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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. Sandbar shark demographic analyses, using known and estimated life history parameters, including fishing mortality (F) at ages and levels estimated in a recent stock assessment, were used to estimate potential population growth and exploitation. Life history tables were constructed by using best estimates of natural mortality (M) of 0.11 or 0.07 for maximum ages of 30 or 60 yr, respectively. Natality was fixed at 2.1 female pups/yr. Fishing mortality ($F=0.05, 0.10, 0.15, 0.20, \text{ or } 0.25$) was simulated to begin at age 8, 10, 15, 20, or 29. The annual population growth rate was highest under a "best-case" scenario of $M=0.05$ ($1/2$ best estimate) and maximum age of 30 yr, but was only 11.9%/yr. At $M=0.11$ for all ages, the population increase rate was 6.4%/yr, and the generation time was about 20 years. At higher juvenile mortality rates, the population growth rate decreased to 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, respectively. It is apparent that sandbar shark populations will decline under any substantial fishing mortality on immature ages and that mature fish can be exploited only at very low levels.

Demographic analysis of the sandbar shark, *Carcharhinus plumbeus*, in the western North Atlantic*

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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 20% of the large-shark fauna of the U.S. east coast and is an important component of recreational and commercial fisheries (Hoff, 1990; Musick et al., 1993; Anonymous¹). Age and growth (Casey et al., 1985; Casey and Natanson, 1992; Sminkey and Musick, 1995), seasonal distribution (Bigelow and Schroeder, 1948; Springer, 1960; Musick et al., 1993), and reproductive biology (Colvocoresses and Musick²) 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 to 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 and growth studies (Casey and Natanson, 1992; Sminkey and Musick, 1995), and a reexamination of fecundity data presented in

Colvocoresses and Musick² have provided updated parameters necessary for a demographic analysis of the sandbar shark. This analysis uses estimates of longevity, age-specific survival, and age-specific natality to construct a life history table which generates estimates of the net reproductive rate per generation, the generation time, and the intrinsic rate of increase of the population (Krebs, 1985). These parameters are useful for management purposes and for input into population models (Krebs, 1985; Hoenig and Gruber, 1990). The objective of this study is to provide an updated demographic analysis of the sandbar shark by estimating population parameters under varying conditions of natural mortality and fishing mortality (i.e. mortality caused by fishing).

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¹ Anonymous. 1992. Fishery management plan for sharks of the Atlantic Ocean. U.S. Dep. Commer., NMFS, NOAA, 10 December 1992.

² Colvocoresses, J. A., and J. A. Musick. 1989. Reproductive biology of the sandbar shark, *Carcharhinus plumbeus*, in the Chesapeake Bight. Abstract, 69th annual meeting, Am. Soc. Ichthyology and Herp.: 17–23 June 1989, San Francisco, CA.

Materials and methods

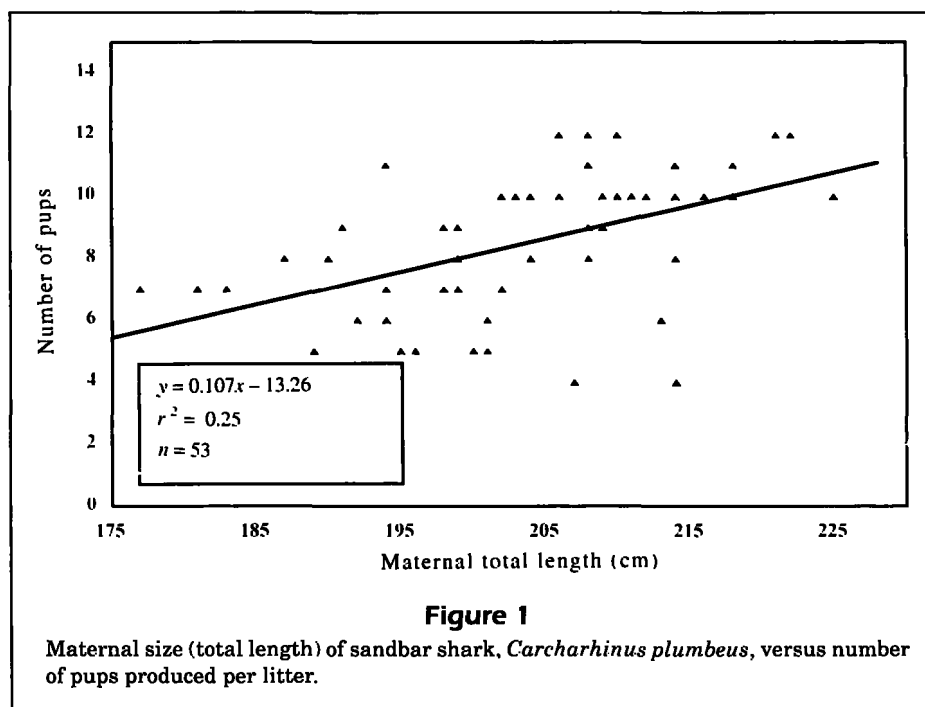
Based on size at maturity (Springer, 1960; Sminkey, 1994) and von Bertalanffy growth equations for sandbar sharks determined by Sminkey and Musick (1995), age at 100% maturity was determined to be 15 years. Casey and Natanson (1992) determined age at maturity to be ca. 29 years on the basis of a von Bertalanffy growth equation derived from tag and recapture information and a similar size at maturity. For this demographic analysis, 15 and 29 years therefore were used in separate trials as conservative estimates of the age at which 100% of females were mature.

The age-specific natality was determined from a reexamination of the data from 50 pregnant sandbar sharks collected from 1974 to 1986 (Colvocoresses and Musick²) and from 3 additional females collected during 1990–92. Results similar to those reported by Colvocoresses and Musick² were obtained. The relationship between maternal size and number of pups was very weak (Fig. 1; $r^2=0.25$), with the average number of pups per litter equal to 8.4 ($n=53$, $SD=2.3$). Sandbar sharks produce a litter once every 2 years (Branstetter³; Musick, unpubl. data) 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 age of maturity.

³ Branstetter, S. 1994. Gulf and South Atlantic Fisheries Development Foundation, Tampa, FL 33609. Personal commun.

The probable maximum age for sandbar sharks differs between the von Bertalanffy growth equation derived from vertebral data (Sminkey and Musick, 1995) and the growth equation from tag and recapture data (Casey and Natanson, 1992). The latter study reported tagged sandbars estimated to be 22 (155 cm fork length, FL), 32 (157 cm FL), and over 40 years old (185 cm FL) at recapture; the 22-year-old was determined to be immature. The first 2 of these ages were estimated on the basis of length at release, a vertebrally derived growth equation (sexes combined) of Casey and Natanson (1992), and on time at liberty. Regarding the 40+ year old shark, Casey and Natanson (1992) stated "since length at first maturity is 150 cm FL, it is reasonable to assume that this individual was over 30 yr old at tagging and over 40 yr at recapture." Casey and Natanson (1992) then suggested that sandbar sharks may live in excess of 50 years. Sminkey and Musick (1995) reported that the oldest individual examined (175 cm FL) was 24 years old (determined by vertebral counts). On the basis of vertebral data of Sminkey and Musick (1995), it seems reasonable to consider the maximum age for sandbar sharks to be about 30 years. For the life history tables, 30 and 60 years were considered as maximum ages in separate trials.

To examine the effects of fishing mortality (F) on the demography of the sandbar shark, 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 to 1991 and is the recommended F for maximum sustainable yield (Anonymous¹). The mean carcass size of all large coastal sharks in the 1986–91 fishery was approximately 24 lb (Anonymous¹), but the mean carcass size landed for sandbar sharks only was approximately 40 lb (Branstetter³). Based on two sandbar shark growth models, 24 and 40 lb correspond to ages 8 and 12 years, respectively (Sminkey and Musick, 1995; Musick, unpubl. data) or 15 and 24 years, respectively (Casey and Natanson, 1992). Considering that a mean is a measure of central tendency, then nearly 50% of the catch was younger than these ages. Therefore, fishing mortality was simulated to begin at 8, 10, 15, 20, and 29 years, which are conservative estimates based on mean carcass sizes.

Annual survival including natural mortality was estimated to be only 0.90 (max. age=30) and 0.93 (max. age=60) following the method of Hoenig (1983), which related maximum age attained to instantaneous total mortality rate (Z). If the maximum age attained was estimated from unexploited or lightly exploited stocks, Z approximates the instantaneous natural mortality rate (M). However, it has been suggested that survival of young-of-year sandbar sharks may be lower (Hoff, 1990). Increased mortality on neonate and age-1 sharks would primarily 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 with survival equal to 0.95 (one-half of estimated mortality rate).

The net reproductive rate (R_0), the generation time (G), and the intrinsic rate of increase of the population (r) were calculated (Krebs, 1985) for each trial.

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 mortality level (F) for sandbar sharks may be recommended to maintain a viable, reproducing population.

Results

Using the growth model for sandbar sharks calculated by Sminkey and Musick (1995) and the best estimate of annual survival rate (0.90) with no in-

creased juvenile mortality, the population will increase at 6.4% per year (Table 1). If natural mortality were lower ("best-case" scenario, survival=0.95), the population could increase at a rate of nearly 12%/yr (Table 2). If there was increased mortality of neonates and age-1 sharks, the population increase rate would range from 2.1%/yr to 7.2%/yr (Table 2). These rates all suggest healthy and increasing populations without fishing. Population replacement ($r=0.0$) was attained with annual survival rates of 0.70 for neonates and 0.85 for age 0+ fish, and 0.50, 0.70, and 0.88 for ages 0, 1, and 1+, respectively (Table 2). Any greater mortality would lead to population declines.

If age at maturity and maximum age are set at 29 and 60 years, respectively, and annual survival is 0.93, the population increase rate will be 3.5%/yr (Table 2). If natural mortality is 0.1 for all ages (annual survival=0.9), the population will decrease at 0.1%/yr (Table 2). With decreased juvenile survival (0.70 for age 0, and 0.50 and 0.70 for ages 0 and 1), the population increase rates are only 2.7% and 1.1%/yr, respectively (Table 2). With similar juvenile mortality rates, population equilibrium is obtained when postjuvenile survival is 0.91 and 0.92 (Table 2).

When fishing mortality is added at the recommended level for maximum sustainable yield [MSY] ($F=0.25$; Anonymous¹), age of maturity is fixed at 15 years, and age at first capture is set at 8 years, the population would decrease by >7%/yr (Table 3). Assuming these ages of first maturity and first capture, we conclude that fishing mortality would have to be reduced to $F=0.10$ to maintain a growing population (Table 3). If a minimum-size limit equivalent to a 15-year-old sandbar shark (135 cm precaudal length, 148 cm fork length, or 178 cm total length) were imposed, fishing mortality could remain at $F=0.25$ and still support an increasing population (Table 3). However, population doubling time ($= \ln(2)/r$) would be about 33 years.

Under an age of maturity of 29 years and a maximum age of 60 years, the population increases at all levels of F up to 0.25, if fishing does not begin until age 29. Population doubling time, however, would increase dramatically as F increased, ranging from 27.7 years if $F=0.05$ to 693 years if $F=0.25$. If fishing begins before age 29, the population could increase only at very low fishing mortality rates (Table 3). The generation time (G) is the period between the birth of the parents and the birth of the offspring. When offspring are produced over a period of time, G is the mean period between the parent's birth and the birth of each offspring. As fishing mortality increases, survival of parents decreases, leading to fewer offspring later in life, therefore G decreases. This result does not suggest more rapid population replacement.

Table 1

Life history table for sandbar shark, *Carcharhinus plumbeus*, using best estimate of natural mortality only, no increased juvenile natural mortality, age at maturity = 15, and maximum age = 30. Column symbols are as follows: X = age in years; l_x = survivorship (annual survival = 90%); m_x = natality (no. of female pups/yr); $X \times l_x \times m_x$ = age-specific reproductive rate; R_0 , net = reproductive rate per generation; G = generation time (yr); r = intrinsic rate of population increase; and % = population increase rate (%/yr).

X	l_x	m_x	$l_x \times m_x$	$X \times l_x \times m_x$	R_0	G	r	%
0	1.00				3.54	20.37	0.062	6.4
1	0.90							
2	0.81							
3	0.73							
4	0.66							
5	0.59							
6	0.53							
7	0.48							
8	0.43							
9	0.39							
10	0.35							
11	0.31							
12	0.28							
13	0.25							
14	0.23							
15	0.21	2.1	0.43	6.51				
16	0.19	2.1	0.39	6.25				
17	0.17	2.1	0.35	5.98				
18	0.15	2.1	0.32	5.70				
19	0.14	2.1	0.28	5.41				
20	0.12	2.1	0.26	5.13				
21	0.11	2.1	0.23	4.85				
22	0.10	2.1	0.21	4.57				
23	0.09	2.1	0.19	4.30				
24	0.08	2.1	0.17	4.04				
25	0.07	2.1	0.15	3.79				
26	0.07	2.1	0.14	3.55				
27	0.06	2.1	0.12	3.32				
28	0.05	2.1	0.11	3.10				
29	0.05	2.1	0.10	2.89				
30	0.04	2.1	0.09	2.69				

Discussion

Demographic analysis using 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 analyses indicate that if fishing mortality continues to target small sandbar sharks, beginning with 8-year-old sharks, at the level of fishing estimated for 1986–91 ($F=0.25$; Anonymous¹), the population will decrease by >7% per year. The population of sandbar sharks along the mid-Atlantic coast declined to about 15% of its previous level over a 13-year span (Musick et al., 1993; Musick et al.⁴), suggesting that this demographic study may be an accurate estimate of potential population changes as a result of excessive fishing mortality. The potential population increase rates reflect an evolu-

tionary strategy not well adapted to sudden and severe population depletions, particularly if applied to many age classes simultaneously or persisting over several years.

Natural mortality is difficult to estimate directly for any fish population; therefore we chose to use the longevity relationship of Hoenig (1983) to estimate this parameter. Additionally, following the example of Hoff (1990), we 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 poten-

⁴ Musick, J. A., E. Branstetter, and T. R. Sminkey. 1994. Trends in shark abundance from 1974 to 1993 for the Chesapeake Bight region of the U.S. mid-Atlantic coast. Contrib. SB-19, Shark evaluation workshop, 14–18 March 1994, Southeast Fisheries Science Center, Natl. Mar. Fish. Serv., Miami, FL 33149, 16 p.

Table 2

Life history parameters for sandbar shark, *Carcharhinus plumbeus*, under two growth models (Sminkey and Musick [1995]: age at maturity = 15, max. age = 30; and Casey and Natanson [1992]: age at maturity = 29, max. age = 60) with varying natural mortality only. Natality is 2.1 female pups/yr. R_0 = net reproductive rate per generation; G = generation time (yr); and r = intrinsic rate of population increase. Negative values are in bold.

Annual survival (%/yr)			R_0	G	r	Population increase rate
Age 0	Age 1	Age 2+				
Age at maturity = 15						
0.70	0.90	0.90	2.76	20.37	0.050	5.1
0.50	0.70	0.90	1.53	20.37	0.021	2.1
0.70	0.85	0.85	1.00	19.44	0.000	0.0
0.50	0.70	0.88	1.00	19.95	0.000	0.0
0.95	0.95	0.95	11.20	21.45	0.113	11.9
0.50	0.70	0.95	5.01	23.16	0.070	7.2
Age at maturity = 29						
0.93	0.93	0.93	3.79	39.05	0.034	3.5
0.90	0.90	0.90	0.97	36.88	-0.001	-0.1
0.70	0.93	0.93	2.84	39.05	0.027	2.7
0.50	0.70	0.93	1.52	39.05	0.011	1.1
0.50	0.70	0.92	1.00	38.28	0.000	0.0
0.75	0.91	0.91	1.00	37.20	0.000	0.0

tial for population growth in the absence of fishing mortality. The annual population increase rate of nearly 12% is modest when compared with teleost reproductive potential (Hoff, 1990) and probably is not actually attainable in sandbar shark populations.

The Casey and Natanson (1992) growth model assumes the maximum age attained is 60 years, resulting in an estimate of $M = 0.07$. However, if natural mortality was 0.10, the life history table predicts a population decrease rate of 0.1% in the absence of any increased neonate mortality or fishing mortality (Table 2). This indicates a nonviable population under natural mortality levels, particularly if neonate and juvenile mortality were higher. Therefore, if sandbar sharks are assumed to grow according to this 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 juvenile sandbar sharks are vulnerable to predation by large coastal sharks. The trials with increased mortality during these years demonstrate the sensitivity to natural mortality estimates in the life history table. If age at maturity is 15 years and mortality is >0.10, the population increase rate is considerably reduced (2.1%–5.1%/yr), suggesting that

Table 3

Life history parameters for sandbar shark, *Carcharhinus plumbeus*, under varying rates of fishing mortality and two growth models (Sminkey and Musick [1995]: age at maturity = 15, max. age = 30; and Casey and Natanson [1992]: age at maturity = 29, max. age = 60). Natality is 2.1 female pups/yr in both models. Age_i = age at which F starts; R_0 = net reproductive rate per generation; G = generation time (yr); r = intrinsic rate of population increase. Negative values are in bold.

Age_i	Instantaneous fishing mortality		R_0	G	r	Population increase rate (%/yr)
	F					
Age at maturity = 15						
Annual survival = 0.90						
8	0.25	0.25	17.29	-0.080	-7.7	
8	0.20	0.40	17.68	-0.051	-5.0	
8	0.15	0.66	18.17	-0.023	-2.2	
8	0.10	1.12	18.77	0.006	0.6	
8	0.05	1.95	19.50	0.034	3.5	
10	0.25	0.42	17.29	-0.051	-5.0	
10	0.20	0.60	17.68	-0.029	-2.8	
10	0.15	0.90	18.17	-0.006	-0.6	
10	0.10	1.37	18.77	0.017	1.7	
10	0.05	2.16	19.50	0.039	4.0	
15	0.25	1.45	17.29	0.021	2.2	
15	0.20	1.64	17.68	0.028	2.8	
15	0.15	1.90	18.17	0.035	3.6	
15	0.10	2.26	18.77	0.043	4.4	
15	0.05	2.77	19.50	0.052	5.4	
Age of maturity = 29						
Annual survival = 0.93						
15	0.25	0.03	31.66	-0.109	-10.4	
15	0.20	0.07	32.23	-0.081	-7.8	
15	0.15	0.18	33.06	-0.052	-5.1	
15	0.10	0.45	34.29	-0.023	-2.3	
15	0.05	1.23	36.19	0.006	0.6	
20	0.25	0.11	31.66	-0.070	-6.8	
20	0.20	0.20	32.23	-0.050	-4.9	
20	0.15	0.37	33.06	-0.030	-2.9	
20	0.10	0.74	34.29	-0.009	-0.9	
20	0.05	1.58	36.19	0.013	1.3	
29	0.25	1.04	31.66	0.001	0.1	
29	0.20	1.20	32.23	0.006	0.6	
29	0.15	1.44	33.06	0.011	1.1	
29	0.10	1.82	34.29	0.017	1.8	
29	0.05	2.47	36.19	0.025	2.5	

the population may be near equilibrium ($r=0.0$) under these conditions (Table 2). However, Musick et al. (1993) and Musick et al.⁴ 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). Assuming this natural mortality level, the population increases at 6.4%/yr (Table 1).

The life history parameters generated by the two growth models with the best estimates for natural mortality, suggest similar population increase potential but on two different time scales. The intrinsic rates of population increase are 0.062 and 0.034 for the growth models of Sminkey and Musick (1995) and Casey and Natanson (1992), but the generation times are 20.37 and 39.05 years, respectively, and population doubling times are 11.2 and 20.4 years, respectively. The life history tables with 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 with both growth models demonstrate the detrimental effect of exploitation on immature fish (Table 3). At fishing mortality levels >0.10 , the population will decline. The ages used for these estimates (8 and 15) correspond to the mean carcass size in the 1986–91 large coastal shark fishery and are 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.⁴ report that the adult coastal stock has already been reduced to only 15% of its abundance in 1980–81. Clearly the sandbar shark, with a slow growth and low net reproductive rate typical of most elasmobranchs, cannot withstand even a low rate of fishing mortality on immature individuals.

Cailliet (1992) used demographic analyses to examine population growth in the leopard shark, *Triakis semifasciata*, including fishing mortality to begin at several ages. The population would replace itself ($r=0$) if fishing began at age 4 at the estimated rate ($F=0.084$) and would slowly increase (0.4–6.4%/yr) if fishing did not begin until later ages (5, 10, 15, 21 years). However, it was demonstrated that if fishing mortality doubled ($F=0.168$), the age at which F starts must be >12 to produce a growing population. Although females first mature at age 17, Cailliet (1992) concluded that a size limit of 110 cm TL (approximately 13 years) would ensure population replacement at this moderately low fishing level.

A demographic analysis of the Pacific angel shark, *Squatina californica*, examined the effects of low fishing mortality rates ($F=0.05, 0.10, 0.20, 0.22$) simulated to begin at age 10 yr (Cailliet et al., 1992). This age was the estimated age of entry into the fishery as well as the approximate age of first maturity.

Cailliet et al. (1992) concluded that the population would grow very slowly (0.4%/yr) at $F=0.20$, would decrease at higher F , and that a size limit above the size of first maturity should be imposed in the absence of better estimates of natural and fishing mortality.

Demographic analyses of the Atlantic sharpnose shark, *Rhizoprionodon terranovae*, classified as a "small coastal" species in the Fishery Management Plan (FMP) for sharks of the Atlantic Ocean, indicated that, in the absence of fishing mortality, the population would increase by only about 4.5%/yr (Cortés, 1995). This best estimate is considerably below the rate derived for "small coastal" sharks of the Atlantic Ocean ($e^r=1.91$; 91%/yr) (Parrack⁵). Furthermore, if fishing mortality continues at the estimated rate for 1986–90 ($F=0.43$) (Anonymous¹), a size limit of about 97 cm TL (nearly 6 years old) would have to be imposed just to allow population replacement (Cortés, 1995). Cortés (1995) demonstrates that extreme modification of the reproductive and survival parameters was required to attain the population increase rate derived by Parrack⁵ and concluded that management of the Atlantic sharpnose under the FMP was based on unrealistic biological parameters.

This demographic analysis of sandbar sharks provides additional life history information on acceptable levels of exploitation. If the current FMP recommendation of $F=0.25$ for MSY (Anonymous¹) 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 135 cm precaudal length or about 23 kg carcass weight (size at first maturity) were imposed and juvenile survival remained high. But, with the current severe depletion of the sandbar shark population of the western North Atlantic, far more restrictive fishing mortality levels must be implemented to allow the population to rebuild itself. Such a conservative approach would also provide a buffer against natural perturbations during the crucial recovery phase.

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⁵ Parrack, M. L. 1990. A preliminary study of shark exploitation during 1986–1989 in the U.S. FCZ. Contrib. MIA-90-493, Southeast Fisheries Science Center, Natl. Mar. Fish. Serv., Miami, FL 33149, 23 p.

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