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Changes in Biological Parameters of Atlantic Sharpnose Shark, *Rhizoprionodon terraenovae*,  
in the Gulf of Mexico: Evidence for Density-dependent Regulation?  
(Elasmobranch Fisheries – Oral)

by

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**Abstract**

In 1993, an assessment of small coastal sharks, largely composed of Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*), determined this group to be fully utilized. Subsequent reductions in commercial quotas for large coastal species have caused increased harvesting of Atlantic sharpnose shark. This increased fishing pressure allowed for the investigation of possible density dependent changes in biological parameters with time. Biological data from the Gulf of Mexico collected in 1979-1984 from published studies were compared to that collected in 1998-2001. For combined sexes, the von Bertalanffy growth parameters were  $L_{\infty}=110.8$  cm total length,  $K=0.39$ , and  $t_0=-0.86$  for 1984 and  $L_{\infty}=94.0$  cm total length,  $K=0.72$ , and  $t_0=-0.88$  for 1998-2001. Median size at maturity decreased from about 78.3 and 80.2 cm total length in 1979-1980 to 71.1 and 75.8 cm total length in 1998-2001 for males and females, respectively. Age at maturity also decreased from 2.3 years to 1.4 years for combined sexes. Litter size was similar between periods (5.0 embryos) as was the average size of embryos close to parturition (32 mm TL, 130-150 g). The observed decrease in length and age at maturity and increased growth ( $K$ ) lends support to the hypothesis of a compensatory response although it could not be determined if the response was due to differences in methodology among studies, anthropogenic influences, or natural causes.

**Introduction**

In 1993, an assessment of small coastal sharks, largely composed of Atlantic sharpnose sharks, *Rhizoprionodon terraenovae*, determined this group to be fully utilized. Subsequent reductions in commercial quotas for blacktip, *Carcharhinus limbatus*, and sandbar, *Carcharhinus plumbeus*, shark have caused increased exploitation of Atlantic sharpnose shark. For example, commercial harvests increased from 42,476.2 kilograms in 1995 to 110,815.5 kilograms in 1999 (Cortés, 2002). Recreational catches of Atlantic sharpnose have also intensified from an estimated 43,490 sharks in 1981 to 122,422 sharks in 2000 (Cortés, 2002). Moreover, Atlantic sharpnose sharks suffer considerable mortality as by-catch in various fisheries and this mortality may exceed the recorded landings for this species. If the abundance of Atlantic sharpnose shark has declined due to increased mortality, it would be reasonable to expect changes in biological parameters due to a density-dependent mechanism.

There have been few studies providing empirical evidence of density-dependent compensation in sharks. A study on the age and growth of sandbar sharks, *Carcharhinus plumbeus*, found an increase in juvenile growth rate after exploitation but this was not accompanied by a decrease in age at maturity (Sminkey and Musick, 1995). Although these results are conflicting perhaps due to methodology (Cortes, 2002), the possibility exists that changes due to density-dependence are much more difficult to quantify for longer lived elasmobranchs like the sandbar shark which does not reach age at maturity until 13 years and has a generation time of 21.1 years (Cortes, 1998). Thus, density-dependent compensation in sharks, if it exists, may be easier to detect for a relatively short-lived elasmobranch like the Atlantic sharpnose shark that has a generation time of 5.76 years (Cortes, 1998). The purpose of this paper is to update the age, growth, and reproduction of the Atlantic sharpnose shark in the northern Gulf of Mexico and provide empirical evidence for potential compensatory changes in biological parameters.

### Materials and Methods

Atlantic sharpnose sharks were collected from the northern Gulf of Mexico from 1998-2001 using gill nets (multiple panels of 8.9 to 20.3 cm stretched mesh sizes) and a 100-hook longline (#15/0 circle hook). The sharks collected were placed on ice and returned to the laboratory. At the laboratory, sharks were measured to the nearest cm for body lengths (PC - precaudal, FL - fork length, TL - total length, and stretched total length (STL), vertebrae collected from the column between the origin and termination of the first dorsal fin, and reproductive condition assessed following Parsons (1983).

Preparation of vertebrae for enhancement and reading of growth bands was performed following Carlson et al. (in press). Growth bands were found to be most apparent using crystal violet stain on sagittal sections with a thickness of 0.5 mm. Based on a previous validation study (Branstetter, 1987), we assigned ages assuming 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 June, (2) growth bands are formed once a year, and (3) the narrow dark marks are deposited in winter. Ages were calculated using the algorithm: age=the birth mark + number of winter marks -1.5. If only the birth mark was present, age was assumed to be 0+.

Growth for male and female sharks was expressed using the von Bertalanffy growth model (von Bertalanffy, 1938) fitted to observed size-at-age data using the equation:

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

where  $L_t$ =predicted length at time  $t$ ;  $L_\infty$ =theoretical asymptotic length;  $K$ =growth coefficient; and  $t_0$ =theoretical age at zero length. Growth model parameters were estimated using Marquardt least-squares non-linear regression. Comparison of growth curves between sexes was performed using  $\chi^2$ -tests of likelihood ratios (Cerrato, 1990). Theoretical longevity was estimated as the age at which 95% of  $L_\infty$  is reached ( $(5 \ln 2)/K$ ; Fabens, 1965).

Median total length at maturity for male and female sharks was determined by fitting a logistic model,  $Y = 1/(1 + e^{-(a+bX)})$ , to the binomial maturity data (immature=0, mature=1) where  $Y$ =maturity and  $X$ =total length (cm) (Mollet *et al.*, 2000). Median total length at maturity was expressed as  $MTL = -a/b$ . The model was fitted using least squares non-linear regression. Length was back transformed to a relative age using data from this study and the corresponding age was fit to the logistic model to determine median age at maturity. Reproductive effort was determined by examining litter size and quantifying the average size and weight of near term embryos.

#### *Comparison of biological parameters*

Length-at-age data ( $n=20$ ) collected in 1984 by Branstetter (1987) and reproductive information ( $n=149$ ) obtained from 1979-1980 by Parsons (1983) was compared to data obtained from 1998-2001 ( $n=350$ ) to test for differences in life history traits. Because of the uncertainties and complexities associated with using back-calculated lengths-at-age (e.g. Rosa Lee's Phenomenon) (Walker *et al.*, 1998), we used observed size-at-age data when comparing growth curves. Growth curves for combined sexes were compared between sampling periods following Cerrato (1990). Observed mean size-at-age and growth rates between ages were compared using a t-test. Sex-specific median size

and age at maturity (combined sexes) obtained through the logistic model were compared using F-tests (Neter *et al.*, 1990).

## Results

Although several length measurements were taken for each individual, previous studies on Atlantic sharpnose shark have reported information in total length, i.e., a straight line from the tip of the snout to the tip of the tail in a natural position, our results are reported in natural TL to provide a direct comparison.

### *Biological parameters 1998-2001*

The precision of band counts was high among authors. The first set of readings resulted in an average percent error (APE) (Beamish and Fournier, 1981) of 3.1%. After consultation, agreement was reached in 304 out of 308 (98.7%) vertebrae. Samples with disagreement were discarded.

Von Bertalanffy growth parameters for Atlantic sharpnose sharks were  $L_{\infty}=95.6$  cm TL,  $K=0.63$  yr<sup>-1</sup>,  $t_0=-1.03$  and  $L_{\infty}=91.9$  cm TL,  $K=0.85$  yr<sup>-1</sup>,  $t_0=-0.73$  for females and males, respectively (Table 1). No significant differences between von Bertalanffy growth curves were found between sexes (log-likelihood ratio=5.55;  $p \geq 0.05$ ) (Fig. 1). The maximum observed age was 9.5+ (female) and 6.5+ years (male) based on vertebral band counts. Theoretical longevity estimates were 5.5 years for females and 4.0 yrs for males, respectively using values obtained through von Bertalanffy growth model.

Median size at maturity was significantly larger ( $F=2.975$ ,  $p < 0.0001$ ) for females (75.8 cm TL) than for males (71.1 cm TL) (Fig. 2). The largest immature shark was 86 cm TL and 80 cm TL and the smallest mature shark was 75 cm TL and 65 cm TL for females and males, respectively. Fitting the corresponding age to the logistic model results in an age of maturity of 1.6 years and 1.3 years for females and males, respectively.

A significant exponential relationship was found for maternal total length and number of embryos (litter size= $0.047 \exp^{(0.048)TL}$ ,  $r^2=0.65$ ). Average litter size was 5.0 ( $\pm 1.8$  S.D.). The mean size of near term embryos was 32.3 STL ( $\pm 2.1$  S.D.) (weight= $130 \pm 29.8$  g).

### *Comparison of biological parameters*

Growth parameters for combined sexes derived for Atlantic sharpnose shark from 1998-2001 show that they attain a smaller theoretical maximum size ( $L_{\infty}$ ) and that they reach  $L_{\infty}$  at a faster rate ( $K$ ) than conspecifics from 1984 (Fig. 1). Von Bertalanffy growth parameters for sharks from 1998-2001 were  $L_{\infty}=94.1$  cm TL,  $K=0.73$  yr<sup>-1</sup>,  $t_0=-0.88$  (Table 1). In 1984,  $L_{\infty}=110.8$  cm TL,  $K=0.39$  yr<sup>-1</sup>,  $t_0=-0.86$ . Significant differences between von Bertalanffy growth curves were found between time periods (log-likelihood ratio=51.14;  $p < 0.01$ ). Maximum age increased by 4 years (5.5 years vs. 9.5 years) from 1984 to 1998-2001.

Observed size-at-age was different between studies but many ages were not significantly different ( $p \geq 0.05$ ) (Table 2). Among younger ages, mean observed size-at-age was larger for 1998-2001. Beyond age 2.5, mean observed size at age was larger for the Atlantic sharpnose from 1984.

Growth rates between ages varied depending on time period. Average growth from observed mean size-at-age data was 25.2 cm TL from age 0 to age 0.5, 11.2 cm TL from age 0.5 to 1.5, and 9.4 cm from age 1.5-2.5 for those sharks obtained during 1998-2001. From 1984, sharks grew 11.9 cm TL from age 0 to age 0.5, 19 cm TL from age 0.5 to 1.5, and 24.6 cm from age 1.5-2.5.

Estimates of size and age at maturity for male and female sharks from 1998-2001 were different than those from 1979-1980 (Fig. 2). Although no significant differences were found ( $F=132.57$ ,  $p \geq 0.05$ ), the size at which 50% of the population reached maturity (MTL) decreased from about 80.2 cm TL in 1979-1980 to 75.8 cm TL in 1998-2001 for females. Male median total length at maturity also decreased from 78.3 to 71.1 cm TL but was not significantly

different ( $F=121.09$ ,  $p \geq 0.05$ ). Using the combined age and growth models, age at maturity decreased from 2.3 in 1979-1980 to 1.4 years in 1998-2001.

Reproductive effort was similar between time periods. Fecundity (number of embryos) was found to increase with size (TL) but the relationship was described by an exponential equation for 1998-2001 while Parsons (1983) described reproductive effort using a linear relationship. Overall, litter size was similar between studies (5.0) and the mean size of near term embryos was  $130 \pm 29.8$  g for 1998-2001 and 95-150 g for 1979-1980.

### Discussion

There are several mechanisms by which density-dependent regulation in shark populations may occur. Holden (1973) hypothesized that when dogfish populations are reduced compensatory increases in fecundity and growth rate (which in turn induces earlier maturity) and or decreases in natural mortality may take place as a result of decreased predation, reduced competition, or increases in available food. Although Holden (1973) proposed that changes in fecundity is the density-dependent mechanism for controlling populations of spiny dogfish, *Squalus acanthias*, off Norway, Wood *et al.* (1979) and Walker (1992) using theoretical simulations proposed natural mortality was the mechanism for regulating spiny dogfish and gummy shark, *Mustelus antarcticus*, populations, respectively. Evidence from this study suggests the mechanism for controlling density dependent regulation in Atlantic sharpnose shark is to increase juvenile growth, which in turn induces a decrease in age and size of maturity.

As discussed by Cailliet *et al.* (1990) and Tanaka *et al.* (1990), detecting differences in growth estimates may difficult to assess. We attempted to minimize some source of bias by re-analyzing the original size-at-age data that might hinder comparison with Branstetter's (1987) original study. However, we were unable to acquire the original vertebrae samples and contend that the difference in growth rates could be due in part to differences in interpretation of growth rings and sample size.

The decline in age and size at maturity and increase in growth rate could be attributable to an increase in food availability. One hypothesis is the increase in food availability is the result of the increased harvest of Atlantic sharpnose sharks from the 1993 through 2001, thus reducing intraspecific competition. However, an alternate hypothesis is the reduction in large coastal sharks, such as blacktips, since the early-1980's have reduced interspecific competition. Although no published quantitative studies and trophic interactions of diet for these species are available, preliminary evidence suggests juvenile blacktip shark and adult Atlantic sharpnose shark occupy similar food niches (Dana Bethea, North Carolina State University, personal communication). Kato (1987) proposed the increased growth rate and decrease in maturity found in minke whales, *Balaenoptera acutorstrata*, was attributable to reduced competition for food with depleted stocks of blue, *B. musculus*, and fin whales, *B. physalus*. Further study on the diet and niche relations on these and other sharks will be necessary to further evaluate this hypothesis.

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Table 1. Life history parameters for Atlantic sharpnose sharks obtained from 1998-2001, 1984 by Branstetter (1987), and 1979-1980 by Parsons (1983). M=values for males and F=values for females. Values are means  $\pm$ 95% confidence limits.

Parameter	1998-2001	1984	1979-1980
Theoretical maximum size ( $L_{\infty}$ cm)	91.9 $\pm$ 6.0 (M) 95.6 $\pm$ 5.9 (F) 94.1 $\pm$ 4.2 (combined sexes)	110.8 $\pm$ 23.8 (combined sexes)	
Growth coefficient ( $K$ yr <sup>-1</sup> )	0.85 $\pm$ 0.36 (M) 0.63 $\pm$ 0.24 (F) 0.72 $\pm$ 0.21 (combined sexes)	0.39 $\pm$ 0.29 (combined sexes)	
Theoretical age at zero length ( $t_0$ yr)	-0.73 $\pm$ 0.38 (M) -1.03 $\pm$ 0.48 (F) -0.88 $\pm$ 0.31 (combined sexes)	-0.86 $\pm$ 0.73 (combined sexes)	
Observed maximum age (yr)	6.5 (M) 9.5 (F)	5.75	
Theoretical maximum age (yr)	4.0 (M) 5.5 (F)	9.9	
Median size at maturity (cm)	71.1 (M) 75.8 (F)		78.3 (M) 80.2 (F)
Median age at maturity (yr)	1.3 (M) 1.6 (F) 1.4 (combined sexes)		2.3 (combined sexes)
Fecundity (pups yr <sup>-1</sup> )	5.0 $\pm$ 0.47		5 range (1-7)
N	350	20	149

Table 2. A comparison of observed mean size at age for combined sexes from 1984 and 1998-2001.

	0	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5
1984	33.6	45.5	64.5	89.0	92.0	96.6	100.0				
S.D.	-	4.7	0.9	-	1.4	2.5	-				
N	1	6	4	1	2	5	1				
P value	-	p $\geq$ 0.05	<0.01	-	p $\geq$ 0.05	p $\geq$ 0.05	-				
1998-2001	38.0	63.2	74.4	83.9	90.4	92.0	94.3	96.0	100.1	98.9	97.3
S.D.	5.7	6.1	7.7	6.4	6.2	5.8	3.9	3.8	1.8	0.8	-
N	26	90	55	53	33	16	10	14	4	2	1

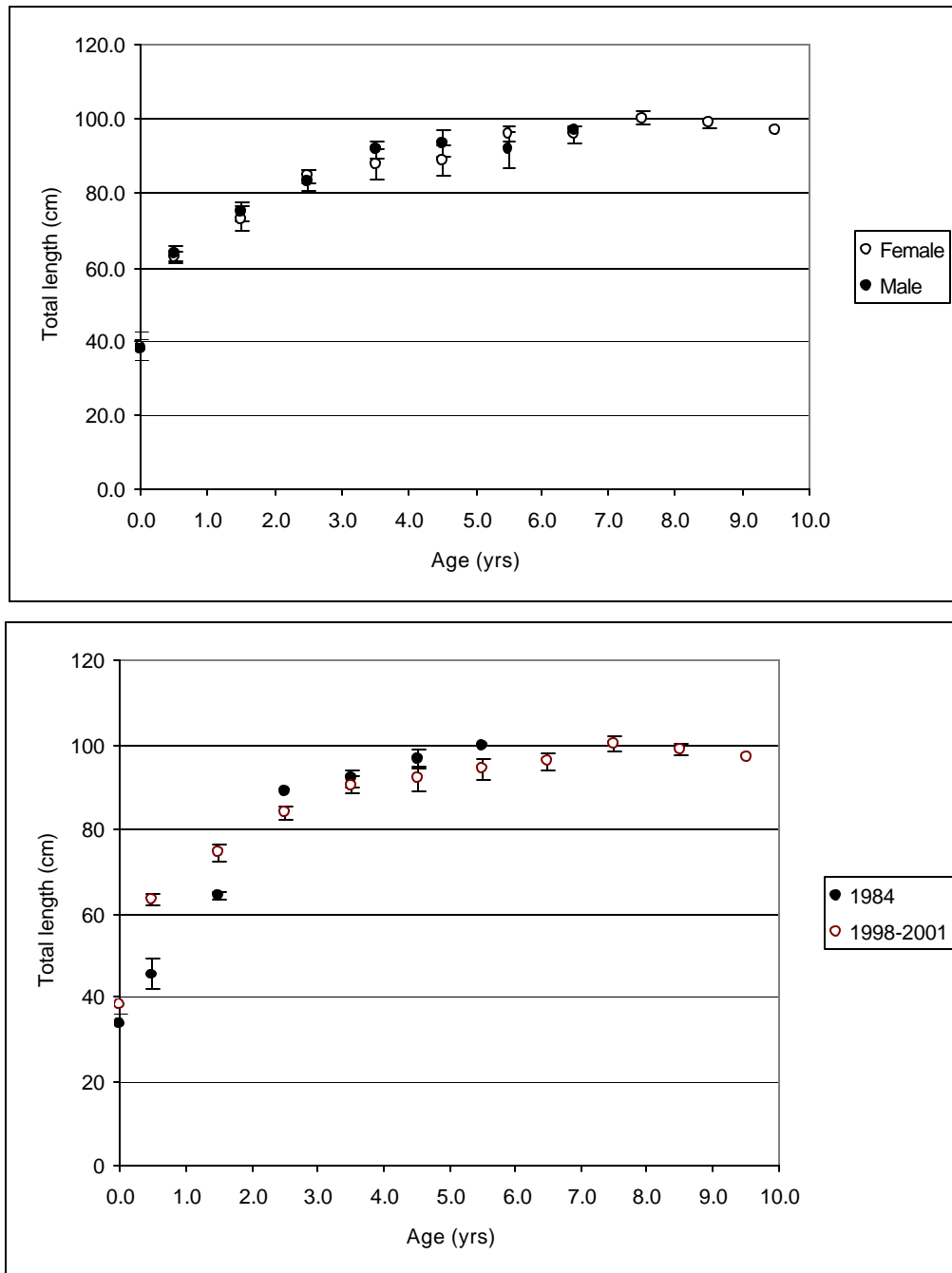


Fig. 1. Von Bertalanffy growth functions of Atlantic sharpnose sharks for (A) male and female from 1998-2001 and (B) from 1984 and 1998-2001 for combined sexes. Vertical bars are 95% confidence limits.

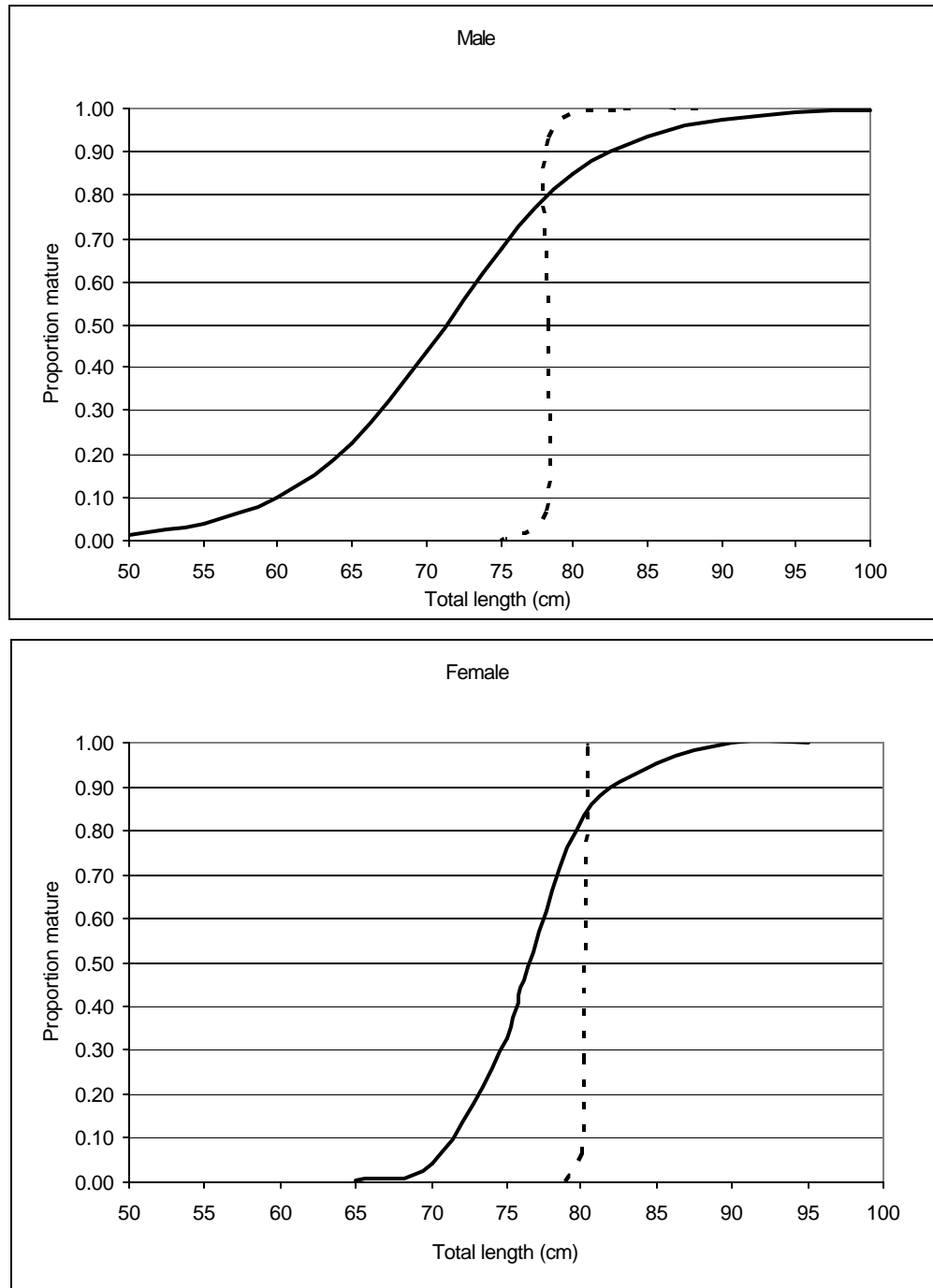


Fig. 2. Total length at maturity of male and female Atlantic sharpnose from 1998-2001 and 1979-2001 as expressed through the logistic model. Models from 1998-2001 are illustrated with a solid line and that from 1979-1980 with a dashed line.