Do differences in life history exist for blacktip sharks, *Carcharhinus limbatus*, from the United States South Atlantic Bight and Eastern Gulf of Mexico?

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SEDAR 29–RD-06

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Environ Biol Fish (2006) 77:279–292
DOI 10.1007/s10641-006-9129-x

ORIGINAL PAPER

Do differences in life history exist for blacktip sharks, *Carcharhinus limbatus*, from the United States South Atlantic Bight and Eastern Gulf of Mexico?

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Received: 12 June 2006 / Accepted: 3 July 2006 / Published online: 6 September 2006
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Synopsis We examined life history traits (e.g., mean length-at-age, growth rate, age-at-maturity) for blacktip sharks collected from two separate geographical areas (eastern Gulf of Mexico and South Atlantic Bight) to address the potential for separate stocks in southeastern US waters. Samples were obtained from fishery-dependent and independent sources. Growth and logistic models were fitted to observed length-at-age and reproductive data, respectively. von Bertalanffy growth parameters derived for blacktip shark from the Gulf of Mexico show that they attain a statistically smaller theoretical maximum length (L_∞ = 141.6 cm vs. L_∞ = 158.5 cm for female and L_∞ = 126.0 cm FL and L_∞ = 147.4 cm FL for male) and have a faster growth rate (k = 0.24 yr^{-1} vs. k = 0.16 yr^{-1} for female and k = 0.27 yr^{-1} vs. k = 0.21 yr^{-1} for male) than conspecifics in the South Atlantic Bight. Median length- and age-at-maturity were significantly different between sex and area. Length at which 50% of the population is mature was 117.3 cm FL for females and 103.4 cm FL for males in the Gulf of Mexico and 126.6 cm FL for females and 116.7 cm FL for males in the South Atlantic Bight. Median age-at-maturity was 5.7 yrs and 4.5 yrs for females and males in the Gulf of Mexico, respectively, while age-at-maturity was 6.7 yrs for females and 5.0 yrs for males for sharks from the South Atlantic Bight. Due to varying statistical results, temporal problems of sampling, and potential for gear bias, we could not definitively conclude that differences in life history characteristics exist.

Keywords Growth · Reproduction · Age · Stock

Introduction

Life history traits are the result of the strategy to which fish populations or stocks have evolved. Growth rates, age-at-maturity, and mortality reflect the underlying dynamics of the population. Estimates of these parameters are thought to be representative of individuals within a presumed stock and can be used to distinguish among

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separate stocks because these parameters are phenotypic expressions of the interaction of genotype and the environment (Begg 2005). Thus, differences in life history traits found between groups of individuals are assumed to be evidence that stocks of fish are geographically isolated and therefore are discrete stocks for management purposes (Ihssen et al. 1981).

Differences in life history between geographically separated stocks of elasmobranchs are becoming more widely documented. In waters off the United States (US), Carlson et al. (2003) noted a larger length-at-maturity for finetooth sharks, *Carcharhinus isodon*, from South Carolina than from the northeast Gulf of Mexico. Blacknose sharks, *Carcharhinus acronotus*, in the US south Atlantic Ocean have significantly lower growth rates (k) and reach maturity later than conspecifics in the Gulf of Mexico (Driggers et al. 2004). Neer and Thompson (2005) reported cownose rays, *Rhinoptera bonasus*, in the Gulf of Mexico have lower estimates of theoretical maximum length and growth rate than those from Chesapeake Bay, Virginia. However, these studies could not rule out that differences were artifacts of low sample sizes, methodology, or inter-annual comparisons.

Blacktip sharks, *Carcharhinus limbatus*, inhabit coastal waters off the United States from Massachusetts through Texas (Compagno 1984; Castro 1996). Blacktip sharks occur within two separate large marine ecosystems (Southeast US Continental Shelf and Gulf of Mexico, Musick et al. 2004), and conventional tagging evidence suggests little exchange between areas (Kohler et al. 1998; Carlson unpublished). However, blacktip sharks are managed as one stock under the current federal management plan (NMFS 2003). If sharks from separate geographic areas are assumed to share similar life history traits but actually differ, information used in the development of age-structured population models could result in errors in stock assessments and, possibly, overexploitation. To address the potential for separate stocks of blacktip sharks in US waters, we examined life history traits (e.g., mean length-at-age, growth rate, age-at-maturity) for sharks collected from two separate geographical areas, the eastern Gulf of Mexico and the South Atlantic Bight.

Materials and methods

Biological samples were collected during 1996–2002 through fishery-independent surveys (Hueter and Manire 1994; Grace and Henwood 1998; Carlson and Brusher 1999) and from fishery-dependent programs (Trent et al. 1997; Burgess and Morgan 2003). Additional reproductive data were also provided from a study by Castro (1996). Precaudal (PC), fork (FL), total (TL), and/or stretched total (STL) length (cm), sex, and maturity state were determined for each shark. When possible, weight was measured to the nearest kg (±0.1).

Age and growth

Vertebrae for age determination (3–6) were collected from either the column below the first dorsal fin or above the branchial chamber of each shark. Vertebral sections were placed on ice after collection and frozen upon return to the laboratory. Thawed vertebrae were cleaned of excess tissue and soaked in a 5% sodium hypochlorite solution for 5–30 min to remove remaining tissue. After cleaning, vertebrae were soaked in distilled water for 30 min and stored in 95% isopropanol. One vertebra was randomly selected, removed from alcohol, dried, fixed to a clear glass slide with resin, and sectioned using a Buehler 82 Isomet[1] low-speed saw.

To determine the most appropriate technique for enhancing visibility of growth bands, sagittal sections were cut from the vertebral centrum at 3 different thicknesses (±0.2 mm) and stained or left unstained (see review in Cailliet and Goldman 2004). Each section was mounted on a glass microscope slide with clear resin and examined using a dissecting microscope under transmitted light.

The annual periodicity of band pair formation was investigated using a marginal increment ratio analysis (MIR), which was calculated as the ratio between the final fully formed band pair and penultimate band (Cailliet and Goldman 2004). We observed that annuli in older adult specimens were compressed; therefore marginal increments

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[1] Reference to trade names does not imply endorsement by NOAA Fisheries Service.

were calculated from randomly selected juvenile specimens below age 5 (e.g., Simpfendorfer 2000; Sulikowski et al. 2003, 2005). Measurements of the last complete band pair and the penultimate band from the centrum edge were taken using a compound microscope and optical micrometer. Mean marginal increment ratios were plotted by month of capture to identify trends in band formation, and a Kruskal–Wallis one-way analysis of variance on ranks was used to test for differences in marginal increment ratios by month.

In developing theoretical growth models, we assumed that (1) the birth mark is the band associated with a pronounced change in angle in the intermedialia and is formed on an arbitrary birth date of 1 May, (2) broad light bands are formed during summer, and (3) narrow dark bands are deposited in winter. Although vertebrae were taken from two different regions of the vertebral column (cervical and thoracic), an independent study found no significant difference in band counts between regions (B. Cullum, Florida Fish and Wildlife Commission, personal communication). Ages (yr) were calculated following the algorithm of Carlson et al. (1999): age = birth mark + number of winter marks –1.5. If only the birth mark was present, age was 0+ yrs. All age estimates from growth band counts were based on the hypothesis of annual growth band deposition (Branstetter 1987; Killam and Parsons 1989).

Vertebrae were read independently and randomly by two readers (JKC & IEB) without knowledge of location, sex, length or date of capture. Vertebral age estimates for which the readers disagreed were reviewed jointly by using a Meiji Techno R2 Dissecting Microscope equipped with a Hitachi KP-D50 Digital Camera and software.[1] Precision among age determinations was evaluated using percent agreement [(PA = Number agreed/Number read)*100] and percent agreement plus or minus 1 yr calculated for 10 cm FL (e.g., 76–85 cm) length intervals (Cailliet and Goldman 2004; Goldman 2004). Bowker's test of symmetry following Hoenig et al. (1995) was used to determine if differences between readers were systematic or due to random error. The Index of Average Percent Error (IAPE, Beamish and Fournier 1981) was calculated to compare the average deviation of readings from the means of all readings for each vertebral section:

$$\mathrm{IAPE} = \frac{1}{N}\sum_{j=1}^{N}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{|x_{ij}-x_j|}{x_j}\right]$$

where N = number of sharks aged; R = number of readings; x_{ij} = ith age estimation of jth shark at ith reading, and x_j = mean age calculated for the jth shark.

Following Carlson and Baremore (2005), several growth models were fitted to the observed length-at-age data: the von Bertalanffy growth model (von Bertalanffy 1938; Beverton and Holt 1957; see also Cailliet et al. this issue), an alternate equation of the von Bertalanffy growth model with a length-at-birth intercept rather than the t_o parameter (Van Dykhuizen and Mollet 1992; Goosen and Smale 1997; Carlson et al. 2003), and a Gompertz growth model (Ricker 1975). All growth model parameters were estimated using Marquardt least-squares non-linear regression and SAS statistical software (PROC NONLIN, SAS Inst., Inc). Models were assessed based on a combination of examining residual mean square error (MSE), coefficient-of-determination (r^2), level of significance ($P < 0.05$), and standard residual analysis.

Several methods were employed to test for differences in age and growth within and between geographic areas. Following Kimura (1980), χ^2-tests of likelihood ratios were used to test for differences in combined parameters within the von Bertalanffy growth model. Comparisons of observed mean length-at-age between ages were made using a Welch modified two-sample t-test (Zar 1984). Growth rates were calculated from predicted fork lengths by the von Bertalanffy growth model. Growth intervals were represented by the time between band deposition (growth interval one is the time between band counts one and two). Sex-specific predicted growth rates (cm yr^{-1}) were compared between the areas.

Length-at-maturity estimation

Maturity was assessed following the guidelines of Castro (1996). To quantitatively assess length-at-maturity, the length at which 50% of the population is mature for male and female sharks was determined (i.e., median length-at-maturity). Data from the Gulf of Mexico and South Atlantic Bight were fitted separately to a logistic model:

$$Y = 1/(1 + e^{-(a+bX)})$$

where Y = the binomial maturity data (immature = 0, mature = 1) and X = length. Median length-at-maturity was expressed as $-a/b$. The model was fitted using maximum likelihood (PROC LOGISTIC, SAS Inst., Inc.) and the effects of area and sex were compared using χ^2-tests of likelihood ratios.

To assess age-at-maturity, lengths were back-transformed to age using each respective von Bertalanffy growth model. Similar to determination of length-at-maturity, ages were fitted to a logistic model using maximum likelihood and the effects of area and sex compared used χ^2-tests of likelihood ratios.

Results

A total of 628 biological samples were collected throughout the study (Fig. 1). Using data collected in this study and that from fishery-independent surveys (Carlson and Brusher 1999; Carlson 2003), several morphometric relationships to convert length measurements were developed. Linear regression formulae were determined as FL = 1.10(PC) + 0.29 (n = 1,096);

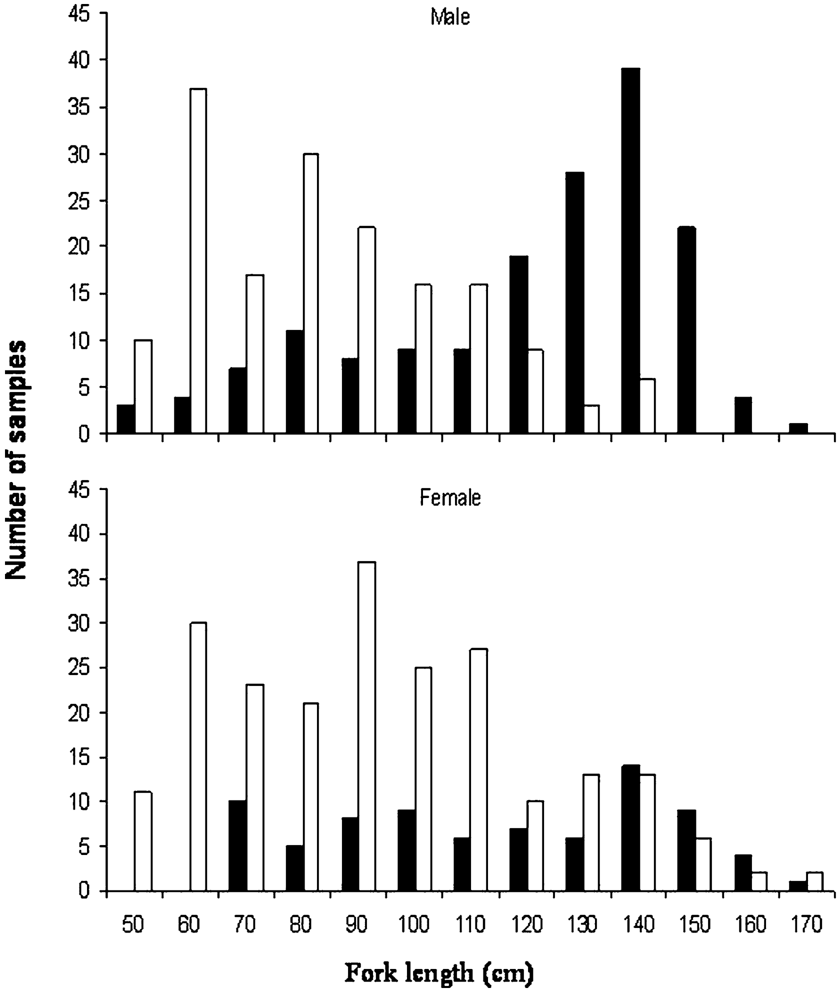


Fig. 1 Length frequency distributions for male and female blacktip sharks collected from the South Atlantic Bight (solid bar) and eastern Gulf of Mexico (open bar)

$TL = 1.12(FL) + 1.12$ ($n = 1{,}248$); and $STL = 1.02(TL) + 0.99$ ($n = 926$). All equations were highly significant ($P < 0.0001$) and had r^2 between 0.98 and 0.99.

Age and growth

Growth bands were found to be most apparent on unstained sagittal sections with a thickness of 0.3 mm (Fig. 2) and less apparent on 0.5 mm and 0.7 mm. The precision of band counts was high between readers and Bowker's test of symmetry (Hoenig et al. 1995) indicated that differences between readers were due to random error (χ^2 test, $P > 0.05$).

The first set of readings resulted in an index of average percent error of 3.9%. Initial percent agreement in all band counts between the readers was 76.5% within 1 band, 94.2% within 2 bands, 98.4% within 3 bands, 99.8% within 4 bands, 100.0% within 5 bands, and 99.8% within 6 bands. When grouped by 10 cm length intervals, agreement for combined sexes was reached for an average of 77.2% and 97.3% ±1 band for sharks less than 105 cm FL (Table 1). Above 105 cm FL, agreement was reached for 46.6% and 71.9% ±1 band of samples initially read. For those samples where band counts differed, consultation resulted in agreement for 608 out of 628 vertebrae. Samples with no resolution were discarded.

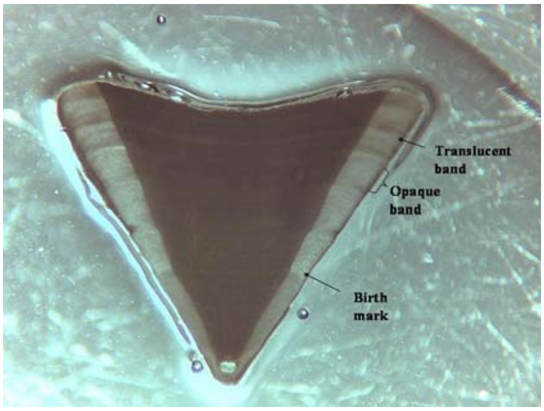


Fig. 2 Sagittal section from a blacktip shark vertebra used for age determination. Translucent bands (winter marks) correspond to thin areas under transmitted light, whereas opaque bands (summer marks) correspond to wide zones

Table 1 Percent agreement and percent agreement ±1 band from the initial set of readings for blacktip shark

FL interval	Total read	Percent agreement	Percent agreement ±1
Sexes combined			
36–45	3	66.7	100.0
46–55	61	100.0	100.0
56–65	62	96.8	100.0
66–75	63	81.0	96.8
76–85	76	68.4	100.0
86–95	58	65.5	93.1
96–105	68	61.8	91.2
106–115	48	52.1	85.4
116–125	39	56.4	89.7
126–135	66	60.6	90.9
136–145	62	54.8	82.3
146–155	18	55.6	83.3
156–165	4	0.0	0.0

A total of 79 vertebral samples were considered usable for marginal increment analyses. Six to 10 samples were available each month except for October and December, which were represented by a sample size of two and three, respectively, and April and November, when no specimens were collected. Marginal increment ratios were significantly different among those 8 months (Kruskal–Wallis, $P < 0.001$) with a distinct trend of increasing monthly increment growth that peaked in May, followed by a sharp decline to a numerical low in June (Fig. 3). Based on this information, the increment analyses support the likelihood that a single opaque band is formed annually on the vertebral centrum during the month of June.

All three growth models fit the data well (e.g., high r^2, low standard deviation of residuals). Because of the general similarity between the models and the ubiquitous use of von Bertalanffy model, we present and compare further age and growth results using only the von Bertalanffy equation. Growth parameters derived for blacktip sharks from the Gulf of Mexico indicated that they attain a smaller theoretical maximum length (L_∞) and that they reach L_∞ at a faster rate (k) than conspecifics in the South Atlantic Bight (Table 2, Fig. 4). von Bertalanffy growth parameters for sharks in the Gulf of Mexico were $L_\infty = 141.6$ cm FL, $k = 0.24$ yr^{-1}, $t_o = -2.18$ yr and $L_\infty = 126$ cm FL, $k = 0.27$ yr^{-1} $t_o = -2.21$ yr for females and males, respectively (Table 2). In the South

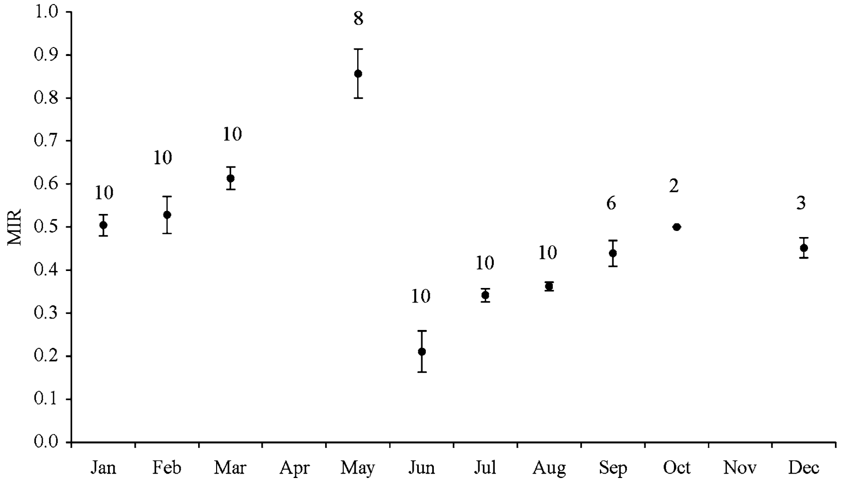


Fig. 3 Mean marginal increment ratio (MIR ± standard error) by month for combined sexes from sharks less than age 5. Numbers above each month represent sample size

Table 2 Von Bertalanffy growth parameters for male, female, and sex combined blacktip sharks

	Male	SE	LCL	UCL	Female	SE	LCL	UCL	Combined	SE	LCL	UCL
Gulf of Mexico												
L_∞ (cm)	126.0	3.50	119.1	132.9	141.6	2.99	135.7	147.5	139.4	2.61	134.2	144.5
k (yr^{-1})	0.27	0.02	0.22	0.33	0.24	0.02	0.20	0.27	0.23	0.01	0.20	0.26
t_o (yr)	–2.21	0.18	–2.57	–1.84	–2.18	0.16	–2.49	–1.87	–2.33	0.13	–2.58	–2.07
N	161				207				368			
South Atlantic Bight												
L_∞ (cm)	147.4	2.60	142.2	152.5	158.5	5.71	147.1	169.8	150.9	2.51	145.9	155.8
k (yr^{-1})	0.21	0.02	0.17	0.24	0.16	0.02	0.11	0.21	0.19	0.01	0.16	0.22
t_o (yr)	–2.58	0.24	–3.06	–2.11	–3.43	0.50	–4.43	–2.43	–2.89	0.23	–3.34	–2.44
N	162				78				240			
Areas combined												
L_∞ (cm)	150.8	2.67	145.6	156.1	148.5	2.49	143.6	153.4	148.7	1.76	145.2	152.2
k (yr^{-1})	0.18	0.01	0.16	0.20	0.21	0.01	0.18	0.23	0.20	0.01	0.18	0.22
t_o (yr)	–2.76	0.15	–3.06	–2.46	–2.42	0.15	–2.74	–2.13	–2.57	0.11	–2.79	–2.36
N	323				285				608			

Estimates are provided for the Gulf of Mexico, South Atlantic Bight, and areas combined. Standard error = SE and 95% lower and upper confidence limits = LCL and UCL, respectively

Atlantic Bight, $L_\infty = 158.5$ cm FL, $k = 0.16$ yr^{-1}, $t_o = -3.43$ yr and $L_\infty = 147.4$ cm FL, $k = 0.21$ yr^{-1}, $t_o = -2.58$ yr for female and male blacktip sharks, respectively. Significant differences between von Bertalanffy growth curves of males and females were found within populations (Gulf log-likelihood ratio = 33.21, $P < 0.001$; Atlantic log-likelihood ratio = 9.32, $P < 0.05$) and between populations (females log-likelihood ratio = 18.65, $P < 0.001$; males log-likelihood ratio = 53.15, $P < 0.001$).

The maximum observed ages were 15.5+ yr (female) and 13.5+ yr (male) for sharks collected in the South Atlantic Bight and 12.5+ yr (female) and 11.5+ yr (male) in the Gulf of Mexico, based on vertebral band counts. Theoretical longevity estimates were 21.6 yr and 14.4 yr for females and 16.6 yr and 12.8 yr for males from South Atlantic Bight and Gulf of Mexico, respectively, using values obtained through von Bertalanffy growth models. The largest female aged in the Gulf of Mexico was 158 cm FL (11.5 yr) and 164 cm FL

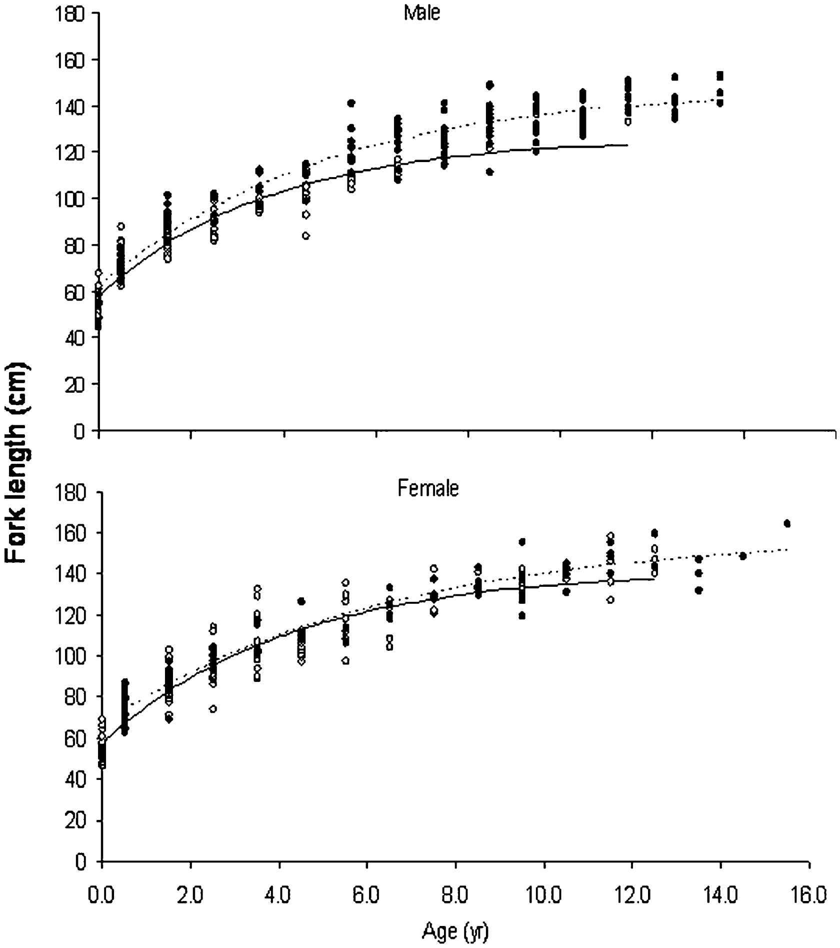


Fig. 4 Von Bertalannfy growth functions fitted to observed length-at-age data for male and female blacktip sharks. Solid circles for sharks and dashed lines = South Atlantic Bight while open circles and solid lines = Gulf of Mexico

(15.5 yr) from the South Atlantic Bight. For male blacktip sharks, the largest shark aged was 136 cm FL (9.5 yr) and 153 cm FL (age 13.5 yr) for the Gulf of Mexico and from the South Atlantic Bight, respectively.

Observed length-at-age and predicted growth rates were not significantly different ($P \geq 0.05$) between most ages for populations in the Gulf of Mexico and South Atlantic Bight (Table 3). Among females, mean observed length-at-age was only statistically different for one of out of 13 age classes (age 4.5). For male sharks, mean observed length-at-age was significantly differences in five of nine age classes (ages 1.5, 2.5, 3.5, 5.5, and 6.5). Predicted growth rates from age 0 yr to 12 yrs were similar among ages, averaging 6.6 cm yr^{-1} and 6.5 cm yr^{-1} for females and 5.5 cm yr^{-1} and 6.5 cm yr^{-1} for males from the Gulf of Mexico and South Atlantic Bight, respectively. Two-factor analysis of variance found no significant differences in growth rates (log transformed) between sexes ($F = 0.549$, df = 1, $P = 0.462$), area ($F = 1.060$, df = 1, $P = 0.308$) or their interaction ($F = 0.116$, df = 1, $P = 0.734$).

Length- and age-at-maturity

Median length- and age-at-maturity were different between sexes and areas. Length of the population at 50% maturity was 117.3 cm FL for females and 103.4 cm FL for males in the Gulf of Mexico (Fig. 5). The largest immature shark was 122 cm FL and 106 cm FL and the smallest mature shark was 109 cm FL and 102 cm FL for females and males, respectively. In the South

Table 3 Mean size-at-age for female and male blacktip sharks from the eastern Gulf of Mexico and South Atlantic Bight

Age	0.0	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5	15.5
Female																	
Gulf	53.6	75.0	85.7	96.5	104.8	105.4	117.5	116.4	126.7	134.5	132.2	139.3	132.2	146.1	–	–	–
SE	0.8	1.1	1.2	1.5	2.6	1.5	3.8	4.4	4.0	3.2	2.5	1.4	5.2	3.4	–	–	–
LCL	52.0	72.7	83.2	93.4	99.4	101.9	108.8	104.1	115.5	120.9	126.4	133.2	126.9	131.6	–	–	–
UCL	55.2	77.4	88.1	99.5	110.3	108.8	126.2	128.7	137.8	148.1	138.0	145.4	155.8	160.6	–	–	–
N	46	27	34	28	19	11	10	5	5	3	8	3	5	3	–	–	–
$P > t$	–	0.17	0.22	0.55	0.28	0.03	0.48	0.24	0.36	0.87	0.47	0.93	0.30	0.29	–	–	–
Atlantic	–	72.4	88.8	98.4	111.9	114.9	110.5	123.9	126.8	134.4	134.6	136.6	144.6	146.1	144.3	148	164
SE	–	1.8	2.2	2.0	4.1	5.6	3.5	3.4	2.2	1.5	1.8	1.3	1.4	3.4	2.8	–	–
LCL		68.6	83.9	93.2	94.1	90.9	66.0	113.1	122.1	131.3	131.0	133.9	141.8	138.2	137.4	–	–
UCL		76.1	93.6	103.6	129.7	139.0	154.9	134.7	131.5	137.4	138.3	139.3	147.3	154.1	151.1	–	–
Male																	
Gulf	54.5	73.3	81.4	89.9	98.2	102.0	108.1	114.6	121.6	121.5	136	130.5	132.9	–	–	–	–
SE	0.6	0.9	0.9	1.9	1.1	3.1	1.2	2.5	7.4	–	–	–	–	–	–	–	–
LCL	53.2	71.3	79.3	85.5	95.7	94.9	105.3	108.7	27.5	–	–	–	–	–	–	–	–
UCL	55.8	75.2	83.4	94.4	100.7	109.1	110.9	120.5	215.6	–	–	–	–	–	–	–	–
N	51	32	26	10	10	9	9	8	2	1	1	1	1	–	–	–	–
$P > t$	0.17	0.43	< 0.01	0.05	< 0.01	0.17	< 0.01	0.02	0.52	–	–	–	–	–	–	–	–
Atlantic	51.9	72.0	90.1	97.0	106.5	109.0	120.6	124.3	125.1	134.2	134.0	135.8	143.4	141.5	147.8	–	–
SE	2.2	1.0	1.8	2.5	2.4	2.7	2.3	2.7	1.9	1.8	1.9	1.4	1.4	3.1	2.9	–	–
LCL	45.5	69.9	86.0	89.2	100.3	101.6	115.5	118.3	120.9	130.4	130.0	132.8	140.4	132.9	5.7		
UCL	57.3	74.0	94.2	104.1	112.6	116.4	125.7	130.2	129.3	137.9	138.1	138.8	149.5	150.1	156.9		
N	7	18	12	5	6	5	12	10	14	21	15	16	12	5	4		

Standard error = SE, 95% lower and upper confidence limits = LCL and UCL, respectively and *N* = sample size. $P > t$ = the probability the *t* statistic is greater than the critical value of the *t* distribution

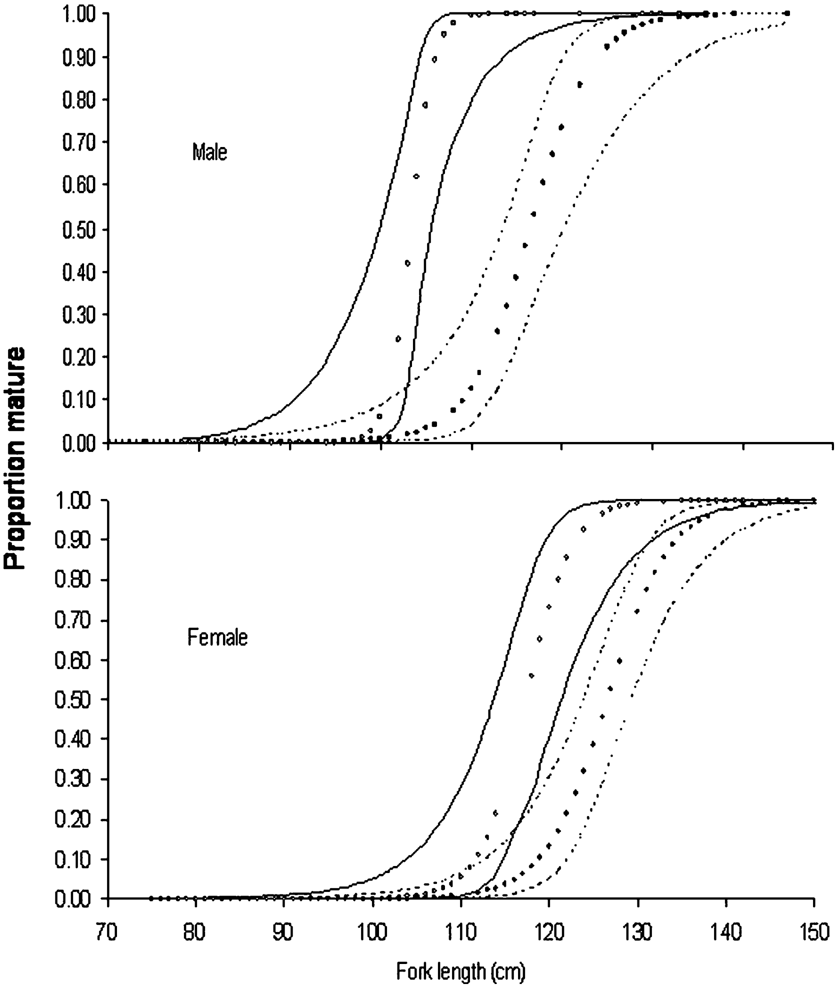


Fig. 5 Logistic models fitted to predicted length-at-maturity for male and female blacktip sharks. Lines = upper and lower 95% confidence intervals of the logistic curve. Solid circles and dashed lines = South Atlantic Bight while open circles and solid lines = Gulf of Mexico

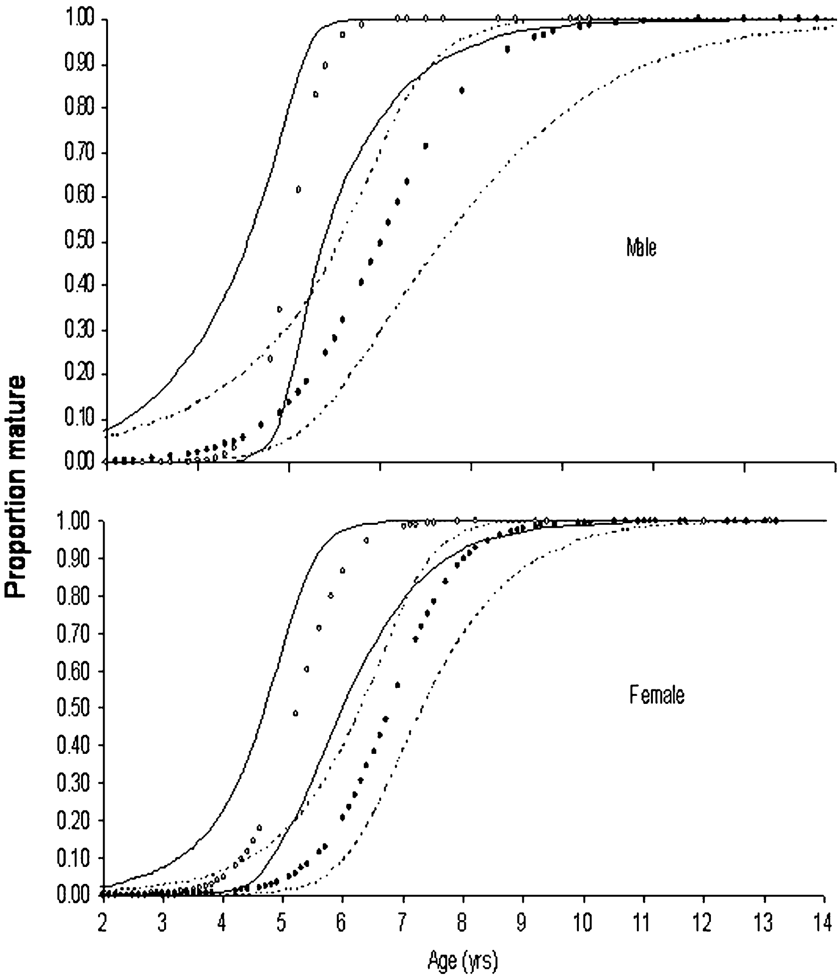
Atlantic Bight, median length-at-maturity was 126.6 cm FL for females and 116.7 cm FL for males (Fig. 5). The largest immature shark was 134 cm FL and 119 cm FL and the smallest mature shark was 112 cm FL and 111 cm FL for females and males, respectively. Significant differences between logistic curves of males and females were found within populations (Gulf log-likelihood ratio = 310.19; $P < 0.0001$) (Atlantic log-likelihood ratio = 262.37; $P < 0.001$) and between populations (females log-likelihood ratio = 18.65; $P < 0.001$) (males log-likelihood ratio = 53.15; $P < 0.001$).

Converting length to age and fitting the logistic model resulted in an age-at-maturity of 5.7 yr and 4.5 yr for females and males in the Gulf of Mexico, respectively (Fig. 6). In the South Atlantic Bight, age-at-maturity was 6.7 yr for females and 5.0 yr for males.

Discussion

Life history parameters of many marine fish stocks have been shown to vary in response to environmental change and to the interaction between genotype and that particular environment (Begg 2005). Regional differences in annual sea surface temperatures are evident between the eastern Gulf of Mexico and the South Atlantic Bight (24.4°C vs. 22.5°C, respectively; NOAA/NOS/Center for Operational Oceanographic Products and Services, http://www.lternet.edu/technology/sensors/arrays.htm). Keeney et al.

Fig. 6 Logistic models fitted to predicted age-at-maturity for male and female blacktip sharks. Lines = upper and lower 95% confidence intervals of the logistic curve. Solid circles and dashed lines = South Atlantic Bight while open circles and solid lines = Gulf of Mexico



(2005) demonstrated genetic heterogeneity and female philopatry, which resulted in multiple genetic reproductive stocks among blacktip sharks in the Gulf of Mexico and South Atlantic Bight. Further, recoveries from conventional tagging of over 6,000 sharks since 1963 suggest very little mixing of sharks between these two areas (Kohler et al. 1998; Carlson unpublished data; J.P. Tyminski, Mote Marine Laboratory, personal communication). Despite these mechanisms that could potentially cause differences in life history traits in blacktip sharks between the South Atlantic Bight and eastern Gulf of Mexico, we could not definitively conclude that they exist. Although significant differences between sexes from each area were found in the overall von Bertalanffy growth models, mean length-at-age was not different for most ages and growth rates were similar. Length- and age-at-maturity differences could have been due to temporal disjunction, since most samples from the South Atlantic Bight (Castro 1996) were collected in 1981–1993 while sharks from the eastern Gulf of Mexico were captured during 1996–2002.

The temporal periodicity of growth zones should be evaluated to fully understand differences in shark stocks. In the current study, minimal marginal increment ratios occurred in sharks captured in June and maximal ratios occurred in sharks captured in May. These results support the hypothesis of that one band pair form annually in the vertebral centra of this species. These results compare favorably to cycles in marginal increments (Cailliet and Goldman 2004) and to annual vertebral band patterns in other shark species examined in both the Gulf of Mexico (Carlson et al. 1999, 2003) and the Atlantic Ocean (Natanson et al. 1995; Conrath et al. 2002). However, Killam and Parsons (1989) suggest ring deposition occurs in January for blacktip sharks captured in Tampa Bay, Florida. The reason for this difference in marginal increment formation between the studies is unknown but may be due to differing techniques. For example, Killam and Parsons (1989) used vernier calipers on whole vertebrae whereas the present study utilized an ocular micrometer on sectioned vertebrae.

Since band counts of the largest and oldest animals in the present study were compressed (too small to discern marginal increments from their widths), marginal increment analysis was only conclusive for juvenile animals (sharks <5 yrs in age). Thus, the annular nature of growth bands was verified for only those age groups. Nevertheless, we assumed that as sharks grew larger and older, the annual nature of growth ring deposition continued throughout their lifetimes (Cailliet and Goldman 2004).

Geographic variation in growth for at least two stocks of starspotted dogfish, *Mustelus manazo*, was proposed by Taniuchi et al. (1983), but a reexamination of their data using cross-exchange and comparative reader analysis found no significant differences (Cailliet et al. 1990). Similarly, Tanaka et al. (1990) reported that differences among band readers and methodologies produce variations in growth for blue shark, *Prionace glauca*, that were artifacts. We attempted to control these factors and feel they had little effect on our results. We suspect the most significant factor in our study that could affect our results was inherent bias associated with gear selectivity. An ideal study would ensure all samples would be collected using a similar fishery-independent gear. Growth models fitted to fishery-dependent data can have biases due to length-selective fishing where more fast-growing sharks, fewer large young sharks, and small old sharks are differentially removed from the stock (Kimura 1980; Walker et al. 1998). In our study, blacktip sharks were collected with a variety of sampling gears from scientific gillnets to commercially fished longlines. This is a common problem when attempting to model growth on sharks with wide ranges in lengths. Blacktip sharks range in length from 35 cm to 170 cm. Gear utilized for catching smaller sharks would not be appropriate for larger sharks. For example, longlines designed to capture smaller sharks (i.e., small hooks, low gangion leader strength) would not be appropriate for sampling larger sharks due to differential catchability as a result of bite-offs from low leader strength (Beerkircher et al. 2003). Conversely, gillnets of larger mesh lengths designed for adult sharks would not be suitable for juvenile sharks as smaller sharks would simply pass through the net. Carlson and Cortés (2003) documented gillnet selectivity for small coastal sharks in US waters, but few controlled experimental studies are available on how gear variation affects catches of sharks or resulting growth models (Walker et al. 1998).

Despite these fundamental biases associated with determining variation in life history traits, at least one study has illustrated that differences in life history traits do occur in shark populations. Lombardi-Carlson et al. (2003) demonstrated increasing length-, age-at-maturity, and mass of near-term embryos in bonnetheads, *Sphyrna tiburo*, with increasing latitude in the eastern Gulf of Mexico. Further, these authors documented an increase in shark growth rate with an increase in latitude (termed countergradient variation, Conover and Present 1990). Along with controlling for sample preparation and reading, Lombardi-Carlson et al. (2003) collected sharks simultaneously in all areas with similar sampling gear to minimize sampling bias.

Estimates of age, growth, and length- and age-at-maturity for male and female blacktip sharks in the Gulf of Mexico were different than those reported by Killam and Parsons (1989) for sharks collected off Tampa Bay, FL. von Bertalanffy growth parameters were $L_\infty = 160$ cm FL, $k = 0.19$, and $L_\infty = 137$ cm FL, $k = 0.28$ during 1985–1987 for females and males, respectively. These indicate an increase in growth and a decrease in theoretical maximum length for sharks collected for our study 11–14 yrs later. Observed maximum age also increased from 10 yrs and 9 yrs in 1985–1987 to 12.5 yrs and 11.5 yrs in the present study. Length- and age-at-maturity decreased from about 110 (age = 4–5 yrs) and 132 cm FL (age = 6–7 yrs) in 1985–1987 to 103 (age = 4.5 yrs) and 117 cm FL (age = 5.7 yrs) in 1996–2001 for males and females, respectively. Blacktip sharks have been heavily harvested in the Gulf of Mexico since the 1980's (NMFS 2003), thus the observed decrease in length- and age-at-maturity and increased growth rate lends support to the potential for a density-dependent compensatory response. Compensatory growth and reproductive responses have been documented in a few species of sharks (Sminkey and Musick 1995; Carlson and Baremore 2003). For reasons previously outlined, it could not be determined if these temporal changes in age and growth were due to differences in methodology, anthropogenic influences, or natural causes.

Given the caveats observed in this study and the current data, we could not definitively conclude that differences in life history characteristics exist between blacktip sharks in the eastern Gulf of Mexico and South Atlantic Bight. A synoptic study sampling the entire geographic range of blacktip sharks (i.e., entire Gulf of Mexico and northwest Atlantic Ocean) would be required to fully resolve the question of separate stocks. The application of archival satellite tags could also help to define spatial distributions and long-term movement patterns, information that can assist in stock discrimination (Punt 2001).

Acknowledgements Ken Goldman, Pete Sheridan and Linda Lombardi provided helpful comments on an earlier version of this manuscript. Lori Hale (NOAA Fisheries Service-Panama City Laboratory) assisted with the processing and reading of samples and Linda Lombardi developed the SAS code for the maturity estimates. George Burgess and Matt Callahan (University of Florida) obtained samples from the directed shark longline fishery. John Tyminski (Mote Marine Laboratory) provided samples off Tampa Bay and Charlotte Harbor, FL. Armando de ron Santiago, C.J. Greene, Matt Rayl, Bill Habich, Mike Farni, Jacques Hill, and Jeff Pulver collected samples from the directed shark gillnet fishery. Mark Grace and Lisa Jones (NOAA Fisheries-Mississippi Laboratory) helped to provide samples during R/V Oregon II longline surveys. Thanks also go to Jose Castro (NOAA Fisheries-Miami Laboratory) who provided data from his blacktip reproduction study.

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