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Authors: Romine, J. G., Musick, J. A., and Johnson, R. A.

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Compensatory Growth of the Sandbar Shark in the Western North Atlantic Including the Gulf of Mexico

J. G. Romine,*[1] J. A. Musick, and R. A. Johnson
Virginia Institute of Marine Science, 1208 Greate Road, Gloucester Point, Virginia 32065, USA

Abstract

The number of Sandbar Sharks *Carcharhinus plumbeus* in the western North Atlantic Ocean has experienced a drastic decline since the early 1980s, reaching a minimum during the early 1990s. Catch rates in the early 1990s were a mere 25% of those during the 1980s. According to several fishery-independent surveys, the low point in Sandbar Shark abundance followed a period of high exploitation. Growth models fit to age–length data collected from 1980 to 1983 and from 2001 to 2004 were compared to investigate potential changes in parameter estimates that might reveal compensatory responses in the Sandbar Shark population. Statistical differences were found between the model parameters for the two time periods, but the differences in growth rates were minimal. The parameters from the three-parameter von Bertalanffy growth model for female sharks during the 1980–1983 and 2000–2004 time periods were as follows: $L_\infty = 188.4$ and 178.3 cm FL; $k = 0.084$ and 0.106; and $t_0 = -4.097$ and -3.41. For males the growth parameters were as follows: $L_\infty = 164.63$ and 173.66 cm; $k = 0.11$ and 0.11; and $t_0 = -3.62$ and -3.33. The estimated age at 50% maturity for female Sandbar Sharks changed from 15 years to 12.49 years between the two time periods.

The Sandbar Shark *Carcharhinus plumbeus* is a common large coastal shark that inhabits temperate and subtropical waters worldwide and attains lengths greater than 2 m (Compagno 1984). In the western North Atlantic Ocean (WNA), this species inhabits nearshore waters out to the edge of the continental shelf from Cape Cod to Brazil (Bigelow and Schroeder 1948; Springer 1960; Garrick 1982). Tagging studies suggest that this region is composed of two unit stocks. One stock is found from Cape Cod south to the northern Yucatan peninsula and throughout the Gulf of Mexico; the other is found from Trinidad to Brazil (Springer 1960; Kohler et al. 1998). Genetic studies conducted on specimens from Virginia waters and the Gulf of Mexico further support the existence of a single stock that utilizes the area of Cape Cod to the northern Yucatan peninsula (Heist et al. 1995).

The Sandbar Shark in the WNA undertakes seasonal migrations from the Gulf of Mexico and Florida to as far north as Cape Cod as water temperatures rise in the spring and returns south as water temperatures decrease in the fall (Springer 1960; Musick and Colvocoresses 1986). Adult males often inhabit waters along the edge of the continental shelf out to depths of 250 m, while juveniles and females are generally found inshore.

The mode of reproduction in the Sandbar Shark is placental viviparity, with females giving birth to well-developed live young. In the WNA, young are approximately 47 cm (FL) at birth (Springer 1960; Castro 1993a; Sminkey and Musick 1995; Cortés 2000; Baremore and Hale 2012), and litter sizes average nine sharks (Springer 1960; Clark and von Schmidt 1965; Sminkey and Musick 1996; Cortés 2000; Baremore and Hale 2012). Due to the advanced development of the pups, a long gestation period of approximately 9–12 months is required (Springer 1960; Clark and von Schmidt 1965; Lawler 1976; Baremore and Hale 2012). Maturity in both males and females has been estimated to occur between 12 and 30 years of age

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*Corresponding author: jromine@usgs.gov
[1]Present address: U.S. Geological Survey, Western Fisheries Research Center, Columbia River Research Laboratory, 5501A Cook-Underwood Road, Cook, Washington 98605, USA.
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at lengths of approximately 148–155 cm FL (Springer 1960; Casey et al. 1985; Sminkey and Musick 1995; Baremore and Hale 2012). Maximum reported lengths are 194 and 187 cm FL for females and males, respectively (Cortés 2000).

Previous studies of the age and growth of Sandbar Sharks from the WNA have yielded mixed results. Lawler (1976) produced unrealistic values for asymptotic length (221 cm FL) and only provided von Bertalanffy growth parameters for female Sandbar Sharks due to a limited sample size for males. Casey et al. (1985) provided a more comprehensive study of the age and growth of Sandbar Sharks in the WNA that had a large sample size ($n = 475$), but they too produced unrealistic asymptotic length estimates (303 cm FL) that resulted in very low growth coefficients ($k = 0.04$ and 0.05 for females and males, respectively). Casey et al. (1985) lacked a representative sample from larger size-classes, which is an inherent problem in conducting an age–growth study on long-lived species. The oldest male in their sample set was estimated to be 15 years old, and the oldest female was estimated to be 21 years old. Through back-calculation, this study estimated maturity to be attained between 12 and 13 years of age. Casey and Natanson (1992) estimated new growth parameters based on tagging experiments and proposed age at maturity to be approximately 30 years and the theoretical maximum size to be 186 cm FL. These estimates more than doubled the previously estimated age at maturity by Casey et al. (1985). Sminkey and Musick (1995) reexamined the age and growth of Sandbar Sharks from samples obtained a decade apart, 1980–1981 and 1991–1992. The sample set from 1991 to 1992 was the largest sample size and had the greatest size range of any study conducted on Sandbar Sharks to date. That study indicated that juvenile growth rates were slightly higher in the later period, but the back-calculated age at maturity (15 for males and 16 years for females) remained unchanged. Merson (1998) estimated that maturity was attained at 19 years of age for females from a back-calculation of age at length using the growth curve from Sminkey and Musick (1995). Back-calculation can underestimate age at length, leading to an inflated estimate of age at maturity (Sminkey and Musick 1995). In 2010, the age at maturity was estimated to be 12.1 and 13.1 years for males and females, respectively (Baremore and Hale 2012). These estimates were the first to use reproductive analysis of directly aged Sandbar Sharks in the WNA. In short, age-at-maturity estimates for Sandbar Sharks in the WNA have ranged from 12 to 30 years since 1985, with the most recent estimates being those estimated by Baremore and Hale (2012).

Andrews et al. (2011) used bomb-radiocarbon aging of five individual Sandbar Sharks to verify the annual periodicity of band pair formation in vertebral centra. This study indicated that the age estimates of sharks older than 10 years of age may not be accurate and could lead to underestimates of age due to band pair compression at the margin of the centra when one is using the methods of aging as defined by Casey et al. (1985). The authors state that many additional band pairs were evident besides those that traversed the intermedialia and that when counted ages are in close agreement with the ages estimated through bomb-radiocarbon analyses.

The Sandbar Sharks in the WNA have experienced drastic reductions in numbers due to overfishing, which reflects the absence of a Fishery Management Plan (FMP) prior to the 1990s. Several indices from fishery-independent and -dependent sources have shown a steady reduction from the late 1970s to the early 1990s, when the lowest abundance was recorded (SEDAR 2010). An FMP for large coastal sharks was adopted in 1993 (NMFS 1993), and Sandbar Sharks were managed as part of the large coastal fishery. Sandbar Sharks have been managed on a species-specific basis since 2008 (NMFS 2008), and landing quotas were reduced drastically as a result of the overfished status revealed by the 2006 stock assessment (SEDAR 2006). Since the early 2000s there has been a gradually increasing trend in Sandbar Shark abundance indices (SEDAR 2010). However, the current abundance estimates remain well below those of the early 1980s.

Compensation for population fluctuations below carrying capacities has been recognized for many oceanic *r*-selected organisms (Clarke 1949; MacArthur and Wilson 1967; Boyce 1979; Fowler 1981). The fishes in this category exhibit high fecundity, rapid growth, and maturity at a young age. Deviations below the carrying capacity for these species often result in changes in growth parameters due to a suite of circumstances (Rose et al. 2001). Often a decrease in population density results in decreased intraspecific competition and thus greater availability of food sources for each individual. As a result, mortality rates and/or reproductive success may change. The increased availability of food sources may result in faster growth, earlier maturity, or higher fecundity (Jensen 1991; Hilborn and Walters 1992; Hayward et al. 1997). An increase in fecundity may occur via either larger offspring or more offspring. Larger offspring would contribute to population growth over time due to the probable increase in survival due to their larger size, whereas more offspring in each litter would have an immediate effect on population size as well as the long-term population increase. However, it is unlikely that compensation takes the form of increased fecundity for two reasons: the advanced nature and large size of Sandbar Shark offspring, and space limitations within the uterus (Baremore and Hale 2012). Increased fecundity can only occur at the cost of reduced offspring size or substantially increased female size (Goodwin et al. 2002; Conrath 2005). Therefore, the most likely compensation for shark species in terms of reproductive output is a decreased age at maturity. Maturity may be reached at an earlier age as a consequence of a faster growth rate, or an increase in the rate of growth and in turn an increase in fecundity at the population level may occur.

Few studies have documented changes in life history parameters for elasmobranchs before and after exploitation. Carlson and Baremore (2003) found significant increases in juvenile growth and earlier maturity in the Atlantic Sharpnose Shark *Rhizoprionodon terraenovae* in the Gulf of Mexico after heavy exploitation,

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but they were unable to rule out their methodology as the cause of these differences. Cassoff et al. (2007) reported changes in life history parameters of the Porbeagle *Lamna nasus* in the WNA following exploitation. Sminkey and Musick (1995) discovered slight differences in size at age among juvenile Sandbar Sharks when samples obtained in 1980–1981 and 1990–1992 were compared. However, the older sharks in their 1990–1992 sample had undergone their fastest growth in the late 1970s and early 1980s, i.e., before the population decline. Greater differences in growth rates may be discovered upon examination of sharks being born during the time of lowest abundance. The Virginia Institute of Marine Science (VIMS) longline survey reported the lowest abundance of Sandbar Sharks in 1993, 1 year after Sminkey and Musick (1995) completed their research.

The present study aimed to continue the investigation into the potential for compensatory changes in Sandbar Shark growth rates in the WNA by comparing the growth rates derived from vertebral centra obtained over two time periods and to provide revised age and growth estimates. In addition, we examined age at maturity between the two time periods.

METHODS

Data collection.—Vertebral centra were primarily obtained from Sandbar Sharks landed by the VIMS longline survey, which operates in Chesapeake Bay, Virginia coastal waters, and North Carolina coastal waters. Samples were collected from 1980 to 1983 and from 2000 to 2004 (hereafter referred to as the VIMS1983 and VIMS2004 data sets). The VIMS1983 data set was augmented by samples collected from shark fishing tournaments held in Virginia Beach, Virginia. The VIMS2004 data set was augmented by samples collected from the Commercial Shark Fishery Observer Program (CSFOP), which primarily operated in the Gulf of Mexico and along the east coast of Florida (Morgan et al. 2009). Samples were also collected by the principal author during National Marine Fisheries Service (NMFS) fishery-independent longline surveys (Henwood et al. 2004) from 2000 to 2004.

At sea, each shark was sexed and a straight-line measurement was taken from the tip of the snout to the fork in the caudal fin (FL; cm). In the VIMS and NMFS surveys, sharks were euthanized and a minimum of five vertebral centra were removed from behind the head just anterior to the origin of the first dorsal fin (McAuley et al. 2006). Centra collected by the CSFOP were removed from the anterior section of the "log" or carcass. Removal of centra from below the first dorsal fin was not practical for fishery-dependent samples because such action would reduce the value of the shark at market. Piercy et al. (2006) showed no difference in band counts for vertebrae taken from below the first dorsal fin (VIMS samples) and posterior to the chondocranium (CSFOP and NMFS samples) for Sandbar Sharks in the WNA; therefore, the use of these vertebrae for comparison was likely valid. Vertebrae were frozen and sent to the Virginia Institute of Marine Science.

At the laboratory, the samples were thawed and excess muscle tissue was removed. The samples were then placed in 75% ethanol until they could be sectioned. All vertebral centra were sagitally sectioned through the focus of the centrum using an isomet rotary diamond saw. Once cut, sections were set to dry for 24 h and then mounted on microscope slides via cover slip mounting medium. The samples were progressively wet-sanded using 300, 400, and 600 fine grit sandpaper until light was readily transmitted through them and the band pairs were readily distinguishable on a dissection microscope.

Maturity was assessed for both male and female sharks. Males were classified as mature if their claspers were deemed fully calcified (i.e., hard) and could be rotated forward (Clark and von Schmidt 1965; Driggers et al. 2004). The maturity status of females was determined by examination of oviducal gland size and uterus width and appearance (Castro 1993b). Pregnant and postpartum females were classified as mature.

Data analyses.—Band pairs were considered an opaque zone combined with a wider translucent zone in the corpus calcareum that may or may not continue across the intermedialia (Sminkey and Musick 1995; Andrews et al. 2011). The birthmark was determined as the first thin opaque band that intersected the inflection, or change in angle, of the corpus calcareum (Casey et al. 1985; Cailliet and Goldman 2004; Cailliet et al. 2006). The formation of annual growth bands up to 12 years of age has been validated for Sandbar Sharks in the WNA from mark–recapture and bomb-radiocarbon aging, so we assumed annual formation (Andrews et al. 2011).

Mounted vertebral sections were examined for age using a dissecting microscope and a video imaging system. Vertebrae were read independently by two readers. Samples were assigned ages without knowledge of the size or sex of the shark. Age estimates for vertebrae that were not consistent between readers were reexamined by both readers until a consensus was reached. The consensus estimate was used in the final analysis. If a consensus age estimate could not be reached, the sample was removed from the study (Cailliet and Goldman 2004). Age was considered to be the total number of band pairs present after the birth mark.

Indices of precision were employed to determine how variable the readers were when assigning ages. The percent agreement (PA) between readers and the PA $\pm$ 1 year were determined by dividing the number of assessed ages agreed upon by the total number of vertebrae examined (Cailliet and Goldman 2004; Goldman 2005). A Bowker and McNemar χ^2 test of symmetry was used to test for systematic reader bias in the assessment of age (Hoenig et al. 1995; Evans and Hoenig 1998).

We fitted two forms of the von Bertalanffy growth model to length-at-age data for males, females, and both sexes combined (von Bertalanffy 1938; Beverton and Holt 1957; Cailliet et al. 2006). The first form of the model (VB2; Fabens 1965) used

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the length-at-birth intercept rather than a theoretical age at zero length and is represented as

$$L_t = L_\infty - (L_\infty - L_0)e^{-kt},$$

where L_t is length at age t, L_∞ is the asymptotic length, L_0 is the length at birth, and k is the growth coefficient. The value of L_0 was estimated from observed at-term embryos and free-swimming young-of-the-year sharks to be 51 cm FL. The second form, a three-parameter von Bertalanffy model (VB3; von Bertalanffy 1938) incorporating the x-intercept (t_0) is represented as

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

All model parameters were estimated using nonlinear least squares and the Gauss–Newton algorithm in R (R Development Core Team 2011). Final model selection was based on the Akaike information criterion corrected for small sample size (AIC_c; Akaike 1973) and mean square error (MSE; Carlson and Baremore 2005). All models were fit to data sets individually (VIMS1983 and VIMS2004) to assess parameter estimates for each time period.

Temporal comparisons between models and model parameters were made using likelihood ratio tests (LRTs; Kimura 1980; Haddon 2001). For this purpose, the data sets were constrained to the lowest maximum age for each data set comparison (Haddon 2001). This was done to remove the potential bias caused by different values of L_∞. For example, if the compared data sets had different maximum ages, the data set with the greater maximum age was truncated to the maximum age of the other data set. The best fit model was then refitted to the truncated data set. These models were then compared using LRTs. In this manner we were able to compare growth over identical age ranges rather than complete growth curves (Haddon 2001).

One assumption of LRTs is homogeneity of variance between data sets; for this reason, Bartlett's test was used to assess the homogeneity of variance between comparison groups in R (R Development Core Team 2011). Model error was assumed to be independent, normally distributed, and homoscedastic. A Shapiro–Wilk test was used to test the assumption of normality. Residual errors were evaluated by examining plots of the residuals for systematic errors.

Age-based maturity ogives were developed for male and female sharks from all time periods for which data were available. Trippel and Harvey (1991) suggested the use of maximum likelihood or probit analysis to estimate the age at which 50% of the population is mature (A50) in populations in which there are successive increases in the proportion of mature fish with increasing age. We used maximum likelihood (ML) methods to estimate A50 from binomial maturity data (0 = immature, 1 = mature). This method takes into account the sample size within each age-class. The negative log-likelihood function that was minimized was

$$-\ln(\mathrm{ML}) = \sum_j \left[n \cdot_j \ln\left[\left(1 + e^{(-b^*(j-A50))}\right)^{-1}\right] + (N_j - n_j) \cdot \ln\left(1 - \left(1 + e^{(-b^*(j-A50))}\right)^{-1}\right)\right],$$

where n_j = is the number of mature fish in age-class j, N_j = the total number of fish in age-class j, and b = the instantaneous rate of fish maturation. Both A50 and b were estimated by minimizing the negative log-likelihood using AD Model Builder. Bias-corrected 95% confidence intervals were constructed using bootstrap methods of estimation (Haddon 2001). Confidence intervals were only estimated for the A50 value, and the steepness parameter (b) was held to the value estimated from the initial fit of the model.

RESULTS

During the period 1980–1983 (VIMS1983 data set), 247 Sandbar Sharks were sampled, 177 females and 70 males (Figure 1). The oldest estimated age for a female shark was 28 years (at a length of 162 cm FL). Lengths for females ranged from 59 to 179 cm FL, with an average of 103.7 cm (SD = 41.1; Figure 1A). Lengths for males ranged from 46 to 161 cm FL, with an average of 73.5 cm (SD = 29.8; Figure 1B). The oldest estimated age for a male Sandbar Shark was 20 years (161 cm FL). The average ages for females and males were 7.3 and 2.7 years, respectively.

Over the period 2000–2004 (VIMS2004 data set), 449 Sandbar Sharks were sampled. Of these, 247 were females ranging in length from 44 to 180 cm FL and 202 were males ranging from 46 to 167 cm FL (Figure 1). The average FL for females was 102.5 cm (SD = 35.6), and that for males was 96.5 cm (SD = 36.3). The oldest estimated age for females was 27 years at a length of 180 cm. The oldest estimated age for males was 22 years and was assigned to a 156 cm shark and a 162 cm shark. The average ages for females and males were 6.33 and 5.53 years, respectively.

The ages estimated by readers were consistent for all three data sets. The percent agreement (PA) for the VIMS1983 samples was 51%. Reader estimates were within 1 year of each other for 86% of the samples and within 2 years for 93% of the samples. For the VIMS2004 data set, PA was 71%. Reader estimates were within 1 year of each other for 95% of the samples and within 2 years for 98% of the samples. Between-reader contingency tables for the VIMS1983 and VIMS2004 data sets revealed that the differences between readers were due to random error rather than systematic error ($\chi^2 = 53.13$, df = 42, $P = 0.12$ and $\chi^2 = 51.00$, df = 36, $P = 0.05$, respectively). The bias between and among readers for all data sets was not systematic; however, older fish (>25 years) led to more error between readers for both data sets (Figure 2).

Based on MSE and AIC values, the VB3 model provided the best fit for males and females for the VIMS1983 data set

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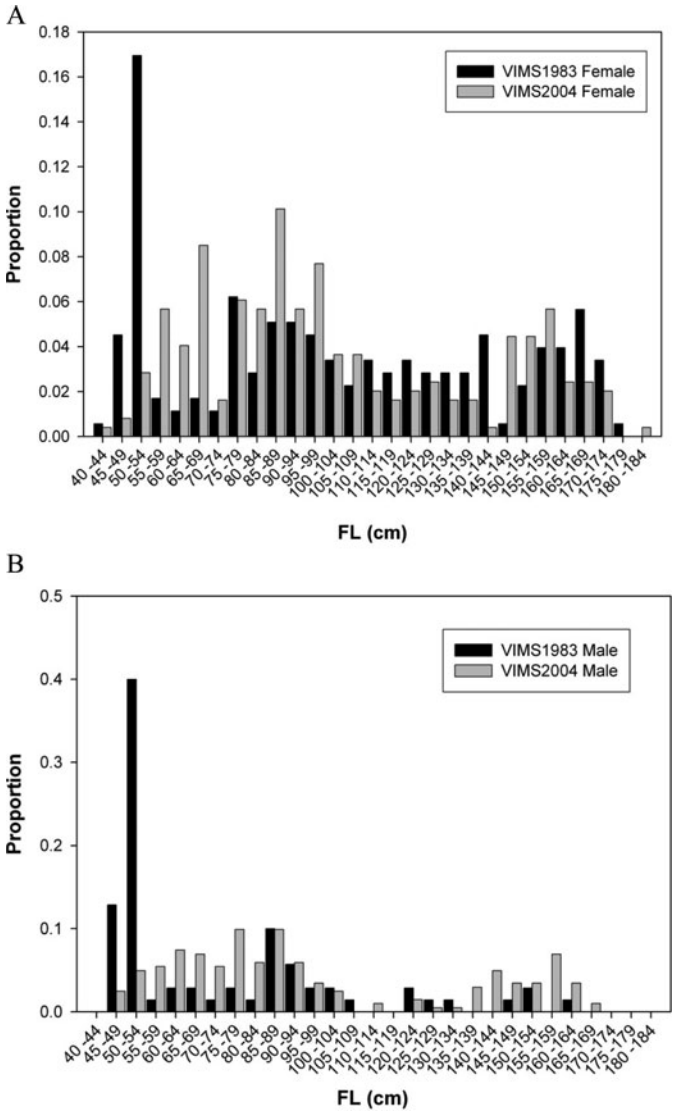


FIGURE 1. Length frequencies of **(A)** female and **(B)** male Sandbar Sharks from the VIMS1983 and VIMS2004 data sets.

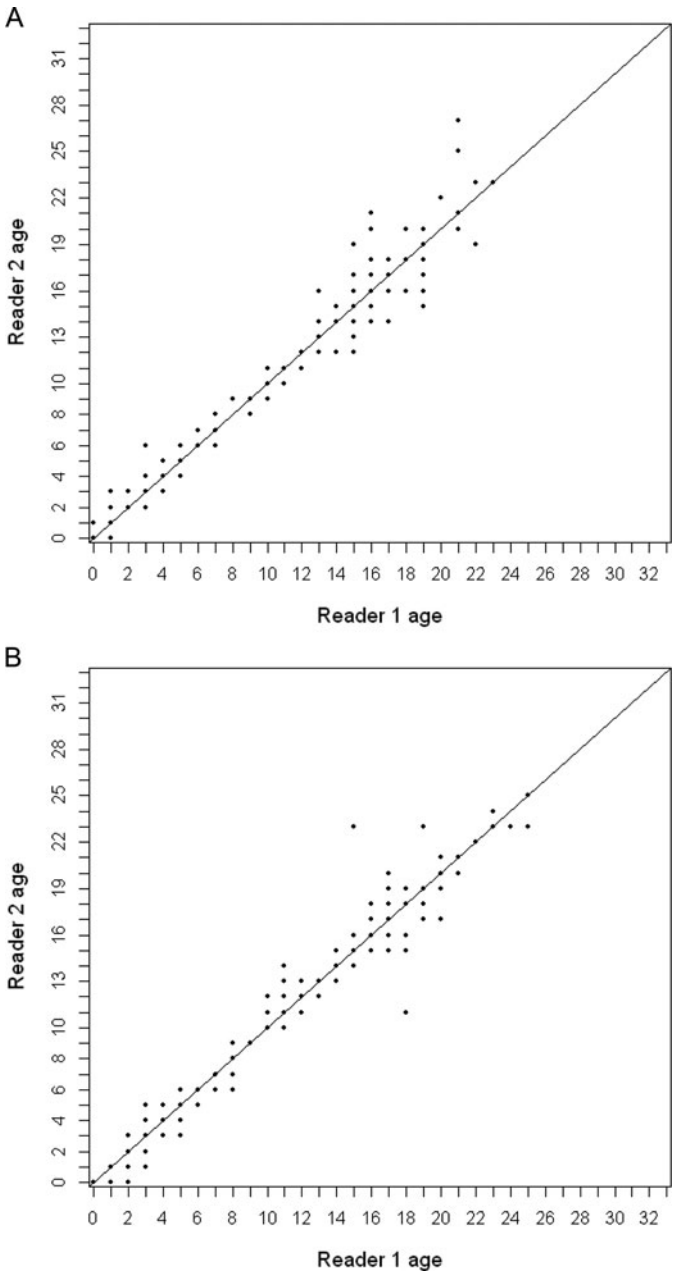


FIGURE 2. Age bias plots for readers 1 and 2 for the VIMS1983 (upper panel) and VIMS2004 (lower panel) data sets. In each panel the solid line has slope of 1 and an intercept of 0, representing no bias between readers.

(Table 1). The VB3 model produced higher estimates of L_∞ and lower estimates of k than the VB2 model, indicating that the VB2 model underestimated the asymptotic length while overestimating growth rates (Figures 3A, 4A, 5). Similarly, the VB3 model provided the best fit for the VIMS2004 male and female data sets (Table 1). Model outputs from the VB2 model were similar, but L_∞ values were slightly underestimated when compared to empirical length data (Figures 3B, 4B, and 5).

To compare temporal differences, the data sets were constrained to the lowest maximum age for each data set comparison (Haddon 2001). Thus, the VIMS2004 data set was truncated to a maximum age of 20 for males and a maximum age of 27 for females. The VB3 model was refit to the truncated data (Table 2). In this way we were able to compare growth over identical age ranges. The assumption of homogeneous variances was not violated at the 0.01 level (females: $K^2 = 4.20$, df $= 1$, $P = 0.041$; males: $K^2 = 3.73$, df $= 1$, $P = 0.054$). The models were then compared using likelihood ratio tests. These likelihood ratio tests revealed significant differences between the VB3 models for females between the VIMS1983 and VIMS2004 data sets ($\chi^2 = 25.06$, df $= 3$, $P < 0.001$); comparison of the VB3 models for males revealed significant differences between those models as well ($\chi^2 = 22.75$, df $= 3$, $P < 0.001$) (Table 3).

The significant difference in the growth models for females between the two time periods was primarily driven by

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TABLE 1. Model fits for all data sets and both sexes. The values in parentheses are the lower and upper 95% confidence limits; AIC_c = AIC corrected for small sample size, MSE = mean square error, and NA = not applicable.

Data set	Model	L_∞	k	t_0	AIC_c	ΔAIC_c	MSE	n
VIMS1983								
Females	VB3	188.26	0.084	−4.078	1,207.40	0	51.3	177
		(180.57, 197.66)	(0.07, 0.10)	(−4.54, −3.67)				
	VB2	183.10	0.094	NA	1,218.89	11.49	55.38	177
		(176.63, 190.62)	(0.08, 0.10)					
Males	VB3	164.17	0.109	−3.612	437.51	0	26.92	70
		(153.54, 178.53)	(0.09, 0.13)	(−4.2, −3.13)				
	VB2	160.18	0.122	NA	444.56	7.05	30.71	70
		(150.49, 172.53)	(0.10, 0.15)					
Sexes combined	VB3	186.29	0.086	−4.02	1,655.49	0	46.14	247
		(179.63, 194.17)	(0.08, 0.1)	(−4.38, −3.7)				
	VB2	181.28	0.095	NA	1,674.86	19.37	50.32	247
		(175.57, 187.8)	(0.09, 0.1)					
VIMS2004								
Females	VB3	178.14	0.107	−3.397	1,596.33	0	36.31	247
		(173.97, 182.83)	(0.10, 0.12)	(−3.71, −3.11)				
	VB2	174.88	0.117	NA	1,606.33	10	38.13	247
		(171.42, 178.60)	(0.11, 0.12)					
Males	VB3	173.52	0.113	−3.323	1,322.71	0	39.25	202
		(168.68, 179.18)	(0.10, 0.12)	(−3.67, −3.01)				
	VB2	169.83	0.125	NA	1,333.14	10.43	41.76	202
		(165.85, 174.20)	(0.12, 0.13)					
Sexes combined	VB3	176.47	0.108	−3.387	2,912.33	0	37.73	449
		(173.22, 180.02)	(0.1, 0.12)	(−3.62, −3.17)				
	VB2	172.88	0.120	NA	2,936.26	23.93	39.98	449
		(170.22, 175.69)	(0.11, 0.13)					

differences in the estimated growth coefficient, k ($\chi^2 = 12.97$, df = 1, $P < 0.001$). The difference between the estimates of L_∞ and t_0 were also significant, though to a lesser extent ($\chi^2 = 7.55$, df = 1, $P = 0.006$ and ($\chi^2 = 8.60$, df = 1, $P = 0.003$, respectively). The difference in the growth models for males was driven by small differences in all model parameters; no individual parameters were significantly different between the time periods. The assumption of normally distributed error was not violated, and skew and kurtosis were minimal for all model fits. There were no significant differences in variance between the VIMS1983 and VIMS2004 data sets for females ($\chi^2 = 4.01$, df = 1, $P = 0.045$) or males between the two time periods ($\chi^2 = 3.35$, df = 1, $P = 0.067$). However, empirically it can be seen that the estimate of the growth coefficient for females was greater for the VIMS2004 data set, while that of L_∞ was lower. For males, the L_∞ value was greater than for the VIMS1983 data, as was the k value.

Maturity ogives were only generated for female sharks due to the paucity of mature males in the VIMS1983 data set. Maturity was determined for 179 female sharks with associated vertebral centra from the VIMS1983 data. Of these, the smallest mature shark was 142 cm FL and was estimated to be 16 years old. The

TABLE 2. Model fits for constrained data sets for both male and female sharks used for temporal comparisons. See Table 1 for additional information.

Data set	Model	Maximum age	L_∞	k	t_0
VIMS1983					
Females	VB3	27	190.89 (182.45, 201.43)	0.081 (0.07, 0.09)	−4.166 (−4.65, −3.74)
Males	VB3	20	164.17 (153.54, 178.53)	0.109 (0.09, 0.13)	−3.612 (−4.20, −3.13)
VIMS2004					
Females	VB3	27	178.14 (173.97, 182.83)	0.107 (0.10, 0.12)	−3.397 (−3.71, −3.1)
Males	VB3	20	174.29 (169.12, 180.37)	0.111 (0.10, 0.12)	−3.348 (−3.71, −3.03)

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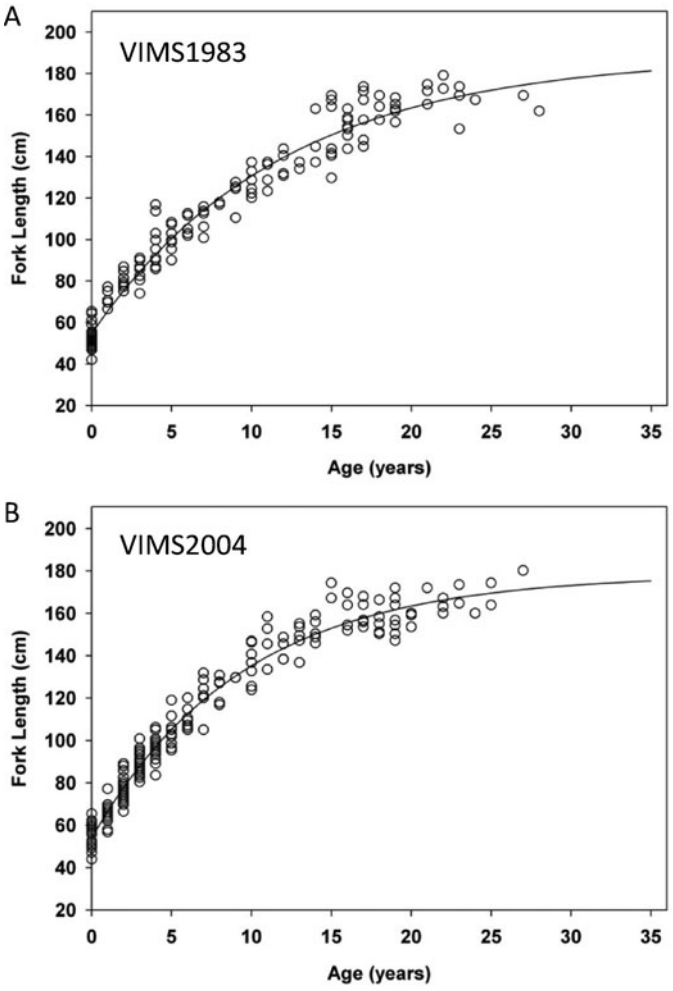


FIGURE 3. VB3 model fits and length-at-age data for female Sandbar Sharks from the **(A)** VIMS1983 and **(B)** VIMS2004 data sets.

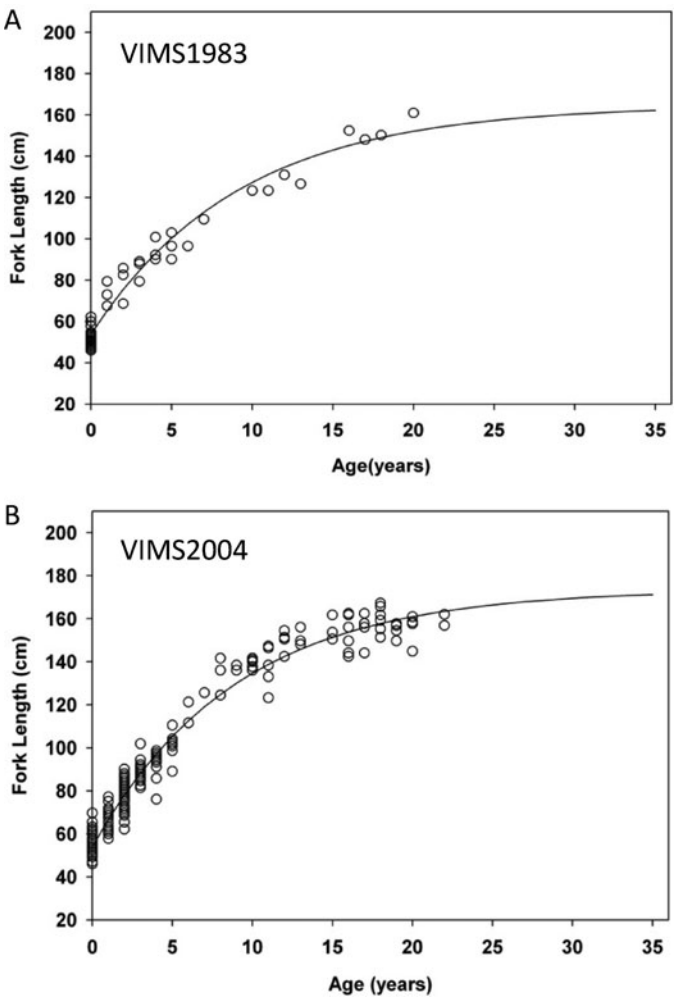


FIGURE 4. VB3 model fits and length-at-age data for male Sandbar Sharks from the **(A)** VIMS1983 and **(B)** VIMS2004 data sets.

largest immature shark was 151 cm and was also estimated to be 16 years old. Maturity was determined for 192 female sharks from the VIMS2004 data set. Of these, the smallest mature shark was 145 cm and was estimated to be 11 years old. The largest immature shark was 147 cm and was estimated to be 13 years of age. The estimate of A50 for female sharks was 15.06 years of age from the VIMS1983 data set and 12.49 years of age from the VIMS2004 data set (Figure 6). The length at 50% maturity for females was 152 and 145 cm FL for VIMS1983 and VIMS2004 samples, respectively; this difference was found to be significant ($F = 7.27$, $P = 0.0001$).

TABLE 3. Results for likelihood ratio tests in temporal comparisons between data sets (VIMS1983 versus VIMS2004) for male and female Sandbar Sharks.

Sex	χ^2	df	P-value
Female	25.06	3	<0.001
Male	22.75	3	<0.001

DISCUSSION

We have shown a significant change in the von Bertalanffy growth parameters for the Sandbar Shark in the western North Atlantic Ocean between the time periods 1980–1983 (VIMS1983 data set) and 2000–2004 (VIMS2004 data set). The growth parameter estimates suggested a greater asymptotic length and lower k value for female sharks when based on the VIMS1983 data set than when based on the VIMS2004 data set (Table 1). Few studies have shown significant changes in growth among K-selected species (Sminkey and Musick 1995; Carlson and Baremore 2003; Sosebee 2005; Cassof et al. 2007). This is the fourth study involving elasmobranchs to demonstrate changes in growth rates following exploitation.

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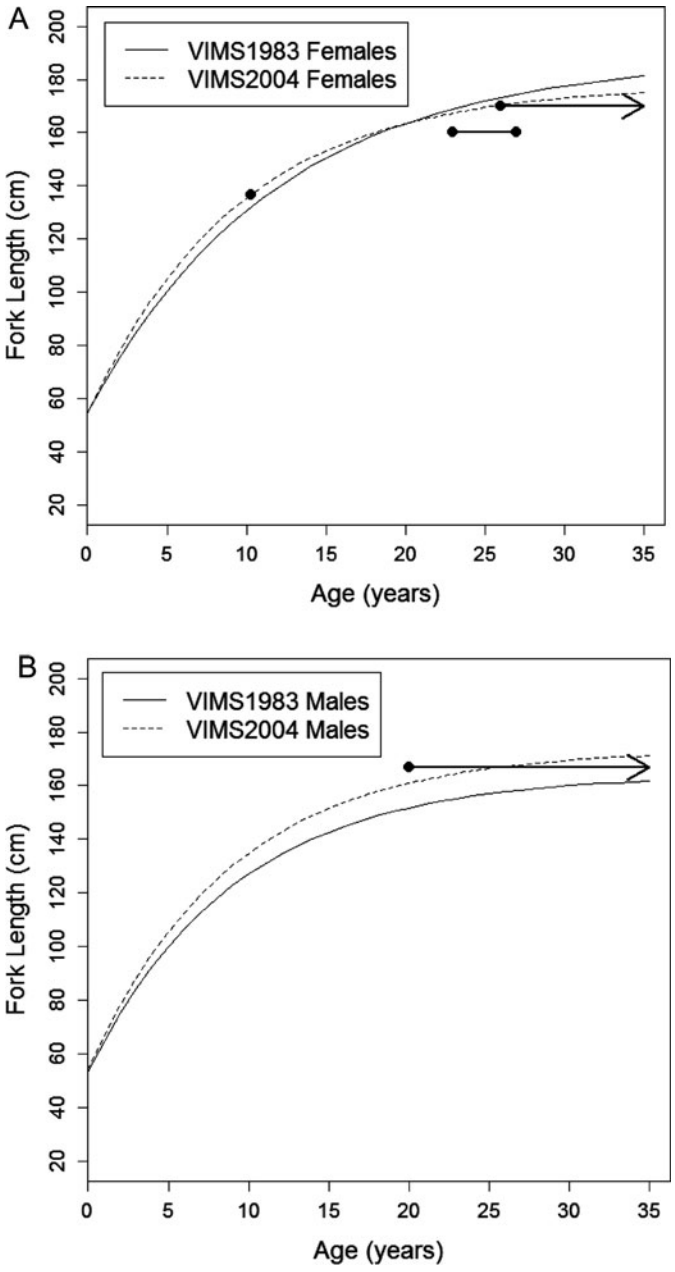


FIGURE 5. Comparison of the results of the VB3 growth model when fitted to the VIMS1983 and VIMS2004 data sets for **(A)** female and **(B)** male Sandbar Sharks. The circles represent the lower and upper estimates of bomb-radiocarbon–validated age–length data for Sandbar Sharks from the WNA (Andrews et al. 2011). A single circle signifies that a single age was given for that sample. Two circles connected with a bar represent the range for a single sample. An arrow signifies that no upper estimate was given.

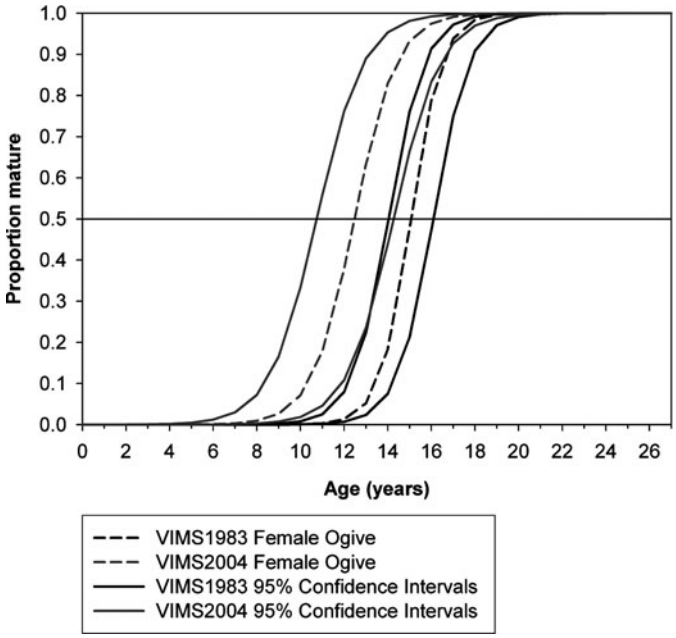


FIGURE 6. Ogives fitted to Sandbar Shark female maturity data for the VIMS1983 and VIMS2004 data sets using maximum likelihood estimation.

Most of the animals in the VIMS1983 and VIMS2004 data sets were landed with identical gear within the same locations. Some sharks from the more recent time period were landed using smaller hooks (9/0 J versus 12/0 circle) with monofilament leaders on the same braided nylon mainline. Samples were also collected by gill nets, recreational gear, and trawl nets for the VIMS2004 data set. These samples comprised less than 1% of the data set, however. This was also the case for the VIMS1983 data set. At-term pups were included in the VIMS1983 data set to account for a lack of neonates within that sample set. Katsanevakis (2006) and Thorson and Simpfendorfer (2009) suggested using multimodel inference to cope with issues of gear selectivity in order to derive more accurate estimates of growth parameters. However, given ΔAIC_c values close to or greater than 10, model averaging resulted in parameter estimates that were almost identical to the best-fit model estimates for all data sets. In addition, we found that the length distributions of both time periods were homogenous and that each size-class comprised approximately similar proportions of the entire data set (Figure 1).

The oldest vertebral centra–based age of Sandbar Sharks from this study was 27 years, which is similar to the maximum estimated age of 25 years from Sminkey and Musick (1995) in the WNA. However, based on our age estimations it is not unreasonable to assume that Sandbar Sharks have longevities much greater than 30 years. A recent study using bomb-radiocarbon dating of Sandbar Shark vertebrae indicated that this species is longer-lived than previously thought and suggested that in some older animals age may be underestimated when it is determined by growth band counting in vertebrae (Andrews et al. 2011). Based on a sample size of four, Andrews et al. (2011) found disagreement between bomb-radiocarbon estimates of age and growth band estimates for three sharks estimated to be older than 20 years through bomb-radiocarbon analyses. These sharks were estimated to be younger than 20 years by growth band counting following the methods of Casey et al. (1985).

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This is understandable given the edge compression of vertebrae in older sharks and the difficulty of discerning bands in this compressed region. It should be noted that the study also validated age determination using growth bands in a shark that was estimated to be 10.3 years of age by both methods.

Other studies using the same bomb-radiocarbon dating methods have validated vertebral centra ages for other long-lived sharks up to 42 years of age (Campana et al. 2002; Passerotti et al. 2010). However, Francis et al. (2007) reported that the ages of Porbeagles from New Zealand that were more than 45 years were underestimated using vertebral centra. The discrepancies between these studies should be examined further to determine whether they stem from the methods used, as was the case with Andrews et al. (2011).

It should be noted that the samples used in Andrews et al. (2011) were prepared using histological methods, as opposed to the methods used in this study. In addition, the age estimation methods that Andrews et al. (2011) used were those described by Casey et al. (1985), which defined growth bands as light and dark regions traversing the entire intermedialia and extending into the corpus calcareum. Andrews et al. (2011) stated that if they had used the band pairs visible in the corpus calcareum the ages estimated from the vertebral centra would have been in line with those estimated through the bomb-radiocarbon analyses and suggested that the aging method used by Casey et al. (1985) is only reliable up to age 12.

Be that as it may, Andrews et al. (2011) suggested that the longevity of Sandbar Sharks in the WNA was probably greater than 30 years prior to the expansion of the shark fishery in the early 1980s. Casey and Natanson's (1992) revision of earlier age and growth estimates (Casey et al. 1985) using tag–recapture data found that tagged Sandbar Sharks in the U.S. Atlantic Ocean were at liberty for over 20 years and suggested a longevity of over 50 years. In addition, they suggested that maturity is not attained until 30 years of age, an extreme contrast to the estimates (12–13 years) presented by Baremore and Hale (2012) and our estimate for females (12.49 years). In the current study, poor band elucidation at the margins may have led to underestimation of counts or ages for some of the largest sharks sampled.

Our growth estimates are generally similar to those reported by Sminkey and Musick (1995), but our estimates present a stark departure from those estimated by Casey et al. (1985). The von Bertalanffy model estimates from this study for males were $k = 0.050$/year, $L_\infty = 257$ cm FL, and $t_0 = -4.5$; those for females were $k = 0.040$/year, $L_\infty = 299$ cm FL, and $t_0 = -4.9$. The values of L_∞ estimated by Casey et al. (1985) are unrealistic given the empirical data. In addition, the growth coefficients are roughly half of our current estimates. Romine (2008) used mark–recapture data and length-based models to estimate growth parameters for Sandbar Sharks in the WNA. That study estimated L_∞ to be 209 cm FL and k to be 0.077 for both sexes combined, which entails a smaller growth coefficient and a larger asymptotic length than our model fits for both sexes combined over both time periods (Table 1). However, caution should be taken with estimates based on tag–recapture data because the variability in the growth of tagged fish is not comparable to the variability associated with length-at-age data and should not be used to verify length-at-age data (Francis 1988).

We have found changes in the parameters of the growth model for Sandbar Sharks in the WNA between the periods 1980–1983 and 2000–2004 that indicate slightly faster growth. We also have found a decrease in the value of A50 for female Sandbar Sharks between the two time periods. However, these revised estimates still depict a fish that is slow growing and susceptible to overfishing. Age-at-length studies should be continued to monitor the status of this population and to provide managers with updated and accurate life history parameters for use in future stock assessments.

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