharks inhabiting the eastern and western Gulf of Mexico (Binstock et al., 2023; Hayne et al., 2024). While speculative, it is possible Blacktip Sharks may also exhibit some degree of natal philopatry in the Gulf of Mexico (Hueter et al., 2004; Swift et al., 2023). Regional philopatry, seasonal residency, and a relatively high site fidelity would contribute to the formation of distinct Blacktip Shark populations, particularly if parturition and breeding site fidelity extends across generations.

The present study emphasizes the need for updated life history parameters for commercially important species like the Blacktip Shark. Regional differences in life history have implications for how quota should be allocated throughout a stock. Ideally, fisheries stock assessments must account for differences in life history parameters as these impact a species' ability to withstand exploitation. For management, it will be important to continue this research to determine if these life history differences are real and not a result of small samples sizes of immature sharks in the western Gulf of Mexico. This will become increasingly important as environmental conditions continue to shift with climate change. Understanding population structure—and how life history differences will influence adaptability in the face of environmental change—remains critical for continued effective conservation and management of Blacktip Sharks in the Gulf of Mexico.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Marine and Coastal Fisheries* online.

DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

There were no ethical guidelines applicable to this study.

FUNDING

Funding for this work was provided by a NMFS Cooperative Research Program award to R.J.D.W. at Texas A&M University.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

ACKNOWLEDGMENTS

We thank members of the NMFS Shark Population and Assessment Program at the Southeast Fisheries Science Center for providing additional data to complement the current study. In particular, we thank H. Moncrief-Cox and A. Mathers for their assistance in procuring archived data and I. Baremore and M. Passerotti for helpful discussions regarding the NMFS archived data. We also thank current and past members of the Marine Fisheries Ecology Program at Mississippi State University who assisted with data collection and sampling throughout the study. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect those of their institution(s).

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