

Age and growth of the blacknose shark, *Carcharhinus acronotus*, in the western North Atlantic Ocean with comments on regional variation in growth rates

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Synopsis

We examined the age and growth of the blacknose shark, *Carcharhinus acronotus*, in the western North Atlantic Ocean by obtaining direct age estimates using vertebral centra. We verified annual deposition of growth increments with marginal increment analysis and validated it by analyzing vertebrae marked with oxytetracycline from a female blacknose shark held in captivity. Von Bertalanffy growth parameters indicated that female blacknose sharks have a lower growth constant (k), a larger theoretical maximum size (L_{∞}), and are longer lived than males. We compared these growth parameters for blacknose sharks in the western North Atlantic Ocean to growth parameters for blacknose sharks collected in the eastern Gulf of Mexico to test for differences between regions. Females in the western North Atlantic Ocean have a significantly lower L_{∞} , lower k , and a higher theoretical longevity than females in the Gulf of Mexico. Males in the western North Atlantic Ocean have a higher L_{∞} , lower k , and higher theoretical longevity than males in the Gulf of Mexico. The significant differences between these life history parameters for blacknose sharks suggest that, when possible, future management initiatives concerning blacknose sharks should consider managing the populations in the western North Atlantic and the Gulf of Mexico as separate stocks.

Introduction

The blacknose shark, *Carcharhinus acronotus*, is found in the coastal waters of the Atlantic Ocean from North Carolina to Brazil, including the Gulf of Mexico (Castro 1983, Compagno 1984). Blacknose sharks are reported to attain a maximum size of 140 cm total length (TL) with the size at birth being approximately 50 cm TL (Castro 1983). Under the Fishery Management Plan for Sharks

(NMFS 1993) the blacknose shark is managed as a small coastal shark, which includes those species that are relatively small, fast-growing and short-lived. Blacknose sharks frequently constitute a portion of the catch in coastal commercial fisheries, with estimated landings of 43–79 metric tons from 1995 to 2000 in the western North Atlantic Ocean (Cortés 2002). Additionally, recreational fishermen in the same region landed 2890–11 831 blacknose sharks from 1995 to 2000 (Cortés 2002).

Regional differences in growth parameters have been suggested to occur among blacknose sharks. Carlson et al. (1999) compared von Bertalanffy growth parameters of blacknose sharks from two regions in the eastern Gulf of Mexico with those reported by Schwartz (1984) off North Carolina and noted that blacknose sharks in the Gulf of Mexico attain a smaller theoretical maximum size and have a higher growth coefficient than conspecifics off North Carolina. However, it could not be determined if these differences in parameter estimates were due to low sample sizes or interpretation of growth rings.

Because variation in growth has been proposed among blacknose sharks, accurate information on each population is important for species-specific management. Given the importance of life history information in the development of age structured population models (Cortés 1999), the objective of this study is to examine the age and growth of the blacknose shark off South Carolina. In particular, for sharks collected off South Carolina we wish to: (1) estimate age and growth for blacknose sharks in the western North Atlantic Ocean and (2) compare these estimates with those determined for blacknose sharks in the eastern Gulf of Mexico to test for differences in growth parameters between the two regions.

Materials and methods

We collected 240 blacknose sharks (112 ♂, 128 ♀), ranging in size from 633 to 1101 mm fork length (FL), from coastal waters off South Carolina, U.S.A., from July 1998 through June 2001. We collected blacknose sharks using longline and hand deployed longline fishing gear. The longline gear consisted of 1852 m (272 kg test monofilament) of mainline with 120 gangions. The hand deployed line gear consisted of 180 m braided rope mainline, with an 18.3 m anchor depth, and supported the use of 50 gangions at 2.8 m intervals. The gangions for both gear types had 63 cm monofilament leaders (91 kg test) and 15/0 tuna circle hooks. The gear was baited with various species of teleosts, as determined by seasonal availability, and set at depths ranging from 2 to 14 m. Soak times were limited to 1 h to reduce mortality rates in non-

target species. All samples were taken from within 5.5 km of the South Carolina coast.

After collection, we recorded sex and measured stretch total length (STL), fork length (FL) and precaudal length (PCL) to the nearest mm over a straight line along the axis of the body. We recorded three different length measurements to obtain conversions for comparisons to other studies which reported only one length measurement. Stretch total length was measured from the anterior most point of the snout to the posterior most point of the upper lobe of the fully extended caudal fin. We measured the mass of each shark to the nearest 0.5 kg, when sampling conditions permitted.

We removed the cervical region of the vertebral column from each specimen and then stored the sample on ice until it could be frozen. For ageing preparation, we removed the basidorsal, interdorsal, basiventral, and interventral cartilages, and remaining muscle tissue from each centrum with a scalpel and forceps. We soaked the vertebrae in 5% sodium hypochlorite for 5–30 min to remove all excess tissue, rinsed them under running tap water and stored them in 50 ml polypropylene containers filled with 95% ethanol.

We measured the diameter of the largest vertebra from each sample, using a digital caliper. After attaching each vertebra to a slide, using thermoplastic glue, we removed a 0.6 mm sagittal section containing the focus using a Buehler Isomet low speed saw. We air dried each vertebra and fixed it to a slide, using a toluene based acrylic mounting medium, before reading. Preliminary vertebrae preparations indicated that the use of chemical stains did not further enhance growth increments and therefore we did not stain vertebrae.

We selected sectioned vertebrae at random and the senior author counted the number of bands on the corpus calcareum twice without knowledge of the date of capture, the size of the shark or the initial band count. A period of 1 month separated the first two age readings. If there was disagreement between the two readings, we conducted a third reading to resolve the discrepancy. The third age reading occurred 2 weeks after the completion of the second age readings. If the third reading did not match one of the previous two we excluded that sample from subsequent analyses. We estimated age by assuming: (1) the birthmark was

formed prior to parturition, (2) the second band was formed approximately 6 months later during the first winter, and (3) the third band was formed 1 year later. Therefore, we subtracted 1.5 from each total band count to calculate age. We calculated the coefficient of variation and index of precision to determine the variability between the age estimates for each sample (Beamish & Fournier 1981, Chang 1982). All readings were done at a magnification of 20X.

We placed one female blacknose shark in the South Carolina Aquarium for validation of growth band formation periodicity. The shark was collected in July of 2000 off the coast of Charleston, SC and acclimated to captivity in holding facilities outside of the aquarium for approximately 9 months. On 27 April 2001 the shark received an interperitoneal injection of oxytetracycline (Promycin) (12 mg kg^{-1} body weight) prior to being placed in the main display aquarium. At the time of injection the shark measured 883 mm FL. The temperature in the $1\,363 \text{ m}^3$ aquarium cycled from 28.3°C for a 4 month period followed by a 2 month transition period to 23.8°C , which was held constant for a 4 month period and then slowly transitioned back to 28.3°C over a 2 month period. There was a constant light cycle of 14.5 h on and 9.5 h off each day. The shark was fed to satiation on a diet of mackerel, *Scomber scombrus*, salmon, *Oncorhynchus* sp., and tuna, *Thunnus* sp., with Mazuri shark/ray vitamins, on a set schedule three times per week. The shark expired on 24 August 2002, measuring 970 mm FL, and the cervical vertebrae were removed to analyze the periodicity of growth increment formation. The vertebrae showed six distinct bands (age 4.5+ years). The periodicity of growth increment formation was determined to be 1 year based on the presence of one growth increment distal to the OTC mark on the corpus calcareum (Figure 1). Therefore, all subsequent vertebral age estimates in this study were based on the formation of one growth increment per year with the exception of the second band which would presumably be incorporated on the vertebral centrum 6 months after parturition when water temperatures decrease with the onset of the first winter. Two additional blacknose sharks, one female and one male, are currently being housed at the South Carolina Aquarium to validate the periodicity of growth band formation in other age classes.

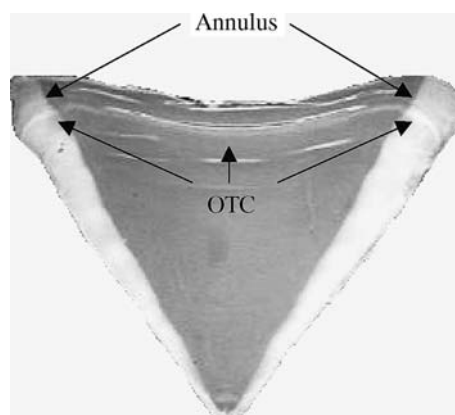


Figure 1. Transverse section of cervical vertebrae from a 970 mm FL, 4.5+ year old female blacknose shark. Oxytetracycline is visible on the corpus calcareum and the intermedialia. Annulus is distal to the oxytetracycline mark and visible only on the corpus calcareum.

There was no significant difference between FL and vertebral diameter (ANCOVA, $F = 0.55$, $p = 0.46$) for males and females, therefore we combined data for both sexes and significant relationships existed between FL and vertebral diameter ($r^2 = 0.93$, $p < 0.01$). This length-vertebral dimension relationship supports the assumption that vertebral size increases proportionally with body length and that vertebrae are suitable for ageing.

We verified the periodicity of band formation using marginal increment analysis. We calculated mean increment ratio (Hayashi 1976, Wintner & Cliff 1999) and plotted it against month of capture to determine the time/season of growth band deposition using the equation $\text{MIR} = (\text{CR} - R_n) / (R_n - R_{n-1})$, where CR = centrum radius, R_n = distance from focus to last fully formed growth band, and R_{n-1} = distance from focus to last fully formed growth band preceding R_n . We took all vertebral measurements for marginal increment analysis along the axis of the corpus calcareum using the image analysis program Optimas (Optimas 1998).

We fitted sex specific observed size at age estimates to the von Bertalanffy growth model (VBGF) using non-linear regression procedures in the program Statgraphics (Statgraphics 2000):

$$L_t = L_\infty(1 - e^{-k(t-t_0)})$$

where L_t = length at age t , L_∞ = theoretical maximum length, k = coefficient of growth, and

t_0 = theoretical age at which length equals zero. We estimated theoretical longevity as the age at which 95% of theoretical maximum size is reached, using the expression $(5(\ln 2))/k$ (Fabens 1965).

To test for differences in age and growth between blacknose sharks from the western North Atlantic Ocean and the eastern Gulf of Mexico, we fitted the observed length-at-age data collected by Carlson et al. (1999) and Carlson (unpublished) to the von Bertalanffy growth model and compared the resulting curves to those obtained in this study using the likelihood ratio test (Cerrato 1990).

Results

There was no statistical difference in body length measurements, FL, PCL and STL, for females and males, consequently we combined data from both sexes to obtain conversions (ANCOVA, FL \rightarrow STL: $F = 0.32$, $p = 0.57$; FL \rightarrow PCL: $F = 1.12$, $p = 0.29$). The relationships between the body length measurements of the blacknose sharks caught during this study were linear ($r^2 = 0.99$,

$p < 0.01$) (Table 1). There was a difference in the relationship between FL and weight for males and females (ANCOVA, $F = 9.35$, $p < 0.01$), therefore, the equations for these relationships are reported separately (Table 1).

We assigned ages to 226 vertebral samples (117 ♀, 109 ♂). After both readings, 76% of the counts agreed, 99.1% were ± 1 year between counts and 100% were within ± 2 years. The mean CV was 0.06 (SD = 0.13) and the mean index of precision was 0.04 (SD = 0.09). The parameters estimated by the VBGF indicated that females attain a larger L_∞ , have a lower k and are longer lived than males (Table 2; Figure 2). We found statistically significant differences between growth models estimated for males and females (likelihood ratio = 24.37, Chi-square p -value < 0.01).

We found a significant difference between the marginal increment widths from early summer to late fall/early winter (F -ratio = 6.65, $p < 0.01$) (Figure 3). This indicated that the vertebral radius increases over summer and fall months, and that growth slows during the winter months at which time the annulus is presumably formed. Because

Table 1. Length (mm) and length-weight (kg) relationships for blacknose sharks.

Conversion	Equation	Regression r^2 value	Regression p -value	ANCOVA F -ratio	ANCOVA p -value	n
FL \rightarrow STL	STL = $45.2829 + 1.18784 * FL$	0.99	<0.01	0.32	0.57	230
FL \rightarrow PCL	PCL = $-15.4285 + 0.927212 * FL$	0.99	<0.01	1.12	0.29	228
FL \rightarrow WT ♀	WT = $\exp(-1.892 + 0.004 * FL)$	0.96	<0.01	9.35	<0.01	120
FL \rightarrow WT ♂	WT = $\exp(-1.673 + 0.004 * FL)$	0.95	<0.01			102

Table 2. Comparison of von Bertalanffy growth function parameter estimates for male and female blacknose sharks in the western North Atlantic Ocean and the Gulf of Mexico based on the results of this study, Schwartz (1984) and Carlson et al. (1999).

Life history parameter	Atlantic Ocean (present study)	Atlantic Ocean (Schwartz 1984)	Gulf of Mexico (Carlson et al. 1999, Carlson unpublished data)
Theoretical maximum size (L_∞)(mm FL)	1058.60 \pm 43.28 ♂ 1135.50 \pm 52.45 ♀	1887 ♂ 1650 ♀	929.80 \pm 11.90 ♂ 1305.20 \pm 59.8 ♀
Growth coefficient (k)	0.21 \pm 0.05 ♂ 0.18 \pm 0.04 ♀	0.117 ♂ 0.138 ♀	0.48 \pm 0.17 ♂ 0.21 \pm 0.16 ♀
Theoretical age at zero size (t_0) (years)	-3.90 \pm 0.90 ♂ -4.07 \pm 0.96 ♀	-2.01 ♂ -2.68 ♀	-0.95 \pm 0.31 ♂ -1.58 \pm 0.16 ♀
Theoretical longevity (years)	16.4 ♂ 19.0 ♀	29.6 ♂ 25.11 ♀	7.2 ♂ 16.5 ♀
N	109 ♂ 117 ♀	30 ♂ 42 ♀	49 ♂ 74 ♀

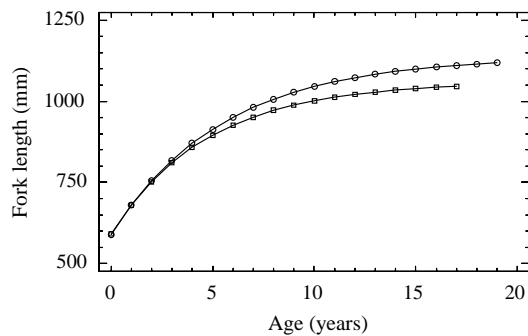


Figure 2. von Bertalanffy growth models for Atlantic Ocean male and female blacknose sharks, based on direct age estimates: \square = male ($L_{\infty} = 1058.64$; $k = 0.21$; $t_0 = -3.90$, $r^2 = 0.90$; $n = 109$), \circ = female ($L_{\infty} = 1135.47$; $k = 0.18$; $t_0 = -4.07$, $r^2 = 0.91$; $n = 117$).

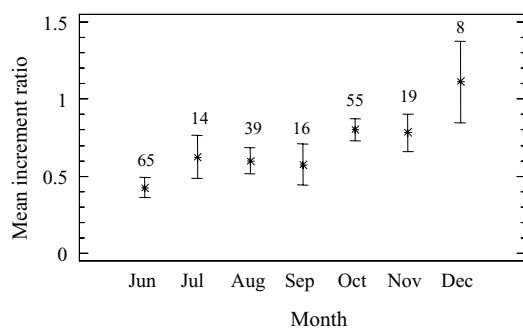


Figure 3. Mean increment ratio by month; $n = 216$. Error bars are 95% confidence intervals. Numbers above error bars represent the number of samples included in the analysis for each month.

blacknose sharks are not present in South Carolina waters during the winter we were not able to collect specimens during the period when growth bands are deposited on vertebral centra. However, it is apparent that the growth bands are deposited during periods of slower growth, i.e. winter, as the marginal increment was significantly more narrow during the early summer than it was in the late fall.

There were statistically significant differences between growth models for each sex between the Gulf of Mexico and the western North Atlantic Ocean (δ likelihood ratio = 129.06, Chi-square p -value < 0.01; ϕ likelihood ratio = 126.96, Chi-square p -value < 0.01). Male blacknose sharks in the Atlantic have a higher L_{∞} , lower k and t_0 than do males in the Gulf of Mexico. Females in the

Atlantic also have a lower k and t_0 ; however, they have smaller L_{∞} than females in the Gulf of Mexico. Both male and female blacknose sharks in the Atlantic have higher theoretical longevity than do conspecifics in the Gulf of Mexico (Table 2).

Discussion

We were able to demonstrate the annual periodicity of growth increment formation on the vertebrae of one female blacknose shark held in captivity which suggests annual deposition of growth bands up to an age of 4.5 years. However, we were not able to validate the formation of annual growth increments for all age classes of blacknose sharks, a requirement proposed by Beamish & McFarlane (1983). The results of the marginal increment analysis strongly indicate that narrow translucent bands observed on vertebral centra of blacknose sharks are formed once a year on the distal edge of the corpus calcareum and intermedialia between January and May. Because we were not able to collect blacknose sharks throughout the year in the coastal waters of South Carolina marginal increment analysis was not able to verify the month of band formation on vertebral centra of blacknose sharks.

The von Bertalanffy growth parameters estimated in this study were dissimilar to the parameter values reported by Schwartz (1984) from the same region of the western North Atlantic (Table 2, Figure 4). Schwartz (1984) reported higher L_{∞} , lower k , and lower t_0 for both male and female blacknose sharks. Carlson et al. (1999) reported similar differences between their data and Schwartz's and attributed the disparity to the assumptions of each study as well as to differing sample sizes for age 0+ and 1+ sharks. Schwartz (1984) did not include individuals estimated to be less than 1 year old and only six individuals between the age of one and two were used in his analysis. Although no neonates were incorporated into the growth model in this study, 18 individuals between age 0+ and 1+ and 30 individuals between age 1+ and 2+ were included. The lack of younger fish in Schwartz's (1984) VBGF may have led to the large L_{∞} and low k values for each sex.

The growth of one recaptured shark supports our growth model. A female blacknose shark

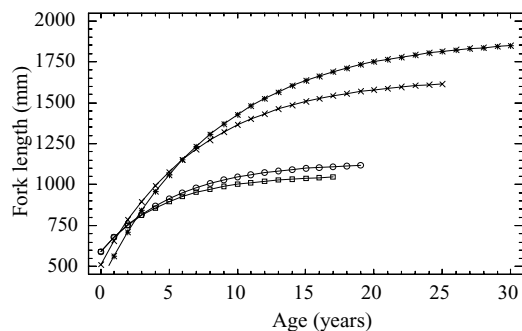


Figure 4. Comparison of von Bertalanffy growth models for blacknose sharks in the western North Atlantic Ocean. \square = males (this study), \circ = females (this study), \times = females (Schwartz 1984) and $*$ = males (Schwartz 1984); von Bertalanffy growth parameter estimates are presented in Table 2. Theoretical maximum ages were calculated using the algorithm $5(\ln 2)/k$ (Fabens 1965).

tagged on 28 August 1997 off Charleston, South Carolina ($32^{\circ}40'83''\text{N}$, $79^{\circ}48'57''\text{W}$), was recaptured on 10 July 2001, by South Carolina Department of Natural Resources biologists, near the North Carolina/South Carolina border ($33^{\circ}03'120''\text{N}$, $79^{\circ}17'85''\text{W}$). The shark was 843 mm FL at time of tagging and 1006 mm FL when recaptured. By back transforming length to age, the shark was 3.4 years old at time of tagging and 7.8 years at time of recapture, which closely fit the actual growth and time at liberty of this shark (Figure 5).

Theoretical age at size zero estimates were higher than expected. However, because intra-uterine growth rates are more rapid than those

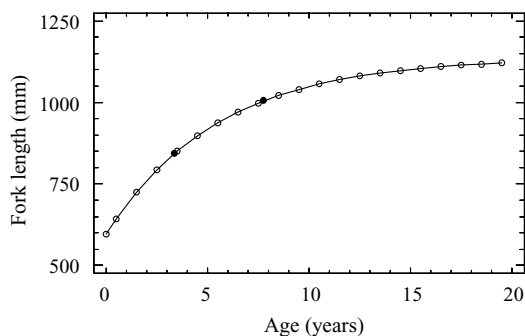


Figure 5. Comparison of VBGF, based on observed data, and tag recapture data. Female blacknose shark tagged on 28 August 1997, FL 843 mm – Recaptured on 10 July 2001, FL 1006 mm; \circ = VBGF from direct age estimates, \bullet = back transformed age from observed VBGF (3.4 and 7.8 years).

after parturition, the high t_0 values in this study might result from the inability of the von Bertalanffy growth function to model intrauterine growth. Because intrauterine growth is sigmoidal and not linear, intrauterine growth of elasmobranchs is not adequately described by the von Bertalanffy growth model. Casey & Natanson (1992) reported high t_0 values for sandbar sharks *Carcharhinus plumbeus*, in the Atlantic and also attributed the inflated values to rapid intrauterine growth. Therefore we assert that the assumption that t_0 represents gestation time is not correct as the von Bertalanffy growth model is logarithmic and thus not capable of detecting more than one inflection point.

Blacknose sharks in the Gulf of Mexico have a higher k than was estimated for blacknose sharks in the western North Atlantic Ocean. Based on observed data, males in the Atlantic grew more slowly than males in the Gulf of Mexico (0.21 vs. 0.48), while the k values for females in the two regions were similar (Atlantic = 0.18, Gulf = 0.21) (Figure 6). The higher k values in the Gulf of Mexico relative to the Atlantic for blacknose sharks followed the same trend reported for tiger sharks, *Galeocerdo cuvieri*, by Branstetter et al. (1987). Regional differences in growth rates have also been reported for blacknose sharks from northwest Florida and Tampa Bay, Florida, two areas within the Gulf of Mexico (Carlson et al. 1999), as well as for blacktip *Carcharhinus limbatus*

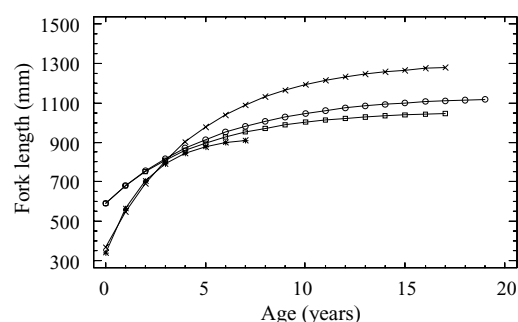


Figure 6. Comparison of von Bertalanffy growth models for blacknose sharks in the western North Atlantic Ocean and the Gulf of Mexico (Carlson et al. 1999); \square = males (this study), \circ = females (this study), \times = females (Carlson et al. 1999) and $*$ = males (Carlson et al. 1999); von Bertalanffy growth parameter estimates are presented in Table 2. Theoretical maximum ages were calculated using the algorithm $5(\ln 2)/k$ (Fabens 1965).

(Wintner & Cliff 1995), spiny dogfish, *Squalus acanthias* (Nammack et al. 1985, Saunders & McFarlane 1993) and bonnethead, *Sphyrna tiburo*, sharks (Parsons 1993 Carlson & Parsons 1997).

Growth coefficients for Atlantic sharpnose sharks *Rhizoprionodon terraenovae*, have been estimated to range between 0.36 and 0.53 (Parsons 1985, Branstetter 1987a) while bonnethead sharks have k values reported to range between 0.28 and 0.69 (Parsons 1993, Carlson & Parsons 1997). Growth coefficient estimates for large coastal sharks range from 0.04, for male dusky sharks, *Carcharhinus obscurus*, to 0.27 for blacktip sharks (sexes combined) (Branstetter 1987b, Natanson et al. 1995). While the k values for blacknose sharks in the Gulf of Mexico were more consistent with the generality that small coastal sharks have higher growth rates and shorter longevities than large coastal sharks, blacknose sharks in the western North Atlantic Ocean appear to be intermediate between the two groups, as also noted by Cortés (2000).

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