Life history parameters for blacktip sharks, *Carcharhinus limbatus*, from the United States South Atlantic Bight and Eastern Gulf of Mexico.

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Introduction

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 size-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 & Thompson (2005) reported cownose rays, *Rhinoptera bonasus*, in the Gulf of Mexico have lower estimates of theoretical maximum size 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et al. 2004), and conventional tagging evidence suggests little exchange between areas (Kohler et al. 1998; Carlson unpublished).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 size-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 & Manire 1994; Grace & Henwood 1998; Carlson & Brusher 1999) and from fishery-dependent programs (Trent et al. 1997; Burgess & Morgan 2003). Additional reproductive data were also provided from a study by Castro (1996) for the South Atlantic Bight. 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 and processed following techniques outlined in Carlson et al. (2003). Specifics for blacktip shark are reported in Carlson et al. (in review).

Several growth models were fitted to the observed size-at-age data: the von Bertalanffy growth model (von Bertalanffy 1938; Beverton and Holt 1957), an alternate equation of the von Bertalanffy growth model with a size-at-birth intercept rather than the t_o parameter, 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 between sex and area. 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 size-at-age between ages were made using a Welch modified two-sample t-test (Zar 1984). Growth rates were calculated from predicted fork sizes 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.

Size-at-maturity estimation

Maturity was assessed following the guidelines of Castro (1996). To quantitatively assess size-at-maturity, the size at which 50% of the population is mature for male and female sharks was determined (i.e., median size-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=size. Median size-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 used χ^2-tests of likelihood ratios.

To assess age-at-maturity, sizes were back-transformed to age using each respective von Bertalanffy growth model. Similar to determination of size-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. Using data collected in this study and that from fishery-independent surveys (Carlson and Brusher 1999), several morphometric relationships to convert length measurements were developed. Linear regression formulae were determined as FL = 1.10(PC) + 0.29 (n=1096); TL = 1.12(FL) + 1.12 (n=1248); and STL = 1.02(TL) + 0.99 (n=926). All equations were highly significant ($p<0.0001$) and had r^2 between 0.98-0.99.

Age and growth

Growth bands were found to be most apparent on unstained sagittal sections with a thickness of 0.3 mm. 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. For those samples were band counts differed, consultation resulted in agreement for 608 out of 628 vertebrae. Samples with disagreement were discarded.

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 2 and 3 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 (Figure 1). 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 age and growth results using only the von Bertalanffy equation. Growth parameters derived for blacktip shark from the Gulf of Mexico indicated that they attain a smaller theoretical maximum size (L_∞) and that they reach L_∞ at a faster rate (k) than conspecifics in the South Atlantic Bight (Table 1; Figure 2). Von Bertalanffy growth parameters for sharks in the Gulf of Mexico were L_∞=141.6 cm FL, k=0.24 yr^{-1}, t_o=-2.18 yr and L_∞=126 cm FL, k=0.27 yr^{-1} t_o=-2.21 yr for females and males, respectively (Table 2). In the South Atlantic Bight, L_∞=158.5 cm FL, k=0.16 yr^{-1}, t_o=-3.43 yr and L_∞=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 (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 size-at-age and predicted growth rates were not significantly different ($p\geq0.05$) between most ages for populations in the Gulf of Mexico and South Atlantic Bight. Among females, mean observed size-at-age was only statistically different for one of out of 13 age classes (age 4.5). For male sharks, mean observed size-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 0-12 years were similar among ages, averaging 6.6 and 6.5 cm yr^{-1} for females and 5.5 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, $p=0.734$).

Size- and age-at-maturity

Median size- and age-at-maturity were different between sexes and areas. Size 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 (Figure 3). 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 Atlantic Bight, median size-at-maturity was 126.6 cm FL for females and 116.7 cm FL for males (Figure 4). 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 size 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. 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. (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 size-at-age was not different for most ages and growth rates were similar. Size- 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.

Estimates of age, growth, and size- and age-at-maturity for male and female blacktip sharks in the Gulf of Mexico were different than those reported by Killam & Parsons (1989) for sharks collected off Tampa Bay, FL. Von Bertalanffy growth parameters were L_∞=160 cm FL, k=0.19, and L_∞=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 size for sharks collected for our study 11-14 years later. Observed maximum age also increased from 10 and 9 years in 1985-1987 to 12.5 and 11.5 years in the present study. Size- 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 size- 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 & Musick 1995; Carlson & 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, it would not be appropriate at this time to manage blacktip sharks as separate stocks. Rather, it would be more acceptable to use the combined estimates from growth models and maturity oogives as inputs to demographic and age-structured stock assessment models (see Table 1 and 2 for combined models). 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).

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Table 1. Von Bertalanffy growth parameters for male, female, and sex combined blacktip sharks. Estimates are provided for the Gulf of Mexico, South Atlantic Bight, and areas combined. Standard error = S.E. and 95% lower and upper confidence limits = L.C.L and U.C.L, respectively.

	Male	S.E.	L.C.L	U.C.L	Female	S.E.	L.C.L	U.C.L	Combined	S.E.	L.C.L	U.C.L
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			

Table 2. Predicted proportion mature for blacktip sharks for combined areas and sexes.

Age	Proportion mature (%)
0	**0.0**
1	**0.2**
2	**0.6**
3	**2.2**
4	**7.7**
5	**23.9**
6	**54.1**
7	**81.6**
8	**94.3**
9	**98.4**
10	**99.6**
11	**99.9**
12	**100.0**
13	**100.0**
14	**100.0**
15	**100.0**

Figure 1. 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.

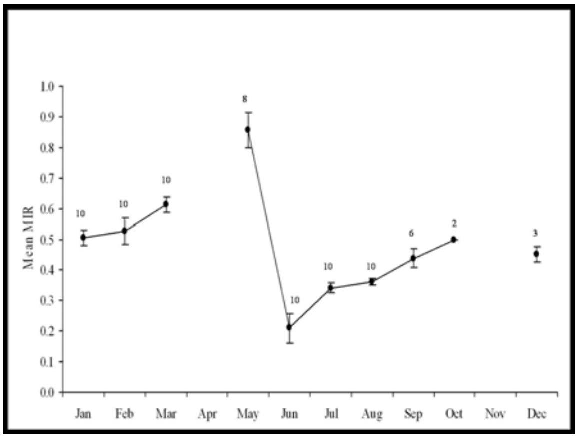

Figure 2. Von Bertalannfy growth functions fitted to observed size-at-age data for male and female blacktip sharks. Solid circles for sharks and dashed lines = South Atlantic Bight while open circles and solid lines = Gulf of Mexico.

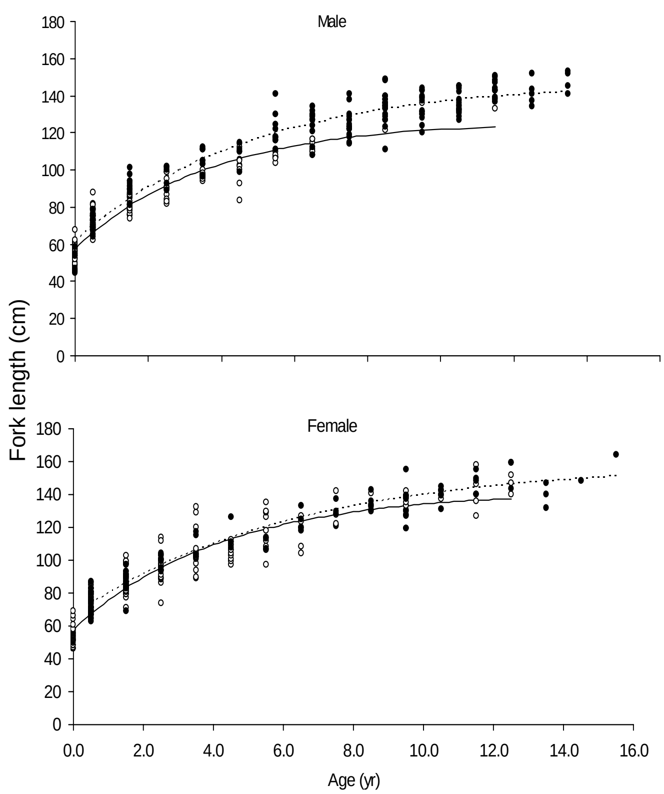

Figure 3. Logistic models fitted to predicted size-at-maturity for male and female blacktip sharks. Lines=upper and lower 95% confidence intervals. Solid circles and dashed lines = South Atlantic Bight while open circles and solid lines = Gulf of Mexico.

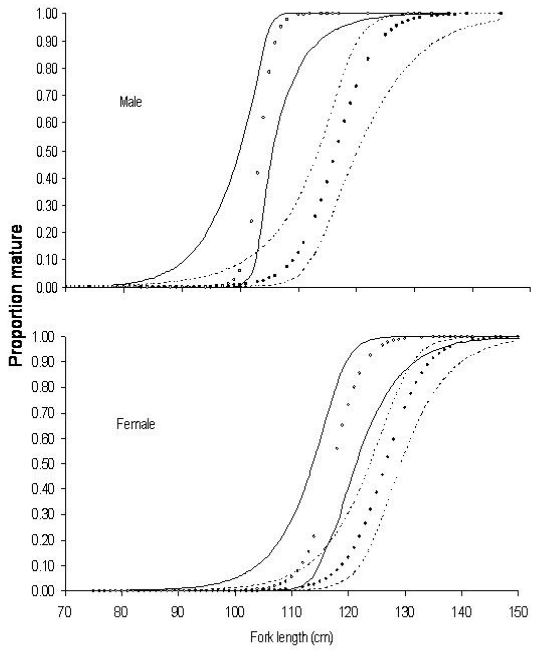

Figure 4. Logistic models fitted to predicted age-at-maturity for male and female blacktip sharks. Lines=upper and lower 95% confidence intervals. Solid circles and dashed lines = South Atlantic Bight while open circles and solid lines = Gulf of Mexico.