Age, growth and population dynamics of the sandbar shark, Carcharhinus plumbeus, at different population levels

Thomas R. Sminkey

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Age, growth and population dynamics of the sandbar shark, 
*Carcharhinus plumbeus*, at different population levels

Sminkey, Thomas Richard, Ph.D.
The College of William and Mary, 1994
AGE, GROWTH AND POPULATION DYNAMICS OF THE SANDBAR SHARK,
CARCHARHINUS PLUMBEUS, AT DIFFERENT POPULATION LEVELS

A Dissertation
Presented to
The Faculty of the School of Marine Science
College of William and Mary in Virginia

In Partial Fulfillment
of the Requirements for the Degree of
Doctor of Philosophy

by
Thomas Richard Sminkey
1994
This dissertation is submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

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ABSTRACT

The objectives of my research were to test the hypothesis that compensatory (density-dependent) growth of sandbar shark (Carcharhinus plumbeus) occurred after severe population reduction, to describe the juvenile sandbar shark fauna present in the Chesapeake Bay during 1980-81 and 1990-93, and to perform demographic analyses to examine potential population growth.

Age and growth of sandbar sharks were investigated by counting rings in vertebral samples collected in 1980-81 and 1991-92. Age at maturity was 15 - 16 years for both sample periods and both sexes. For sexes combined, the von Bertalanffy growth parameters were $L_\infty=199$ cm precaudal length (PCL), $K=0.057$, $t_0=-4.9$ years for the 1980-81 sample and $L_\infty=164$ cm PCL, $K=0.089$, $t_0=-3.8$ years for the 1991-92 sample. Significant differences in size at age and annual incremental growth of juveniles suggest a small increase in juvenile sandbar shark growth rate between the two sampling periods.

Annual catches of sharks $>105$ cm PCL declined substantially between survey periods. Males and females were present in a 1:1 ratio. During 1980-81 juveniles ranged in age from 0-7 yr, but in 1990-93 few sandbar sharks over age 4 were taken. Based on the best estimate of fishing mortality the population ranged from 10,087 to 8509 sharks from 1989-1993. Annual year-class size was variable but all estimates were within one order of magnitude. Juvenile sandbar sharks declined in abundance by approximately 15% between 1989 and 1993.

The annual population growth rate was highest under a scenario of natural mortality ($M$) = 0.05 and maximum age of 30 yr, but was only 11.9%/yr. At higher juvenile mortality rates and adult $M$ fixed at 0.10, the best estimate of $M$ for sandbar sharks, population growth rate was only 2.6%/yr. Adding fishing mortality ($F$) at immature ages caused the population to decline unless $F$ levels were < 0.10 and 0.05 at maximum age = 30 and 60 yr, respectively. It is apparent that sandbar shark populations will decline under any substantial fishing mortality on immature ages, and mature fish can only be exploited at very low levels of fishing mortality.
AGE, GROWTH AND POPULATION DYNAMICS OF THE SANDBAR SHARK,
CARCHARHINUS PLUMBEUS, AT DIFFERENT POPULATION LEVELS
Chapter 1

A COMPARISON OF GROWTH RATES OF SANDBAR SHARKS, *CARCHARHINUS PLUMBEUS*, BEFORE AND AFTER POPULATION DEPLETION
Abstract

Recent studies have shown that by 1991 the sandbar shark (*Carcharhinus plumbeus*) population along the Atlantic coast of the U.S. had declined in abundance to ca. 20% of its level in the late 1970's. This phenomenon allowed us to test the hypothesis that compensatory (density-dependent) growth occurred after severe population reduction. Age and growth of sandbar sharks were investigated by counting rings in vertebral samples collected in 1980 - 1981 and 1991 - 1992. The collections included 188 sharks from 1980 - 1981 and 412 sharks from 1990 - 1991 ranging in length from 51 - 172 cm precaudal length (PCL). All sharks were mature at lengths > 136 cm PCL. Minimum and maximum ring counts, which included a birth mark, were 1 and 25. Age at maturity was 15 - 16 years for both sample periods and both sexes. For sexes combined, the von Bertalanffy growth parameters were $L_\infty=199$ cm PCL, $K=0.057$, $t_0=-4.9$ years for the 1980 - 1981 sample and $L_\infty=164$ cm PCL, $K=0.089$, $t_0=-3.8$ years for the 1991 - 1992 sample. Significant differences in size at age and annual incremental growth of juveniles suggest a small increase in juvenile sandbar shark growth rate between the two sampling periods.
Introduction

The sandbar shark, *Carcharhinus plumbeus*, is a large, predominately coastal species which ranges from Cape Cod to Brazil in the western North Atlantic (Bigelow and Schroeder 1948; Springer 1960; Garrick 1982). It is the most common large coastal shark in Virginia waters (Musick et al. 1993). The lower Chesapeake Bay and Eastern Shore lagoon system are important nursery grounds for neonate and juvenile sandbar sharks. Pregnant females seasonally enter these areas to pup from late May through late June (Musick and Colvocoresses 1986). Mature male sandbar sharks are uncommon in Virginia waters.

The life history of the sandbar shark has been described in detail (Bigelow and Schroeder 1948; Springer 1960). Like most elasmobranchs, the reproductive strategy of the sandbar shark includes production of a few large offspring (avg. 9 per litter), a relatively long gestation period (9-12 months) (Springer 1960; Clark and Von Schmidt 1965; Lawler 1976) and first maturity at late age (Casey et al. 1985; Casey and Natanson 1992). Such a "K" selected species could easily be overexploited to dangerously low levels in a directed and unrestricted fishery (Nammack et al. 1985; Hoff 1990; Pratt and Casey 1990).
Historically shark fisheries along the Atlantic Coast of the U. S. have been small and short-lived. During the 1940's and 1950's sharks were caught for their vitamin A-rich livers and for their hides with these fisheries concentrated in Florida (Springer 1960; Casey et al. 1978). Small scale fishing effort for sharks continued during the 1960's including a small commercial shark fishery near Great Machipongo Inlet on the eastern shore of Virginia (Hoese 1962; Casey et al. 1983). Total U. S. commercial landings of pelagic, or large, sharks (all sharks except dogfish) from the Atlantic Ocean and Gulf of Mexico in the 1960's and 1970's ranged from 38 t (1971) to 608 t (1967) (Anderson 1985; Anderson 1990).

During the 1980's, interest in sharks for both food and recreation greatly increased. Shark meat became increasingly popular and the demand for dried shark fins for export to Asia contributed to the proliferation of directed fisheries (Hoff and Musick 1990; Fritchey 1989). Total commercial landings in the Atlantic rose from 331 t in 1980 to 984 t in 1986, an increase of nearly 300% in only 6 years (Anderson 1990). In the Gulf of Mexico landings nearly tripled from 1979 (61 t) to 1980 (171 t) then continued to increase to 561 t in 1986 (Anderson 1990). Combining the landings from the Atlantic and Gulf of Mexico, there was a six-fold increase from the late 1970's to 1986, a span of only 10 years.
Because of its abundance throughout the region, the sandbar shark is an important component in these historical and current fishery efforts. The species comprises about 20% of the large-shark fauna and is second only to the blue shark in recreational catches along the east coast (Hoff 1990). Additionally, although species composition is not well documented in the commercial fishery, the sandbar shark is one of the primary species caught by the directed fishery in the southeast U.S. because of its fin/carcass ratio (Anonymous 1991). A decline in abundance by nearly 2/3 of adolescent and adult sandbar sharks in Virginia waters (Musick et al. 1993) is at least partially attributable to these intense fishing efforts.

Hoff and Musick (1990) reviewed the informational needs to effectively manage a shark fishery and, among others, identified the lack of accurate age estimates as contributing to the failure to develop a shark management plan. In order to properly manage a species, accurate growth information is essential.

Age and growth of the sandbar shark was previously investigated in the northwest Atlantic (Lawler 1976; Casey et al. 1985; Casey and Natanson 1992) and Hawaii (Wass 1973), but several aspects of these studies warrant reexamination. The parameter $L_\infty$ of the von Bertalanffy growth functions (VBGF) of Lawler (1976) and Casey et al. (1985) was large relative to the maximum reported size for
the species, and sample sizes at older ages in both studies were small. As a result, the VBGFs may not have realistically described growth for this species. Further, these studies were done before the rapid expansion of both the commercial and recreational fisheries for sharks. The more recent study by Casey and Natanson (1992) developed the growth model based upon tag/length-increment data which may not be comparable to models derived from age-length data (Francis 1988). In a study using captive animals (Wass 1973), the calculated asymptotic size (139.4 cm precaudal length: PCL) and the age at maturity (ca. 3 years) of sandbar sharks from the Pacific Ocean were considerably lower than those determined by Lawler (1976), Casey et al. (1985) and Casey and Natanson (1992). These differences suggest that sandbar shark growth may be faster in the Pacific than in the Atlantic, or that the growth of captive sharks does not accurately represent growth in the wild, or both factors may be true.

If sandbar shark growth is affected by density-dependent factors, then lower intraspecific competition for food and other resources may lead to faster growth, particularly among juvenile sandbar sharks. Three possible mechanisms for density-dependence in elasmobranch populations have been categorized as 1) compensatory decreases in natural mortality, 2) compensatory increases in fecundity when food is more available or through decreased
uterine mortality, and 3) compensatory increase in growth rate when food is more abundant resulting in earlier maturity and greater fecundity for each age-class (this assumes maturity and fecundity are size-related rather than age-related) (Holden 1973; Hoenig and Gruber 1990).

Given the importance of accurate and timely growth models to fishery management and population modeling efforts, there were two objectives of this study. First, growth of sandbar sharks from the Chesapeake Bay and coastal Virginia waters were modeled using two collections of vertebrae to investigate the possibility of compensatory growth. One sample was collected during 1980-1981 and archived, and fresh material was collected in 1991-1992. The null hypothesis was that there is no difference in growth between the time periods. The second objective was to compare the resulting age/growth analyses with the growth models of Casey et al. (1985) (vertebral analysis) and Casey and Natanson (1992) (tag/length-increment analysis).
Methods and Materials

Sandbar sharks were collected from sites in the Chesapeake Bay, Virginia and adjacent coastal waters using longline fishing gear. Additional samples were obtained from off the west coast of Florida in September, 1991 and February, 1992. The Florida sandbar sharks were mostly mature males, which are uncommon in Virginia waters. Results of genetic studies on sandbar sharks of the western North Atlantic, using animals collected from Virginia, the eastern Gulf of Mexico and the Yucatan area of Mexico, are consistent with an hypothesis of one population (E. Heist, pers. comm.). Collections were made monthly from May to October during 1991 and 1992. Archived samples were collected from the same sites and seasons in 1980 and 1981. After euthanizing a shark, a sample of several vertebrae was removed from below the origin of the first dorsal fin (vertebrae nos. 25-30). Vertebrae were trimmed, packed on ice, and frozen until processing, or fixed in formalin, rinsed, and preserved in isopropyl alcohol for later processing. Samples were collected from both sexes and all available sizes.

A total of 602 vertebral samples were processed for analysis. The collection from 1980-81 contained vertebrae
Figure 1. Sagittal section through a 5+ year-old sandbar shark vertebra.
from 38 males and 150 females, ranging in length from 51 - 172 cm precaudal length (PCL). In 1991-92 223 male and 191 female sandbar sharks were collected, ranging in length from 43 - 161 cm. Preparation of vertebrae followed the method of Branstetter and Stiles (1987). Vertebrae were thawed (if frozen), cleaned and air-dried. Sagittal sections were cut from the center of the centrum, polished with fine-grit wet sandpaper and air-dried. Although stains have previously been used to enhance ring contrast (Stevens 1975; Hoenig and Brown 1988), satisfactory results were obtained without stains.

Initial ageing of the prepared vertebrae sections was conducted using transmitted light on a binocular dissecting scope at 60X or 120X magnification. Banding patterns were readily discernible in sections, and a light and dark band pair were considered a growth increment with the narrow opaque ring counted as the annulus (Fig. 1). Vertebral radius and distance from focus to each annulus were measured using a dissecting microscope with transmitted light and a Biosonics video imaging and digitizing system. Additional blind readings were used to check precision of age determinations (all readings were by the senior author). The Index of Average Percentage Error (IAPE) (Beamish and Fournier 1981) was used to estimate error in counting annuli:

\[ \text{IAPE} = \frac{1}{N} \sum \left( \frac{1}{R} \sum \left( \frac{|X_{ij} - X_{j}|}{X_{j}} \right) \right) \times 100, \]
where $N$ is the number of fish aged, $R$ is the number of readings, $X_{ij}$ is the age of the $j$th fish at the $i$th reading, and $X_{j}$ is the mean age of the $j$th fish. Body length on vertebral radius regressions were computed to test for isometric growth.

In an attempt to determine the periodicity of ring formation in the vertebrae, marginal increment analysis was performed on samples from juveniles which were more numerous and faster growing. The margin, or growth of vertebra from the last annulus to the edge, was converted to the percent of the last full growth band and was averaged by month.

Body lengths at previous ages were back-calculated from vertebral measurements. Previous studies have most often used the Dahl-Lea direct proportion method, or the Fraser-Lee regression relationship. More recent studies (Campana 1990; Francis 1990; Ricker 1992) have shown that these estimators may not be totally appropriate.

Francis (1990) recommended 3 points to be followed in back-calculating fish lengths (from scales). First, use only back-calculation formulae which follow either the scale proportional (SPH) or the body proportional (BPH) hypotheses. Accordingly, the Dahl-Lea method would only be appropriate when the body:scale regression passes through the origin. Furthermore, Francis (1990) noted that if the regression is linear but does not pass through the origin, the commonly used Fraser-Lee equation should be rejected in
favor of the Hile equation or the BPH equation. Secondly, it was recommended that both the SPH and BPH be used for each fish population and the difference in back-calculations be used as a measure of the imprecision of back-calculation. And thirdly, comparison of back-calculations with observed lengths should be used not only to corroborate the back-calculations, but also to assess which method, BPH or SPH, produces more accurate results.

Campana (1990) proposed the use of a biologically derived intercept, in a modified Fraser-Lee equation:

\[ L_a = L_c + \left[ (O_a - O_c) \frac{(L_c - L_0)}{(O_c - O_0)} \right] \]

where: the biological intercept is at fish length = \( L_0 \) and otolith radius = \( O_0 \), and \( L_a \) = length at age \( a \), \( L_c \) = length at capture, \( O_a \) = otolith distance from focus to annulus \( a \), and \( O_c \) = otolith radius at capture. He defined the biological intercept as the fish and otolith size at which proportionality of fish and otolith growth is initiated. (Any structure used for ageing and proportional back-calculation may be substituted for his use of the otolith.) Using a cohort simulation model, Campana (1990) showed that his equation produced more accurate back-calculated lengths then did the Fraser-Lee model.

In this study the Campana (1990) equation was used with the size at birth as the biologically determined constant. Additionally, both the Hile and BPH equations (Francis 1990) for back-calculation were used and the results of all
three methods were compared. Duncan's multiple range test (SAS 1979) was used to test for differences between sexes and samples in the mean back-calculated lengths.

The mean back-calculated lengths at age for males and females, separately, were used to solve the von Bertalanffy growth equation (von Bertalanffy 1938), which is:

\[ L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right) \]

where:
- \( L_t \) = length at age \( t \)
- \( L_\infty \) = asymptotic length
- \( K \) = growth coefficient
- \( t_0 \) = age when length is theoretically zero.

Data were fitted to the equation using the NLIN procedure with MARQUARDT option of SAS (1979) computer software. Using Monte Carlo simulations this iterative method was shown to produce the most accurate and precise estimates of known parameters and was easier to use than a traditional linear fitting technique (Vaughan and Kanciruk 1982).

Growth models of sandbar sharks from the two sampling periods were compared statistically using various techniques. We directly compared incremental growth by age. By reparameterizing the von Bertalanffy growth model Gallucci and Quinn (1979) propose the use of a new parameter, \( \Omega = K \cdot L_\infty \), which corresponds to the growth rate near \( t_0 \). Bernard (1981) proposes the use of Hotelling's \( T^2 \) and subsequent modification of it to an F statistic for testing of growth parameters when those parameters are
correlated. The method of Kappenman (1981) for comparing growth curves based on the sum of squares of the differences between observed and predicted lengths (from an appropriate growth model) was also utilized. The 1991-92 results also were compared with the reported analyses of Casey et al. (1985) and Casey and Natanson (1992).
Results

Maturity

Estimated sizes at maturity were based on 73 male sandbar sharks from the recent Florida sample and 281 females collected by VIMS from 1976-1992, which were measured and examined for reproductive stage. Eleven immature males were 122 - 136 cm PCL, two maturing males were 134 and 139 cm, and the mature males were 129 - 156 cm. The smallest mature female was 126 cm PCL and the largest immature was 140 cm PCL. With the exception of the latter shark, all females > 134.5 cm PCL were mature and of those from 126-134 cm PCL ca. 25% (7/27) were mature. Springer (1960) reported the size of maturity was 71" TL (135 cm PCL) for males and 72" TL (137 cm PCL) for females. PCL (cm) can be converted to TL (cm) using the equation: $TL = 1.34*PCL - 0.64$ (n>800; $r^2=0.99$).

Age/Growth

Following the second reading of all vertebrae a consensus age was determined for those samples which differed in age, and measurements were taken for back-calculation of size-at-age. Vertebrae from two individuals were discarded as unreconcilable after the second reading.
Following the third reading the percent agreement and the IAPE between the second and third readings were determined. The same age was estimated in 59% of the samples; 89% agreed within 1 year, 98% agreed within 2 years and 100% agreed within 3 years (only 9 additional samples). The IAPE was 7.9. Vertebral radius vs. length regression equations for single sex and sexes combined for both time periods were all significant (prob.<0.001):

1980-81, female: \[ PCL = 12.5 \times VR + 28.1 \quad (r^2=0.96, \ N=150) \]

1980-81, male: \[ PCL = 13.0 \times VR + 25.4 \quad (r^2=0.95, \ N=38) \]

1980-81, both: \[ PCL = 12.5 \times VR + 27.6 \quad (r^2=0.96, \ N=188) \]

1991-92, female: \[ PCL = 13.8 \times VR + 13.6 \quad (r^2=0.98, \ N=183) \]

1991-92, male: \[ PCL = 13.9 \times VR + 13.6 \quad (r^2=0.96, \ N=152) \]

1991-92, both: \[ PCL = 13.8 \times VR + 13.8 \quad (r^2=0.97, \ N=335) \]

Coefficients from these equations were used in the Hilei and BPH back-calculation equations.

Large average margins on vertebrae in May and June are followed by a smaller margin in July (Table 1). This pattern suggests annual rings form sometime in late June or early July, or that the rings are not easily discernable until after summer growth has begun.

Back-calculated mean lengths-at-age from both sample periods in the present study were larger than those estimated by Casey et al. (1985) for ages 0-9 for male sandbar sharks and for ages 0-10 for females (Table 2). At older ages the back-calculated lengths of Casey et al.
Table 1. Marginal increment analysis of sandbar shark vertebral growth. Margin = % of last complete growth band.

<table>
<thead>
<tr>
<th>Month</th>
<th>N</th>
<th>Average Margin</th>
<th>SD</th>
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<tbody>
<tr>
<td>May</td>
<td>23</td>
<td>78</td>
<td>33</td>
</tr>
<tr>
<td>June</td>
<td>52</td>
<td>76</td>
<td>37</td>
</tr>
<tr>
<td>July</td>
<td>63</td>
<td>48</td>
<td>27</td>
</tr>
<tr>
<td>Aug.</td>
<td>105</td>
<td>51</td>
<td>25</td>
</tr>
<tr>
<td>Sept.</td>
<td>35</td>
<td>72</td>
<td>34</td>
</tr>
<tr>
<td>Oct.</td>
<td>33</td>
<td>81</td>
<td>29</td>
</tr>
<tr>
<td>Year</td>
<td>Female Mean</td>
<td>Female SD</td>
<td>Male Mean</td>
</tr>
<tr>
<td>------</td>
<td>-------------</td>
<td>-----------</td>
<td>-----------</td>
</tr>
<tr>
<td>1980</td>
<td>70.646</td>
<td>6.031</td>
<td>72.500</td>
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<td>71.650</td>
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</tr>
<tr>
<td>1985</td>
<td>75.650</td>
<td>6.031</td>
<td>77.500</td>
</tr>
</tbody>
</table>

*From fork length using: FL = 1.17FL + 1.*
Table 3. Sandbar shark back-calculated precaudal length (cm) at age. Sexes combined (B = birth). Lengths from Casey et al. (1980) converted from fork length using: F L  =  1.1*PCL +  1.

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(1980 in year)
Table 4. Juvenile sandbar shark annual growth increments (cm) by sample period for sexes combined.

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* Significant difference at $\alpha = 0.10$
** Significant difference at $\alpha = 0.05$
(1985) were larger for both sexes. Lengths back-calculated using the Hile, and BPH equations were similar to those calculated by the Campana equation (Table 3). At older ages, with small sample sizes, the difference became 0. Results of the Duncan multiple range test indicated that for the 1991-92 period the back-calculated mean lengths for male and female sandbar sharks were the same at all ages tested (0-19; α=0.05; n>1). For the 1980-81 period the mean lengths of males and females were different only for ages 12, 13, 16 and 18. When sexes were combined and the comparison made between sample collection periods the mean lengths were different for ages 4-7 and 16-19.

Significant differences in mean annual growth increments of juveniles collected during the two periods were only present in the 2nd, 3rd, 5th and 6th year of growth (Table 4). There were no significant differences between periods in older increments.

Von Bertalanffy parameters which fit best for the 1980-81 period were:
- females: \( L_\infty = 197 \text{ cm PCL}, \ K = 0.059, \ t_0 = -4.8 \text{ yr} \) (Fig. 2a),
- males: \( L_\infty = 184 \text{ cm PCL}, \ K = 0.059, \ t_0 = -5.4 \text{ yr} \) (Fig. 2a),
- combined: \( L_\infty = 199 \text{ cm PCL}, \ K = 0.057, \ t_0 = -4.9 \text{ yr} \) (Fig. 2b). The 1991-92 period yielded best-fit parameters of:
- females: \( L_\infty = 165 \text{ cm PCL}, \ K = 0.086, \ t_0 = -3.9 \text{ yr} \) (Fig. 3a),
- males: \( L_\infty = 166 \text{ cm PCL}, \ K = 0.087, \ t_0 = -3.8 \text{ yr} \) (Fig. 3a),
- combined: \( L_\infty = 164 \text{ cm PCL}, \ K = 0.089, \ t_0 = -3.8 \text{ yr} \) (Fig. 3b).
Figure 2. Von Bertalanffy growth curves for sandbar shark, *Carcharhinus plumbeus*, from 1980-81 samples. (A) Male and female separate. (B) Sexes combined, with mean back-calculated lengths included.
Figure 3. Von Bertalanffy growth curves for sandbar shark, *Carcharhinus plumbeus*, from 1991-92 samples. (A) Male and female separate. (B) Sexes combined, with mean back-calculated lengths included.
A) Female
- $L_\infty = 165$ cm
- $K = 0.086$
- $T_D = -3.9$
- $N = 191$

B) Male
- $L_\infty = 166$ cm
- $K = 0.087$
- $T_D = -3.8$
- $N = 221$

**BACK-CALCULATION**

**V8GF PREDICTED**
Figure 4. Von Bertalanffy growth curves for sandbar sharks for sexes combined from 1980-81 and 1991-92 samples with curves from Casey et al. (1985) and Casey and Natanson (1992). FL was converted to PCL using FL = 1.1*PCL + 1.
growth curves for the sexes combined for both time periods predict larger sizes at young ages for than the models estimated by Casey et al. (1985) and Casey and Natanson (1992) (Fig. 4). The sizes at ages > 11 predicted by the models of both time periods are smaller than those estimated by Casey et al. (1985) but are larger than those estimated by Casey and Natanson (1990) (Fig. 4).

Comparison of growth parameters using the methods of Bernard (1981), Gallucci and Quinn (1979) and Kappenman (1981) provided varying results. Regardless of method, there was no significant difference in growth between male and female sandbar sharks collected in 1991-92. For those collected in 1980-81 the reparameterization technique of Bernard (1981), which used all three von Bertalanffy parameters, indicated there was a significant difference between growth of male and female sharks ($T^2>3900$, prob.<<0.05). However, the reparameterization technique of Gallucci and Quinn (1979), which uses only $K$ and $L_\infty$, indicated no significant difference in growth between sexes ($H=1.97$, prob.>0.10). The Kappenman (1981) method also resulted in a significant difference in growth between sexes (prob.<0.05). When sexes were combined, all three tests found a significant difference between growth of sandbar sharks from separate time periods.
Discussion

The linear regression of vertebral radius on length was statistically significant indicating a proportional relationship between the two. As vertebral radius increases (vertebral growth) the length increases (somatic growth) in a linear, and predictable, way. Further, the elasmobranch cartilaginous skeleton is a "closed system" with respect to calcium deposition, in that once incorporated into the tissue, calcium is not lost due to resorption or remodeling (Cailliet et al. 1983). It is likely that the observed density differences in centra ring patterns are due to differences in mineralization during different growth phases (Cailliet et al. 1983). Therefore, the vertebra seems to be a suitable structure for back-calculating length at specific vertebral sizes, which can be converted to ages when a constant temporal periodicity of the rings can be ascertained.

The temporal nature of the marks in the vertebrae of the sandbar shark has not been fully resolved. Casey et al. (1985) considered the time of ring formation to be January. Our study, using juvenile sandbar sharks ages 0-8 (45-110 cm PCL), examined marginal growth of the vertebrae directly. The average marginal growth in May and June was similar to
that in October (78%, 76% & 81% of previous annual increment, respectively), and marginal growth in July, August and September was 48%, 51%, & 72%. It seems likely that annual growth is not continuous but, in fact, is composed of seasons - one of rapid growth and short duration (July - October) and one of little, or no somatic growth (October - July). This trend is similar to that observed by Casey et al. (1985). Here, the growth period is from July - September with nearly 75% of annual growth completed by the end of September. The period of rapid growth reported by Casey et al. (1985) was from June - August and was from July - September in the current study. This indicates that the rapid growth period is probably not regulated by the solar year, but may be mitigated by water temperature or seasonal availability of food. The probable interpretation of these marginal analyses is that the ring is formed during the slow growth period of the winter months, but because it is compacted on the edge of the vertebral centra, it may not be distinguished as a valid mark until after the rapid growth of the summer months has added contrasting material to the outer edge of the vertebra. The alternative may be ring formation in June, just prior to the rapid-growth season. This second hypothesis would contradict the periodicity determined for many congeneric species (Branstetter and Stiles 1987, Killam and Parsons 1989, Bonfil et al. 1993). In any case, the error of incorrectly placing the time of
ring formation by six months would only be a problem when analyzing observed length at age and placing those sharks collected in January - June in the wrong age class. If age and growth modeling is based on back-calculated size at previous ages this error is eliminated.

Campana (1990), Francis (1990), and Ricker (1992) discussed, at length, the importance of using the correct method of back-calculating lengths of fishes at previous ages from marks on hard parts used for ageing. This study selected three methods for comparison in a practical application (Campana 1990; Francis 1990). The results indicated little difference between mean lengths at age using three recommended equations (Table 3). At ages > 3 all three mean lengths agree within +/- 2 cm for both sample periods, with smaller differences at older ages. The original authors' discussions centered on the error associated with the back-calculated length vs. the actual length at a given age. For practical purposes the present study finds very similar results among methods suggesting all three equations estimate previous size at age equally well for the sandbar sharks used in this study. The use of lengths calculated with the Campana (1990) equation for estimating von Bertalanffy parameters was based on the inclusion of an independently estimated size at a known age (length at birth). Campana (1990) contended the error associated with the estimated size at age approaches 0 as
the ages approach the known age, in this case birth. In future studies of size at age in elasmobranchs we recommend the use of the Campana back-calculation equation because of its accuracy and ease of calculation when size at birth can be independently estimated.

Casey et al. (1985) and Branstetter (1987) validated annual vertebral rings in sandbar sharks using tag-recapture and/or tetracycline injection information. Branstetter (1987) used 2 juvenile sharks, which were 67 and 69 cm TL at injection. Casey et al. (1985) obtained vertebrae from 6 juvenile female sandbar sharks at liberty from 1-5 years and from one male sandbar shark, recaptured after 8 years (152 cm FL). In each fish, the number of vertebral rings between tagging (from back-calculation) and recapture and the number of years at liberty agreed. The male shark in the Casey et al. (1985) study was slightly larger than the minimum size at maturity (150 cm FL) reported by Springer (1960). Although this shark is a sample of 1, the conclusion, based partially on it, by Casey et al. (1985) of annual ring deposition partly met the requirement of Beamish and McFarlane (1983) that ring periodicity must be proven in all age classes to be accurately validated.

In a later paper, Casey and Natanson (1992) questioned the annual periodicity of vertebral rings, particularly at ages older than 5-6. They based their re-examination of age in sandbar sharks on previously reported tag-recapture
information (Casey et al. 1985) and on 12 additional recaptures (total N=33). A vertebral sample from one sandbar shark at liberty 3.3 years (127 cm FL at recapture) contained only 2 rings subsequent to tagging (from back-calculated vertebral radius at tagging). However, its growth increment of only 2.1 cm/yr was well below that expected for a sandbar shark of its size (ca. 7 cm/yr: Casey et al. 1985 & ca. 5 cm/yr: present study). If the vertebral radius:length relationship for such a slow growing individual is even slightly different from the average ratio derived by the linear regression of Casey et al. (1985), then the calculated vertebral radius at tagging may be incorrect. Such an error could lead to inadvertent exclusion of one (or more) rings (Francis 1990).

Although the annual periodicity of the vertebral rings has not been validated for all age classes, there is acceptable evidence suggesting that the periodicity is annual in juveniles through the age and size of first maturity in sandbar sharks (Branstetter 1987; Casey et al. 1985). Contrary evidence (Casey and Natanson 1992) is limited, but does raise the possibility that the annual periodicity does not persist throughout the life span of this shark, particularly among females carrying pups. Given the data presented here, we have accepted the hypothesis of annual ring formation in the vertebrae and have based resultant VBGF models on back-calculated sizes at age using
vertebral growth rings.  

The $L_m$ of the VBGF is a theoretical maximum size attained by the fish. In the case of a model derived from mean lengths-at-age this parameter is also a mean (Francis 1988). Here, $L_m$ is a maximum mean length at a theoretical maximum age and it need not be larger than the actual maximum reported size for an individual. Springer (1960) reported that over a 20-year survey of commercial shark landings in Florida he never saw a female sandbar shark longer than 234 cm TL (174 cm PCL) or a male sandbar shark longer than 226 cm TL (168 cm PCL) (TL converted to PCL using $\text{TL} = 1.34 \times \text{PCL} - 0.64$; both sexes; $r^2 = 0.99$, $n > 800$). Only 2 female sandbar sharks exceeding 165 cm PCL (172, 174 cm) have been captured by the VIMS longline survey from 1974-1993. Consequently, the estimates of $L_m$ from the 1990-91 sample (females: $L_m = 165$, males: $L_m = 166$, sexes combined: $L_m = 164$) seem reasonable as an estimate of maximum mean length. The estimates of $L_m$ from the 1980-81 period, by sex and sexes combined (females: $L_m = 197$, males: $L_m = 184$, sexes combined: $L_m = 199$) are higher and may represent a theoretical maximum length rather than an actual attainable size for the species.

The VBGFs of sandbar sharks when sexes are combined are significantly different between sampling periods based on statistical tests specifically designed for the VBGF (Bernard 1981; Galluci and Quinn 1979; Kappenman 1981).
Whether these differences reflect real growth differences and whether they are the result of some density-dependent factor is much harder to assess (Tanaka et al. 1990). Based on a long-term sampling survey of Virginia waters the relative abundance of sandbar sharks declined by approximately two-thirds from 1974 - 1991 (Musick et al. 1993). If growth of sandbar sharks was density-dependent this decline in abundance could manifest itself in increased growth rates, particularly of juveniles. That the growth coefficient, K, increased between the 1980-81 VBGF (K=0.057) and the 1991-92 VBGF (K=0.089) indicates an increase in growth rate; however, the $L_m$ of the latter VBGF is considerably lower ($L_m$=164) than that of the former VBGF ($L_m$=199). Because $L_m$ and K are inversely correlated in the VBGF the higher K may merely indicate that growth more rapidly approaches a more realistic asymptote in the latter model. Conversely, the significantly larger mean lengths at ages 4-7 and the larger annual growth increments through the seventh year of life (from the 1991-92 sample) support that early growth of sandbar sharks was actually faster. However, both models predict similar ages at maturity, 15-16 yr, suggesting that any increase in early growth has not been large enough or persisted long enough to decrease the age of first maturity.

Density-dependent growth of fish, primarily during the immature phase of the life history, has previously been
documented for several teleosts. Chadwick (1987) reported a significant decline in fork length of Atlantic salmon, *Salmo salar*, with an increase in number of age 4+ smolts. Both an increase in growth rate and a decrease in age at first spawning have been associated with declines in catch/effort following intensive fisheries for two separate stocks of herring (Iles 1967; Motoda and Hirano 1963; reported in Murphy 1977). However, it may be difficult to demonstrate density effects on growth in some elasmobranchs due to long generation times and life-spans.

Musick et al. (1993) found that the relative abundance of juvenile sandbar sharks in the Chesapeake Bay was similar to and higher in 1990 and 1991 than in 1980 and 1981, respectively. This apparent increase in abundance was probably due to increased survival of young-of-year because of a decline in abundance of large coastal sharks (their principle predators) (Musick et al. 1993). Such an increase in abundance of juveniles may have precluded any increase in growth rate due to density-dependent factors in young-of-year and other early ages. However, abundance of older juveniles (>4 yr) was much lower in 1990-91 compared to 1980-81 (Musick et al. 1993). It was primarily in these ages (4-7 yr old) that we find evidence of higher growth rates in the present study. Considering these factors, and the relatively short time elapsed (10-11 yr) between samples in this study compared to the life span of this species, it
is probable that the growth rate of juvenile sandbar sharks was slightly higher in 1991-92 than in 1980-81, that the age at first maturity was unchanged, and that any population-level consequences may not become apparent until several more years have passed.
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Chapter 2

POPULATION DYNAMICS OF SANDBAR SHARKS, CARCHARHINUS PLUMBEUS, OF CHESAPEAKE BAY, VIRGINIA
Abstract

Recent studies have shown that by 1991 the sandbar shark (Carcharhinus plumbeus) population along the Atlantic coast of the U.S. had declined in abundance to ca. 20% of its level in the late 1970's. Concomitant with this decline, a long-term survey of the shark fauna of Virginia's waters, including the Chesapeake Bay, was conducted by the Virginia Institute of Marine Science. Analysis of catches yielded sufficient data to describe the juvenile sandbar shark fauna present in the Chesapeake Bay during 1980-81 and 1990-93. Males and females up to 100 cm pre-caudal (PCL) were present in a 1:1 ratio. Annual catches of sharks >105 cm PCL declined substantially between survey periods. During 1980-81 juveniles ranged in age from 0-7 yr, but in 1990-93 few sandbar sharks over age 4 were taken. A VPA was constructed to estimate the population size of juveniles seasonally resident in the Bay during 1989-1993. Based on the best estimate of fishing mortality the population ranged from 10,087 to 8509 sharks from 1989-1993. Annual year-class size was variable but all estimates were within one order of magnitude. Juvenile sandbar sharks declined in abundance by approximately 15% between 1989 and 1993.
Introduction

The sandbar shark, *Carcharhinus plumbeus*, ranges from Cape Cod to Brazil in the western North Atlantic (Bigelow and Schroeder 1948; Springer 1960; Garrick 1982) and is the most common large coastal shark in Virginia waters (Musick et al. 1993). The lower Chesapeake Bay and Eastern Shore lagoon system is an important nursery ground for neonate and juvenile sandbar sharks, providing protection from large oceanic predators and an ample supply of food (Hoese 1962; Musick and Colvocoresses 1986; Branstetter 1990). Pregnant females seasonally enter these areas to give birth from late May through late June (Musick and Colvocoresses 1986). Juvenile sandbar sharks are resident in the lower Chesapeake Bay from June through September.

The sandbar shark comprises about 20% of the large-shark fauna of the U.S. east coast and is an important component of recreational and commercial fisheries. It is second only to the blue shark in recreational catches (Hoff 1990) and, although species composition is not documented in the commercial fishery, the sandbar shark is one of the primary species taken by the directed fishery in the southeast U.S. (Anonymous 1991; Musick et al. 1993). Like most elasmobranchs the reproductive strategy of the sandbar
shark includes a few large offspring (avg. 9 per litter), a relatively long gestation period (9-12 months) and first maturity at late age (Springer 1960; Lawler 1976; Casey et al. 1985). Such a "K" selected species could easily be overexploited to dangerously low levels in a directed and unrestricted fishery (Nammack et al. 1985; Branstetter 1990; Hoff 1990; Pratt and Casey 1990).

Total U. S. commercial landings of pelagic, or large, sharks (all sharks except dogfish) from the Atlantic Ocean and Gulf of Mexico in the 1960's and 1970's have ranged from 38 t (1971) to 608 t (1967) (Anderson 1985; Anderson 1990). During the 1980's, interest in sharks for both food and recreation greatly increased. Shark meat became increasingly popular and the demand for dried shark fins for export to Asia spawned directed fisheries (Fritchey 1989; Hoff and Musick 1990). Total commercial landings in the Atlantic rose from 331 t in 1980 to 984 t in 1986, an increase of nearly 300% in only 6 years (Anderson 1990). In the Gulf of Mexico landings nearly tripled from 1979 (61 t) to 1980 (171 t) then continued to increase to 561 t in 1986 (Anderson 1990). Combining the landings from the Atlantic and Gulf of Mexico, there was a six-fold increase from the late 1970's to 1986, a span of only 10 years.

Hoff and Musick (1990) reviewed the informational needs to effectively manage a shark fishery and identified the knowledge of nursery grounds as a critical element for
management and modeling purposes. Specifically, the potential for a direct stock and recruitment relationship in sharks requires detailed knowledge of quantitative, geographic and temporal aspects of nursery areas. By 1991 the sandbar shark population along the Atlantic coast of the U.S. had been depleted by overfishing to ca. 15% of the levels in the late 1970's (Musick et al. 1993). However, Musick et al. noted an apparent increase in abundance of juvenile sandbar sharks in the lower Chesapeake Bay between 1980-81 and 1990-91. This observation was derived from results of surveys at fixed locations in the Bay and did not include additional information on age or size structure of the juvenile population during either time period. The apparent enigma was explained by the hypothesis that although young of the year recruitment probably declined proportional to the decline in mature females, survivorship increased dramatically because of a concomitant decrease in all large sharks, which are predatory on young sandbars.

The objectives of this paper are to describe the population of juvenile sandbar sharks in the lower Chesapeake Bay during 1980-81 and 1990-93 and to report changes in population demographics and abundance between time periods.
Methods and Materials

Sandbar sharks were collected from sites in Chesapeake Bay, Virginia using "Yankee-type" tarred-nylon and steel cable longline fishing gear. The "standard" set consisted of 100 hooks spaced at 18m intervals and fished for 4 hours. However, some sets varied in the number of hooks fished, so all results have been standardized to 100 hooks. The time fished varied on occasion but was not included in effort calculations because the effective fishing time of bait in the lower Chesapeake Bay was considerably less than 4 hours due to scavenging by blue crabs and fouling by algae. Bait was teleost fish, usually mackerel, bluefish or menhaden, cut in small pieces so as not to exclude the smallest sharks. A detailed description of the longline gear and sampling methodology was given by Musick et al. (1993).

Collections were made monthly from May to October from 1990-92 and from June to September in 1993. Sites in the Bay consisted of fixed stations at Kiptopeke and Middle Grounds (Fig. 5; K & M), which were fished on a regular basis, and additional random stations (Fig. 5; unnumbered). Archived samples were collected from the same fixed sites and seasons in 1980 and 1981. All sandbar sharks caught were measured to the nearest cm (precaudal length, PCL; fork
Figure 5. Sample stations in Chesapeake Bay, Virginia. K: Kiptopeke, M: Middle Grounds, and random stations.
length, FL; total length, TL), weighed (lbs.) and sexed. A subsample was sacrificed to collect biological samples and the remainder was released alive. Dart or roto tags were applied when available if time permitted.

Sandbar shark catches by month, station, sex, and length group were summarized to illustrate changes in population demographics between time periods. Age frequencies were calculated from size at age data (Sminkey and Musick, submitted). Catch-per-unit-effort (CPUE) was calculated by dividing the total number of sandbar sharks caught by the actual number of hooks fished and multiplying by 100. The CPUE by month was calculated for the fixed stations to examine changes in relative abundance between time periods. A virtual population analysis was carried out to estimate juvenile cohort size and inter-annual variability. Natural and fishing mortality rate estimates for input to the VPA were derived from life history traits (Hoenig 1983) and recent sandbar shark stock assessments (Parrack 1990; Musick et al. 1993). Natural mortality (M) was estimated to be 0.10 following the method of Hoenig (1983).

The VPA was constructed following the methods of Vaughn et al. (1992). Because the early sample period included only two years (1980 & 1981) and fishing effort was sporadic and low between sample periods (1982-88), the VPA could only be constructed for the latter sample period (1990-93) plus
1989. Total number of sandbar sharks caught in Chesapeake Bay was summed by year, and a length frequency was constructed for each year. A subsample of aged fish was used to create an age-length key. The number of sharks per age in the annual catches was calculated using the matrix equation 2 of Vaughn et al. (1992), where the landings in number are multiplied by the proportions at age for each length frequency. In addition to the catch-at-age data, an estimate of $F$, the instantaneous fishing mortality coefficient, for the final year and oldest cohort (age 5 in 1993) was required for the linked cohort method of VPA.

**Determination of Terminal Fishing Mortality ($F$)**

Terminal $F$ was selected based on Parrack's (1992) estimate of mean $F=0.25$ for large coastal sharks for 1986-91. The sandbar shark was a primary target of commercial longliners (Musick et al. 1993) so presumably this species suffered mortality equal to, or greater than, $F=0.25$. However, the mean carcass size in the commercial fishery was ca. 24 lbs (Parrack 1992), which translates to a 7-9 year old fish (Sminkey, unpubl. data). Although the mean size includes smaller, as well as larger, individuals, fishing mortality would not have impacted the young juveniles (ages 0 - 3), which seasonally inhabit Chesapeake Bay, during that time period.

Fishing effort and gear catchability probably was low
during Bay survey sampling. Our tarred-nylon and steel
cable gear used in this survey is less efficient than the
monofilament longlines used in the commercial fishery
(Branstetter and Musick, in press). Further, effort was not
restricted to known areas of sandbar shark concentration
within the Bay. The fixed sites were selected as
representative of the shark stocks present in the Bay during
the 1970's and on occasion have yielded high catches. Total
gear fished (600-1000 hooks/year) was less than a typical
single day for one commercial longliner (ca. 75 hooks/mile x
10 miles gear = ca. 750 hooks/day) (S. Branstetter, personal
communication). If catchability remains constant over the
sample period for the gear type used, then the catch (or F)
is proportional to the effort. Considering the small effort
in this study, the type of sampling gear and the
experimental design it seems reasonable to conclude that the
resultant F on one year-class was very low. Therefore, an
initial estimate of terminal F=0.005 was used.

Further evidence suggesting very low mortality caused
by the survey can be derived from tag/recapture data. If
the population in the Bay is considered "closed" and
seasonally resident to the Bay then one would expect a
relatively high recapture rate if the survey removals were a
large percentage of the stock and fishing effort was not
reduced after tag release. During 1990-93 a total of 156
tags were applied to juvenile sandbar sharks (ages 0-3)
caught and released in Chesapeake Bay, but none was ever recaptured. In 1992 alone, 62 sharks were tagged from July to September. In 1993 when additional random Bay stations were sampled there were still no tag recaptures. This apparent elusiveness of tagged juvenile sandbar sharks suggests a large stock with typical catches of 10-20 fish being a small percentage of the total number present.
Results

Catch-per-unit-effort (CPUE) of sandbar sharks from the Chesapeake Bay was highest during June - September at most sites in both time periods, demonstrating the seasonality of the population (Fig. 6, Table 5). CPUE was very low in May regardless of time period. Although effort was low in October, the CPUE was high in 1990-93 relative to 1980-81. At the Kiptopeke station monthly CPUE was higher in all months during 1990-93 than the respective months during 1980-81. The August, 1980-81 CPUE at Kiptopeke and the Middle Ground was relatively low compared to July and September as a result of low catches in August, 1980 (Table 5). August catches in 1990-93 were relatively high at all stations (Table 5).

Very few large sandbar sharks (>105 cm PCL) were caught in the Bay (Fig. 7). In 1980-81 10 females ranging from 140-165 cm PCL were caught. In contrast, only one sandbar shark >105 cm PCL, also a female, was taken during the entire 1990-93 sampling period (Fig. 7). No male sandbar sharks over 95 cm PCL were caught in the Bay during either sample period. Further, the length frequency analysis indicates that sandbar sharks >75 cm PCL became progressively less abundant from 1990 to 1993 with only 4
Table 5. Monthly sandbar shark catches (N) and effort (No. hooks) during longline surveys from 1980-81 and 1990-93 at Chesapeake Bay stations (N/Hooks). K = Kiptopeke, M = Middle Ground, E = random Bay site.

<table>
<thead>
<tr>
<th>SITE</th>
<th>YEAR</th>
<th>MONTH</th>
<th>K</th>
<th>M</th>
<th>E</th>
<th>TOTAL</th>
</tr>
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<td></td>
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<td>1/200</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>June</td>
<td>9/100</td>
<td>6/100</td>
<td>15/200</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>July</td>
<td>13/100</td>
<td>24/100</td>
<td>37/200</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Aug.</td>
<td>2/100</td>
<td>0/100</td>
<td>2/200</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sept.</td>
<td>12/100</td>
<td>8/100</td>
<td>20/200</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oct.</td>
<td>1/100</td>
<td>1/100</td>
<td>2/200</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1981</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>July</td>
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<td>10/100</td>
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<td>0/100</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1990</td>
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</tr>
<tr>
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<td></td>
</tr>
<tr>
<td></td>
<td></td>
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<td>40/393</td>
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<tr>
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<tr>
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</tr>
<tr>
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<tr>
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<td></td>
<td></td>
<td>Sept.</td>
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<td>9/100</td>
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<td>Oct.</td>
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<td></td>
</tr>
<tr>
<td></td>
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<tr>
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<td></td>
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<td>29/780</td>
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</tr>
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<td></td>
<td>18/100</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>Oct.</td>
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</table>
Figure 6. Sandbar shark catch-per-effort from Kiptopeke, Middle Ground and lower Chesapeake Bay, Virginia.
Figure 7. Length frequencies of sandbar sharks caught in Chesapeake Bay by sample year.
Figure 8. Age frequencies (percent) of sandbar sharks caught in Chesapeake Bay by sample year.
Table 6. Age-length key for Chesapeake Bay sandbar sharks collected during 1991-92 reported as frequency occurrence of age within length group.

<table>
<thead>
<tr>
<th>LENGTH GROUP</th>
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<th>5</th>
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<td>0.4000</td>
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</table>

Table 7. Chesapeake Bay population estimates of sandbar sharks by age class from 1989 to 1993. VPA input parameters were: \( M=0.10 \) and \( F=0.005 \) for 1993, ages 4 & 5.

<table>
<thead>
<tr>
<th>Year</th>
<th>0</th>
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<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>0 - 3 Total</th>
<th>Total</th>
</tr>
</thead>
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<td>3002</td>
<td>1278</td>
<td>3428</td>
<td>1416</td>
<td>705</td>
<td>258</td>
<td>9124</td>
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<td>2418</td>
<td>2715</td>
<td>1153</td>
<td>3100</td>
<td>710</td>
<td>141</td>
<td>9386</td>
<td>10,237</td>
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<td>1934</td>
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<td>2432</td>
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<td>138</td>
<td>7544</td>
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<td>1909</td>
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<td>307</td>
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<td>2736</td>
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<td>825</td>
<td>1056</td>
<td>97</td>
<td>7356</td>
<td>8,509</td>
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</table>
sharks over 85 cm PCL caught during 1991-93 (Fig. 7). Excluding the females >140cm PCL, the annual ratio of male:female sandbar sharks caught in Chesapeake Bay did not differ significantly from 1:1 ($\chi^2$, 1 d.f., prob.>0.25 for all years).

Age frequencies of juvenile sandbar sharks caught in Chesapeake Bay were composed of 8 and 9 year-classes in 1980 and 1981, respectively, but only 6 or 7 year-classes in 1990-93 (Fig. 8). In both 1991 and 1993 no fish older than age 5 was caught (Fig. 8). The relative contribution of age 4-6 fish declined during the 1990's while the proportion of 0-2 year old sharks increased to nearly 90% of the total caught in 1993 (Fig. 8).

The age-length key for sandbar sharks, constructed from the aged subsample collected during 1991-92, indicates all fish 85-94 cm PCL are age 3 and all fish 95-99 cm PCL are age 5 (Table 6). However, these results are based on small sample sizes (only fish caught in that length group) and are representative only of the juveniles caught in the Chesapeake Bay.

Virtual Population Analysis

Age 0 cohort size estimated by the VPA, with terminal $F=0.005$, ranged from 1934-3071 (Table 7). There were fewer than 400 age 5 sandbar sharks each year, and only 97 age 5 fish were present in 1993. Annual population estimates of 0-3 year old sandbar sharks ranged from 7356-9386 and,
Table 8. Chesapeake Bay population estimates of sandbar sharks by age class from 1989 to 1993. VPA input parameters were: M=0.10 and F=0.010 for 1993, ages 4 & 5.

<table>
<thead>
<tr>
<th>Year</th>
<th>0</th>
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<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>Total</th>
<th>Total</th>
</tr>
</thead>
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<td>1731</td>
<td>737</td>
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<td>5,224</td>
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<td>1431</td>
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<td>1564</td>
<td>369</td>
<td>72</td>
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<td>5,386</td>
</tr>
<tr>
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<td>1183</td>
<td>1270</td>
<td>528</td>
<td>770</td>
<td>70</td>
<td>4,021</td>
<td>4,861</td>
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<tr>
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<td>1685</td>
<td>907</td>
<td>1018</td>
<td>1088</td>
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<td>153</td>
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<td>5,097</td>
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<tr>
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<td>762</td>
<td>420</td>
<td>529</td>
<td>48</td>
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</table>

Table 9. Chesapeake Bay population estimates of sandbar sharks by age class from 1989 to 1993. VPA input parameters were: M=0.10 and F=0.020 for 1993, ages 4 & 5.

<table>
<thead>
<tr>
<th>Year</th>
<th>0</th>
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<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>Total</th>
<th>Total</th>
</tr>
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<tbody>
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<td>201</td>
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<td>2,980</td>
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<td>690</td>
<td>287</td>
<td>400</td>
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</tr>
<tr>
<td>1992</td>
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<td>492</td>
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<td>562</td>
<td>125</td>
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<td>2,688</td>
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<td>1993</td>
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<td>212</td>
<td>266</td>
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<td>2,120</td>
<td>2,410</td>
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</table>
including the 4 and 5 year old sharks, the population in the Bay ranged from 8509-10,237 (Table 7). The age 0-3 fish were 82-92% of the total number of juvenile sandbar sharks in the Bay.

In the second simulation, terminal F was doubled (F=0.01). The resultant population estimates were reduced nearly in half (4399-5386; Table 8). Cohort size ranged between 1040-1685 age 0 sharks and 48-153 age 5 sharks. Increasing the terminal F to 0.02 decreased the population estimates further (2410-2980; Table 9).
Discussion

Monthly CPUE at the two fixed stations in the Bay were similar between the two sample periods for June, July, and September (Fig. 6). The low CPUE of the August 1980-81 sample is a result of the very low catches in August, 1980 at both the Kiptopeke and Middle Ground stations (Table 5). Potential causes of anomalously low catches for that season are sampling biases (i.e. bait condition, bait type or excess fouling of baits while fishing) or short-term environmental fluctuation (tide stage, low bottom dissolved O$_2$, depressed local food supply with resultant stock dispersal or random stock movement in aggregate). Such small-scale variability in fish availability can become a serious factor in population studies if sampling effort is small, as in 1980-81 when Kiptopeke was sampled only once monthly in 1980. Conversely, a longer time series or additional sampling within a short period would be preferable for estimating relative abundance.

Random stations (E in Table 5) were not included in the calculation of monthly CPUE for the Bay (Fig. 6) because none were sampled in 1980-81 and those fished in 1990-93 were an attempt to survey the geographical limits of the sandbar shark nursery. Consequently, the catch rates of
these samples were quite variable even during June-September when CPUE was generally high at stations K and M (Table 5). This lack of consistently high CPUE may be an indication that these areas are not prime nursery habitat and are infrequently or variably utilized by juveniles. Unfortunately, because there are no abundance estimates from random sites in 1980-81, the range of the nursery during that time cannot be assessed.

One potential explanation for the continued high relative abundance of juveniles within the Bay while the adult coastal stock has declined precipitously (Musick et al. 1993) is a contraction of the nursery range to the preferred habitat. This reduction in spatial distribution could support the similar CPUEs between time periods at Kiptopeke and the Middle Ground even if the actual total abundance of juvenile sandbar sharks throughout the Bay had declined.

Another probable factor is increased survival of young-of-year sandbar sharks due to the depletion of the large coastal sharks, which are the only significant source of predation on neonates (Branstetter 1990). Following the first year of life the sandbar sharks are less vulnerable to most predators so natural mortality is very low. The increased survival of the neonates may offset lower production leading to the continued high abundance of juveniles.
Within the 1980-81 sample period the Middle Ground site (only station sampled in 1981; Table 5) supported somewhat larger juvenile sandbar sharks (Fig. 7). Unlike all other sample years, when Kiptopeke was sampled, there were very few sandbar sharks <70 cm PCL taken in 1981. The Middle Ground site is more centrally located near the mouth of the Bay (Fig. 5) and is a more exposed and physically dynamic environment. The smaller juveniles, ages 0-1, seem to prefer the more protected area of Kiptopeke.

Length and age frequencies of juvenile sandbar sharks in 1980-81 and 1990-93 suggest a decline in abundance of older juveniles between the two sample periods (Fig. 7 & 8). Although the Middle Ground station was not as extensively sampled in 1990-93, that reduction in effort alone cannot account for the decline in abundance first of fish >80 cm PCL, then, in 1992-93, of fish >75 cm PCL. This steady ‘juvenescence’ of the sandbar shark population of Chesapeake Bay seems indicative of increased winter mortality of juveniles, which migrate offshore and south of Cape Hatteras during the winter. Although the mean carcass size in the shark fishery is estimated to be ca. 24 lbs. (7-9 year old sandbar shark; Sminkey and Musick, in press), that figure was derived from catch data collected during 1986-91 and included all large coastal species. Because of the decline in abundance of large coastal species, particularly sandbar sharks (Musick et al. 1993), the winter commercial fishery
may now be removing sandbar sharks as young as 4-5 years old.

A footnote to the length frequency analysis of juvenile sandbar sharks caught in the Bay is the number of large (>140 cm PCL) sharks caught per sample period. These sandbar sharks were all mature females and either carrying pups or postpartum. A strong indication of the overall decline in abundance of this species was the occurrence of only one fish of this size during 1990-93 (Fig. 7) even though effort was not substantially reduced relative to 1980-81 (Table 5).

Virtual Population Analysis

There are no underlying statistical assumptions in the calculations of the VPA (Hilborn and Walters 1992). There are, however, three basic assumptions. The first is that there are no fish alive at some age. In the current case there are no fish older than age 5 in the juvenile stock. Secondly, the natural mortality rate must be known. This parameter has been calculated based on longevity for the species (Hoenig 1983) and M=0.1 is considered a conservative estimate for a large carcharhinid shark. Further, the only predators on juvenile sandbar sharks are the large coastal sharks, which have been seriously depleted (Musick et al. 1993). Therefore, survival of young-of-year sandbar sharks has likely increased. The third assumption is no net
immigration or emigration. There is a net emigration. However, this is age-class dependent and probably does not occur during the seasonal habitation of the Chesapeake Bay. Beginning in the 4th year of life (age 3+) the full cohort does not return to the lower Bay during the summer. By the 7th year (age 6+) the entire cohort remains outside Chesapeake Bay. Therefore, the emigration is included as increased natural mortality from age 3-4 and 4-5.

The three VPA constructions indicate considerable variability in year-class size, yet all estimates are within one order of magnitude. By varying $F$ the absolute size of age-classes varied but the relative sizes within the VPA remained similar among simulations. Choice of the most appropriate terminal $F$ is somewhat subjective because available data were not sufficient to directly estimate the value of $F$ due to survey removals. Hence, the three simulations were carried out with $F$ selected as reasonable estimates based on the amount, type, and inferred catchability of the gear. The choice of $F=0.005$ for the oldest age-class is considered the best estimate and evaluation of the resultant virtual population allows an analysis of the dynamics of the juvenile population of sandbar sharks in Chesapeake Bay from 1989-93.

During the present study juvenile catch rates remained relatively high leading to relatively stable total population estimates. However, the adult stock of sandbar
sharks is in serious decline (Musick et al. 1993) and, owing
to the direct stock-recruitment relationship of
elasmobranchs (Fogarty et al. 1989; Hoenig and Gruber 1993),
eventually the juvenile stocks should decline if the parent
stock remains low. It is of further note that the total
population estimates already indicate a small decline from
1989-1993 (10,087-8509; Table 7). This trend may be the
result of random sampling error or may be indicative of
smaller cohorts during the 1990's. The exception seems to
be the 1992 year-class; this cohort is the largest in the
population, second only to the 1987 year-class (age 2 in
1989). These two cohorts, if surviving to maturity, could
be important components in an overall stock recovery along
the Atlantic coast.
Literature Cited


Hoff, T. B., and J. A. Musick. 1990. Western North Atlantic shark-fishery management problems and informational requirements. pp455-472. In: H. L. Pratt, Jr., S. H. Gruber and T. Taniuchi (ed.) Elasmobranchs as living resources: Advances in the biology, ecology, systematics, and the status of the fisheries. NOAA Tech. Rep. NMFS 90.


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Chapter 3
DEMOGRAPHIC ANALYSIS OF SANDBAR SHARKS
IN THE WESTERN NORTH ATLANTIC
Abstract

The sandbar shark, *Carcharhinus plumbeus*, is the most common large coastal shark in Virginia waters and is an important component of recreational and commercial fisheries along the east coast of the United States. Population studies of the sandbar shark have been limited to a time series of relative abundance in Virginia waters and a demographic analysis based on previously published life history parameters. However, the latter study did not include estimates of fishing mortality and its impact on population demographics. Applying known and estimated life history parameters this study has included fishing mortality (F) at ages and levels estimated in a recent stock assessment. Life history tables were constructed with F=0.5, 0.10, 0.15, 0.20, or 0.25 beginning at age 8, 15, or 30. Natural mortality (M) was set at 0.10 or 0.05 for maximum ages of 30 or 60 yr, respectively. Natality was set at 2.1 female pups/yr. The annual population growth rate was highest under a scenario of M=0.05 and maximum age of 30 yr, but was only 11.9%/yr. At higher juvenile mortality rates and adult M fixed at 0.10, which is the best estimate of M for sandbar sharks, population growth rate was only 2.6%/yr. Adding fishing mortality at immature ages caused
the population to decline unless $F$ levels were $< 0.10$ and 0.05 at maximum age = 30 and 60 yr, respectively. It is apparent that sandbar shark populations will decline under any substantial fishing mortality on immature ages, and mature fish can only be exploited at very low levels of fishing mortality.
Introduction

The sandbar shark, *Carcharhinus plumbeus*, ranges from Cape Cod to Brazil in the western North Atlantic (Bigelow and Schroeder 1948; Springer 1960; Garrick 1982) and is the most common large coastal shark in Virginia waters (Musick et al. 1993). It comprises about 20% of the large-shark fauna of the U.S. east coast and is an important component of recreational and commercial fisheries (Hoff 1990; Anonymous 1991; Musick et al. 1993). Age and growth (Casey et al. 1985; Casey and Natanson 1992; present study), seasonal distribution (Bigelow and Schroeder 1948; Springer 1960; Musick et al. 1993), and reproductive biology (Colvocoresses and Musick 1989) of the sandbar shark have been studied, but population studies have been limited to a time series of relative abundance in Virginia waters (Musick et al. 1993) and a demographic analysis based on previously published life history parameters (Hoff 1990).

The recent increase in fishing pressure on sandbar sharks and subsequent decline in abundance (Musick et al. 1993), revised age/growth studies (Casey and Natanson 1992; present study) and a reexamination of fecundity data presented in Colvocoresses and Musick (1989) have provided updated parameters necessary for a demographic analysis of
the sandbar shark. This analysis utilizes estimates of longevity, survival, and age-specific natality to construct a life history table which generates estimates of the net reproductive rate, the generation time, and the intrinsic rate of increase of the population (Krebs 1978). These parameters are useful for management and as input into population models (Krebs 1978; Hoenig and Gruber 1990). The objective of this study is to provide an updated demographic analysis of the sandbar shark, estimating population parameters under varying conditions of natural and fishing mortality.
Methods

Based on the size at maturity and the von Bertalanffy growth equations for sandbar sharks determined in this study, the age at maturity was determined to be 15 or 16 years. Casey and Natanson (1992) had estimated the age at maturity to be ca. 29 years based on a von Bertalanffy growth equation derived from tag/recapture information and a size at maturity reported in the literature. For my demographic analysis I considered both 15 and 29 years in separate trials.

The age-specific natality was determined from a re-examination of data from 50 pregnant female sandbar sharks collected from 1974-1986 with 3 additional females collected during 1990-1992 (see Colvocoresses and Musick 1989 for previous summary of data). Results similar to those reported by Colvocoresses and Musick (1989) were obtained. The relationship between maternal size and number of pups was very weak ($r^2=0.25$), with the average number of pups per litter equal to 8.4 (s.d.=2.3). Sandbar sharks produce a litter once every 2 years (Colvocoresses and Musick 1989) with a sex ratio not significantly different from 1:1. Thus, age-specific natality was fixed at 2.1 female pups per year beginning with the age of maturity.
The probable maximum age of sandbar sharks differs between the vertebrally derived von Bertalanffy growth equation (present study) and the growth equation from tag/recapture data (Casey and Natanson 1992). The latter study reported tagged sandbars 22, 32, and over 40 years old at recapture, with the 22 year old determined to be immature. Casey and Natanson suggested that sandbar sharks may live in excess of 50 years. The present vertebral age/growth study reports the oldest individual examined to be 24 years old. Based on the vertebral data it seems reasonable to consider the maximum age for sandbar sharks to be ca. 30 years. For the life history tables, 30 & 60 years were considered as maximum ages in separate trials.

The net reproductive rate ($R_0$), the generation time ($G$), and the intrinsic rate of increase of the population ($r$) were calculated (Krebs 1978).

To examine the effects of fishing mortality ($F$) on the demography of the sandbar sharks, the survivorship function was modified in several trials to include fishing mortality. Values of $F$ included 0.25, 0.20, 0.15, 0.10 and 0.05. $F = 0.25$ was the approximate level of mortality on large coastal sharks in the fishery from 1986-1991 and is the recommended $F$ for maximum sustainable yield (Anonymous 1992). Fishing mortality was simulated to begin at 8 years (age corresponding to mean carcass size in the 1986-91 fishery: Branstetter, pers. comm.; current study), 15 years, and 29
years.

Natural mortality (M) was estimated to be 0.10 following the method of Hoenig (1983). However, it has been suggested that survival of young-of-year sandbar sharks may be lower (Hoff 1990). Higher mortality on neonate and age 1 sharks would result from predation by larger sharks (Springer 1960 Branstetter 1990). Therefore, natural mortality during the first two years of life was varied in the life history tables. But, the population of large predatory sharks in coastal Virginia waters has been severely depleted (Musick et al. 1993), potentially reducing the mortality rate on juvenile sandbar sharks. Following Hoff (1990), a best-case life history table was constructed using instantaneous natural mortality equal to 0.05 (one-half of estimated M).

The effects of exploitation can be assessed from the value and sign of the intrinsic rate of increase. Based upon the outcome, an appropriate minimum size (age) and fishing level (F) for sandbar sharks may be recommended to maintain a viable, reproducing population.
Results

Using the growth model for sandbar sharks determined in this study (Chapter 1) and M=0.05, the annual survival rate of sandbar sharks is about 90% and the population will increase at almost 12% per year (Table 10). If, however, the natural mortality is higher (M=0.10) or there is increased mortality of neonates and age 1 sharks then the population increase rate ranges from 2.6%/yr to 7.1%/yr (Table 11). These rates all suggest healthy and increasing populations without fishing.

Under the growth model of Casey and Natanson (1992), which estimates age at maturity of 29 years, and with the assumption of a maximum age of 60, the population increase rates are 5.3%/yr and 0.2%/yr for natural mortalities of 0.05 and 0.10 for all ages, respectively (Table 11). When neonate and age 1 mortality is increased but natural mortality is kept at 0.05 for all ages > 1 then the population increase rate declines to 2.9%/yr (Table 11). If natural mortality at ages > 1 is 0.10 and neonate survival is only 75% then the population increase rate is negative (Table 11). Similarly, if the natural mortality of neonates is 50% and age 1 fish suffer 30% annual mortality then the population declines by 1.9%/yr (Table 11).
Table 10. Life history table for sandbar shark, *Carcharhinus plumbeus*, under very low natural mortality only, age at maturity = 15, and maximum age = 30. Column symbols are: X, age in years; l_x, survivorship (natural mortality, M = 0.05); m_x, natality (# female pups/yr); l_x*m_x, age specific reproductive rate; R_0, net reproductive rate per generation; G, generation time (years); r, intrinsic rate of population increase; %, population increase rate (%/yr).

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<tr>
<th>X</th>
<th>l_x</th>
<th>m_x</th>
<th>l_x*m_x</th>
<th>X<em>l_x</em>m_x</th>
<th>R_0</th>
<th>G</th>
<th>r</th>
<th>%</th>
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Table 11. Life history parameters for *Carcharhinus plumbeus* under two growth models (this study: age at maturity = 15, max. age = 30; Casey and Natanson (1992): age at maturity = 29, max. age = 60) with varying natural mortality only. Natality is fixed at 2.1 female pups per year. $R_0$, net reproductive rate per generation; $G$, generation time (years); $r$, intrinsic rate of population increase.

<table>
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<th>Population Increase Rate (%/yr)</th>
<th>Annual Survival</th>
<th>Age of Maturity = 15</th>
<th>Age of Maturity = 29</th>
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<td>Age 1</td>
<td>Age 2+</td>
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<td>0.75</td>
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Table 12. Life history parameters for *Carcharhinus plumbeus* under varying rates of fishing mortality and two growth models (this study: age at maturity = 15, max. age = 30, M=0.10; Casey and Natanson: age at maturity = 29, max. age = 60, M=0.05). Natality is 2.1 female pups/yr in both models. Age, age at which F starts; $R_0$, net reproductive rate per generation; G, generation time (years); r, intrinsic rate of population increase.

<table>
<thead>
<tr>
<th>Instantaneous Fishing Mortality</th>
<th>R₀</th>
<th>G</th>
<th>r</th>
<th>Rate (%)/yr</th>
</tr>
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<tr>
<td>Age of Maturity = 15</td>
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<tr>
<td>M = 0.10</td>
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<tr>
<td>8 0.25</td>
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If fishing mortality is added at the recommended level for MSY (F=0.25; Anonymous 1992), the age of maturity is 15 yr, and the age at first capture is set at 8 yr, the population would decrease by >7%/yr (Table 12). Under these ages of first maturity and first capture fishing mortality would have to be reduced to F=0.10 to maintain a growing population (Table 12). However, if fishing were delayed until a minimum size equivalent to a 15 year old sandbar shark (134 cm PCL, 148 cm FL, 178 cm TL), then the fishing mortality could remain at F = 0.25 and still support an increasing population (Table 12).

Under the conditions of the growth model of Casey and Natanson (1992) the population could increase at all levels of F up to 0.25 if fishing does not begin until age 29. However, if fishing begins at age 15 the population could increase only at very low fishing mortality rates (Table 12). Unlike results obtained using the previous growth model (age at maturity = 15 yr), the generation time was over 30 years.
Discussion

Demographic analysis utilizing life history tables is a useful tool for fishery managers to evaluate potential population changes under various conditions of fishing mortality (Hoenig and Gruber 1990). In this study, the demographic analysis indicates that if fishing mortality continues to target small sandbar sharks ca. 8 years old at the level of fishing estimated for 1986-91 (ca. F=0.25; Anonymous 1992) the population will decrease by > 7% per year. The population of sandbar sharks along the mid-Atlantic coast did decline to nearly 15% of its previous level over a 13 year span (Musick et al. 1993; Musick et al. 1994) suggesting that this demographic study may be an accurate estimate of potential population changes as a result of excessive fishing mortality.

Natural mortality is difficult to estimate directly for any fish population so I chose to use the longevity relationship of Hoenig (1983) to estimate this parameter. Additionally, following the example of Hoff (1990), I reduced the natural mortality by half to examine the 'best-case' population under the conditions of the vertebrally derived growth model. This simulation may indicate the maximum potential for population growth in the absence of
fishing mortality. The annual population increase rate of nearly 12% is modest when compared to teleost reproductive potential (Hoff 1990), but probably is not actually attainable in sandbar shark populations.

Under the parameters of the Casey and Natanson (1992) growth model the maximum age attained is assumed to be 60 yr and natural mortality is ca. 0.05. However, if natural mortality were 0.10 the life history table predicts a population increase rate of only 0.2% in the absence of any increased neonate mortality or fishing mortality (Table 11). If mortality of neonate or age 1 sharks is higher than 0.10, the life history table predicts a population decrease (Table 11). This indicates a non-viable population which would become extinct under natural predation levels. Therefore, under the assumptions of the Casey and Natanson (1992) growth model it seems reasonable to accept the lower estimate of natural mortality.

There is great uncertainty regarding age-specific natural mortality during the first two years of life when the juvenile sandbar sharks are vulnerable to predation by large coastal sharks. The trials with increased mortality during these years demonstrate their sensitivity to natural mortality estimates in the life history table. If age at maturity is 15 yr and mortality is > 0.10, the population increase rate is considerably reduced (minimum = 2.6%/yr) suggesting the population may be near equilibrium ($r = 0.0$).
under these conditions (Table 11). However, Musick et al. (1993) and Musick et al. (1994) suggest that the apparent stable abundance of juvenile sandbar sharks in the Chesapeake Bay is the result of a marked decrease in the large coastal shark population. In this case juvenile survival is probably less dependent upon predation and may be age-independent (M=0.10 for all ages). Under this natural mortality level the population increases at 6.9%/yr (Table 11).

The life history parameters generated by the two growth models using the best estimates for natural mortality suggest similar population increase potential but on two different time scales. The intrinsic rates of population increase are 0.067 and 0.050 for the growth models of the present study and Casey and Natanson (1992), but the generation times are 20.46 and 40.31 years, respectively (Table 11). The life history tables using the vertebral growth model agree well with the results of Hoff (1990), although he used an age/fecundity relationship.

The effects of fishing mortality on the intrinsic rate of increase using both growth models demonstrates the detrimental effect of exploitation on immature fish (Table 12). At fishing mortality levels > 0.10 the population will decline. The age used for these estimates (8 & 15) correspond to the mean carcass size in the 1986-91 large coastal shark fishery and is based upon the most recent data
available. At the currently estimated fishing mortality level (0.25) these populations are not viable and will eventually collapse. The recent analyses of Musick et al. (1993) and Musick et al. (1994) report that the adult coastal stock has already been reduced to only 15% of its abundance in 1980-81. Clearly the sandbar shark, with slow growth and low net reproductive rate, cannot withstand even low fishing mortality on immature individuals.

This demographic analysis of sandbar sharks provides life history information to determine acceptable levels of exploitation. If the current fishery management plan recommendation of F=0.25 for MSY (Anonymous 1992) is implemented in an unrestricted fishery, the sandbar shark population will not recover. This level of fishing would be acceptable for a healthy population if a minimum size limit of 134 cm precaudal length or ca. 20 kg carcass weight (size at first maturity) were imposed and juvenile survival remains high. But, with the current severe depletion of the sandbar shark population of the western Atlantic, far more restrictive fishing mortality levels should be implemented to allow the population to rebuild itself at a faster rate. Such a conservative approach would also provide a buffer against natural perturbations during the crucial recovery phase.
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Appendix

A REVIEW OF BACK-CALCULATION METHODS
Discussion

In a review of back-calculation of fish lengths, Francis (1990) focuses on the hypotheses behind proportional methods and the proper and improper use of two regressions that are inherent in the use of the back-calculation formulas (BCF). These two basic regressions relate scale size to fish length (In his discussion scale was used to denote any hard part used in ageing fish; in this review the terminology will follow the original author's, where feasible). The most common form of the relationships between scale size (S) and length (L) is linear, and the regression equations are:

\[ S = a + bL, \quad (1) \]

\[ L = c + dS \quad (2) \]

for the regressions of S on L and L on S, respectively.

Whitney and Carlander (1956) first stated the two hypotheses as: "if the scale were 10% larger when the fish was caught than the average scale for that size of fish, the scale would be 10% larger than normal throughout the life", and "if a fish at time of capture were 10% smaller than the average fish with that size of scale, the fish would be 10% smaller than the expected length for the size of that scale throughout life". Francis (1990) calls these two hypotheses
the scale proportional (SPH) and the body proportional (BPH) hypotheses, respectively. He then reviews in detail the application, if any, of SPH and BPH to previously reported back-calculation theories and BCF's, supporting or refuting those methods he asserts to be proper approximating tools.

The Dahl-Lea direct proportion method (Lea 1910) assumes the scale grows at the same proportional rate as the fish and the BCF is:

\[ L_i = \frac{(S_i / S_c)}{L_c} \]  
(3)

where: \( L_i \) is the length at age \( i \), \( L_c \) is the length at capture, \( S_i \) is the distance from the focus to the annual mark \( i \) on the scale, \( S_c \) is the scale radius at capture. This equation will pass through the origin.

The Fraser-Lee method proposes "that the growth increment of the scale is, on the average ..., a constant proportion of the growth increment of the fish" (Lee 1920). The BCF is:

\[ L_i = c + \left[ \frac{(L_c - c)}{S_c} \right] * S_i \]  
(4)

where: \( L_i \) is the calculated fish length at age \( i \), \( L_c \) is the measured fish length at capture, \( S_i \) is the distance from the focus to annual mark \( i \) on the scale, \( S_c \) is the scale radius at capture, and \( c \) is a constant originally intended to be the length of the fish at the time of scale formation (Lee 1920) but commonly used as the \( L \)-intercept of the regression of length on scale (equation 2).

Hile's (1941) assumption was "that the percentage or
relative deviation of the ... radius of any single scale from the theoretical ... radius is constant at the time of formation of all annuli". Francis (1990) points out two problems with applying this theory to practical BCFs. First, "and at the time of capture" must be added to extend the model equation to:

\[ \frac{h(L_1)}{S_1} = \frac{h(L_2)}{S_2} = \cdots = \frac{h(L_n)}{S_n} = \frac{h(L_c)}{S_c} \]

where: \( h(L_i) \) is the "theoretical scale radius" at length \( L_i \) (Hile 1941). Secondly, the "theoretical scale radius" is not defined by Hile. Francis (1990) interprets \( h(L) \) as the mean scale radius for fish of length \( L \), derived from the regression of \( S \) on \( L \) (equation 1). When the length:scale relationship is linear this first interpretation (referred to as Hile\(_1\)) results in the BCF:

\[ L_1 = -\left(\frac{a}{b}\right) + \left[ \frac{(L_c + a/b)}{S_c} \right] * S_1 \]  \hspace{1cm} (5)

where \( a \) and \( b \) are from equation 1. This equation is the same as the Fraser-Lee except \( c \) is replaced by \( -(a/b) \), the \( L \)-intercept of the regression of \( S \) on \( L \), and this intercept will always be less than \( c \) (Francis 1990). Therefore, back-calculations from Hile\(_1\) will always be lower than those from the Fraser-Lee method.

The alternative interpretation of Hile's hypothesis, Hile\(_2\), is derived from the regression of \( L \) on \( S \) and defines the "theoretical scale radius" for a fish of length \( L \) as such that the mean length of all fish with scales of that radius is \( L \) (Francis 1990). When the length:scale
relationship is linear the resultant BCF is the Fraser-Lee equation (4).

In reviewing the hypotheses of Whitney and Carlander (1956) Francis (1990) showed that the SPH and BPH, unlike the hypotheses of Lee (1920) and Hile (1941), may be translated into BCFs without further assumptions being made. When the length:scale relationship is linear the SPH equation is the same as Hile, which was a modification of Hile's original hypothesis (Francis 1990). The BPH was a new hypothesis and, in the linear case, Francis (1990) translates it to the BCF:

$$L_i = \frac{(c + dS_i)/(c + dS)}{1} * L_c$$

where c and d are from the regression of L on S (equation 2).

Francis (1990) then explained that the Dahl-Lea method is just a special case of the linear forms of the two hypotheses: Hile (5) if a = 0, and the BPH equation (6) if c = 0. He agreed with Whitney and Carlander (1956) that the Fraser-Lee BCF is according to neither of these two hypotheses, but would follow SPH if c were the L-intercept of S on L rather than L on S ((1) rather than (2)). However, he found the conclusions of Whitney and Carlander (1956) to be "confusing and unconvincing" and this author must concur. Francis (1990) did not agree with the assessment (reiterated by Carlander 1981) that when a linear regression is used, BPH produces the same back-calculated
lengths as the Fraser-Lee. He asserted that when a comparison of the Fraser-Lee BCF and the BPH BCF is made that fact becomes clear.

The alternative to proportional methods of back-calculating lengths at previous ages is the "regression" method. The BCF is:

\[ L_i = h(S_i) \]  

(7)

where the length:scale relationship is described by the equation \( L = h(S) \) for some function \( h \). Francis (1990) rejected the use of this method based on the loss of information by ignoring the size at capture of both the fish and the scale. Whitney and Carlander (1956) compared back-calculated lengths from a number of scales from the same fish calculated by the Fraser-Lee method and the regression method and found lower variability in the estimates from the former technique. Francis (1990) proposed that this lower variability may be a measure of the lost information. Carlander (1981) cautioned on the use of the regression method, "a new method ... introduced without evaluation ... and evidently without recognition that it is different from the traditional methods", for direct back-calculations. As Lagler (1956) warned, the various regressions should not be used for predictive purposes. They describe a relationship between scale size and body size for an average fish, but do not account for individual variation. The variance of lengths estimated from the regression line increases as the
distance from the mean value on the regression increases (Carlander 1981). Further, Carlander (1981) cautioned that in some fish the back-calculated length at the last annulus may be larger than the length at capture. He suggested that because of the ease in calculating regressions with modern computers inadequate samples (from the population) may be used resulting in erroneous calculated lengths. Carlander (1981) advocated the use of traditional proportion methods of back-calculation, either the Fraser-Lee or the Dahl-Lea.

Following the review and rejection of the regression backcalculation method, Francis (1990) then discussed which length:scale regression (L on S or S on L) to use when applying either the SPH or BPH models. He concluded that the choice of which hypothesis will be followed will determine which length:scale regression to use. If SPH is chosen then the S on L regression is appropriate and will not result in bias. For BPH the L on S regression should be used but the sample may need to be modified to insure that for the smallest and largest scale sizes used the full range of body sizes is included.

In his final discussion, Francis (1990) recommended 3 points to be followed in back-calculating fish lengths from scales. First, use only BCFs which follow either SPH or BPH. In particular, when the length:scale relationship is linear, Fraser-Lee should be rejected in favor of the Hile, equation or the BPH equation. Secondly, it was recommended
that both the SPH and BPH be used for each fish population and the difference in back-calculations be used as a measure of the imprecision of back-calculation. And thirdly, comparison of back-calculations with observed lengths should be used not only to validate the back-calculations, but also to assess which method, BPH or SPH, produces more accurate results.

Ricker (1992) also recommended the use of proportional back-calculation methods. He additionally showed that the point of origin of the back-calculation should be determined biologically or be located on a central axis that is symmetrical with respect to fish length and scale radius, computed from a sample that is symmetrical transversely to that axis when plotted with an absolute slope of 45°. Key components of Ricker's (1992) method are the symmetrical sample and the range of lengths and scale sizes in the sample. He suggested use of the Fraser-Lee equation with the fixed parameter estimated from the symmetrical regression line.

Campana (1990) presented a compelling argument that refutes the accuracy of the Fraser-Lee equation. He explained that while this proportional method assumes that any deviation of an individual measurement from the overall fish length:otolith regression will be observed proportionally at back-calculated lengths, it will consistently underestimate previous lengths at age if the
fish length: otolith size ratio varies systematically with somatic growth rate as recent studies have demonstrated (reviewed in Campana 1990). Campana (1990) proposed the use of a biologically derived intercept, \( c \) in the Fraser-Lee equation, in a modification of that equation:

\[
L_a = L_c + [(O_a - O_c)*(L_c - L_0)/(O_c - O_0)]
\]  

where: the biological intercept is at fish length = \( L_0 \) and otolith radius = \( O_0 \). He defined the biological intercept as the fish and otolith size at which proportionality of fish and otolith growth is initiated. Using a cohort simulation model he showed that his equation produced more accurate back-calculated lengths than did the Fraser-Lee (maximum error Campana = 42% vs. Fraser-Lee = 159% at lower limit of data) and further, that the error associated with the Fraser-Lee method continued to increase as the back-calculations approached the intercept (date of hatch in his simulation) whereas error associated with his model decreased to 0 as the intercept was approached (Fig. 7; Campana 1990). For elasmobranchs, it may be useful to use the birth mark on the vertebrae as the biological intercept since birth size may have a relatively narrow range and can be verified by measurements from recent neonates and full-term pups.
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