Demographic analysis of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, in the Gulf of Mexico

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Abstract.—The Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, is a small coastal species caught in recreational fisheries and as bycatch in the shrimp trawl and longline fisheries in the Gulf of Mexico. Demographic analyses incorporating the best available information on validated age and growth, age at maturity (t_{mat}), maximum age (t_{max}), reproductive habits, and age-specific natural mortality and fecundity were performed. An initial set of three life history tables based on input parameters t_{mat}=4, t_{max}=10, constant age 1+ survivorship (S=0.657), and varying first year survivorship (S_0=0.432, scenario 1; S_0=0.512, scenario 2; S_0=0.657, scenario 3 or best case scenario) yielded net reproductive rates (R_0) ranging from 0.844 to 1.284, a generation length (G) of 5.8 years, and instantaneous rates of population change (r) ranging from –0.029 to 0.044. Further simulations were performed to test the sensitivity of the computed demographic parameter values to modifications in various input biological parameter values (scenarios 4 through 14). Overall, manipulations of biological parameters m_x, t_{mat}, and t_{max} caused large variations in demographic parameters r, $t_{\times 2}$, and R_0, while G remained relatively stable. All the demographic parameters proved more sensitive to changes in S than to changes in S_0. The initial set of analyses (scenarios 1 through 3) was then rerun with the estimated mean fishing mortality from 1986 to 1989 (F=0.428) added to natural mortality. Age 6+ sharks can enter the fishery under the best case scenario only to allow the population to replace itself. Ages at first capture (A_{rep}) with F=0.428 that would allow full population replacement were also calculated for scenarios 4 through 14. This study indicates that management of *R. terraenovae* under the Federal Management Plan (FMP) for sharks of the Atlantic Ocean is based on unrealistic biological characteristics for this species.

Manuscript accepted 31 May 1994.
Fishery Bulletin 93:57–66 (1995).

The Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, is an abundant coastal carcharhinid species found in shelf waters of the western North Atlantic and Gulf of Mexico (Compagno, 1984), reported to reach a maximum size of approximately 110 cm total length (Compagno, 1984). Although not targeted by any U.S. commercial fisheries, in the Gulf of Mexico it is caught in recreational fisheries and discarded as bycatch in the shrimp trawl fishery (NMFS, 1993) and shark and reef fish longline fisheries (person. obs.). However, age at first entry in the various fisheries is unknown. *R. terraenovae* is grouped under the "small coastal" species category in the Federal Management Plan (FMP) for sharks of the Atlantic Ocean, which determined that this species group was not overfished, based on a stock assessment resulting in an estimate of finite rate of population increase (e^r) of 1.91. Thus, no quotas or size limits exist for this species despite its importance in several fisheries.

Biological and life history characteristics of *R. terraenovae* in the Gulf of Mexico are now well documented (Parsons, 1983, 1985; Branstetter, 1986, 1987). However, this information has not yet been applied to analyses of the population dynamics of this species, nor have the results of such analyses been published. Furthermore, as is the case with most shark species, sufficient information necessary for stock assessment is lacking (Hoff, 1990). Because long-term records of catch and effort or the age composition by species are not available, traditional surplus production models or more elaborate age-structured methods of stock assessment have seldom been used for sharks. Owing to the paucity of fisheries data, several investigators have used demographic analysis to gain insight into the population dynamics and exploitation rates of shark resources. This type of analysis has been utilized to construct life history tables or Leslie matrices (Caughley, 1977; Krebs, 1985), which are summaries of age-specific mortality and fertility rates operating on a population with the assumption of a stable age distribution. This technique allows estimation of parameters important to the dynamics of any given population. Thus, Hoenig and Gruber (1990), Cailliet (1992), and Cailliet et al. (1992) produced estimates of population dynamics by applying a demographic analysis of the lemon shark, *Negaprion brevirostris*, the leopard shark, *Triakis semifasciata*, and the angel shark, *Squatina californica*, respectively. Hoff (1990), in addition, estimated maximum sustainable yield for the sandbar shark, *Carcharhinus plumbeus*, in a modified stock production model incorporating life history information.

This study was prompted by the existence of validated age and growth data (Branstetter and McEachran, 1986) and reproductive information (Parsons, 1983) on *R. terraenovae*, which provided several important parameters needed for construction of a life history table, i.e. lifespan, fecundity, and age at maturity.

The purpose of this study was 1) to produce, using the life history table approach and the best biological information available, reliable estimates of demographic parameters for *R. terraenovae* in the Gulf of Mexico, 2) to assess the sensitivity of the computed demographic parameters of the population to a variety of biological (input) parameter manipulations and harvest scenarios, and 3) to compare the resultant rates of population increase with that calculated for the "small coastal" shark group in the FMP for sharks of the Atlantic Ocean and to evaluate the biological basis of the stock assessment on which present management measures are based.

Materials and methods

Life history tables incorporating the best biological information available on *R. terraenovae* in the Gulf of Mexico were constructed. Maximum age (lifespan or longevity; t_{max}) has been estimated to be 8 to 10 years (Branstetter, 1987), and age at maturity (t_{mat}) for females has been estimated at 4 years (Branstetter, 1987), and from 2.4 to 3.9 years (Parsons, 1985). For this study, it was assumed that all females reproduced after reaching maturity. Parsons (1983) reported that parturition was annual, gestation period was 10 to 11 months, and sex ratios at birth were 1:1. He also found a significant relationship between total length of gravid females and number of offspring. Fecundity at size was calculated from the regression equation $Y = -8.4109 + 0.1396X$ (r=0.50, P<0.001, n=78; Parsons[1]), where X is female total length and Y is number of offspring. Female length at age was obtained from the von Bertalanffy growth function for both sexes combined derived by Branstetter (1987): $L_t = L_\infty (1-e^{-K(t-t_0)})$, where K=0.359, L_∞=108, and t_0=–0.985. Number of offspring was further divided by two, because the natality function (m_x) at age represents the number of female offspring per female parent and sex ratios at birth are 1:1 and parturition is annual (Parsons, 1983). Reports of unusually large litter sizes in tropical populations of *R. terraenovae* were also incorporated in some of the analyses that follow by doubling fecundity at age (m_x).

[1] Parsons, G. Univ. Mississippi, MI 38677. Personal commun., 1993.

The instantaneous natural mortality rate (M) was calculated from Hoenig's (1983) equation relating maximum age to total mortality rate, derived from data pertaining to unexploited or lightly exploited stocks. A value of 0.42 for Z (instantaneous total mortality rate) was derived from the regression equation $\ln(Z) = 1.46 - 1.01 \ln(t_{max})$, where t_{max} is longevity in years. Assuming that maximum age was determined from a time when there was no fishing directed at this species, Z can be approximated to M. The proportion of survivors at the start of each age interval (x) was $l_x = N_0(e^{-Mx})$, where N_0 is the number of individuals at time 0.

Demographic parameters were computed following methodology by Krebs (1985) and included R_0 (net reproductive rate per generation), G (generation length in years), and r (intrinsic rate of population change). All the values of r reported in this study were refined by using the Euler equation (Wilson and Bossert, 1971; Krebs, 1985):

$$\sum_{x=0}^{\infty} l_x m_x e^{-rx} = 1.$$

The finite or annual rate of change (e^r) was then calculated from the refined values of r. In addition, the theoretical population doubling or halving time in years ($t_{\times 2}$) assuming a stable age distribution was computed as $(\ln 2)/r$ or $(\ln 0.5)/r$, respectively (Krebs, 1985).

The initial set of analyses, consisting of three different scenarios, was run by using the most reliable input biological parameters: t_{max}=10, t_{mat}=4, m_x=baseline age-specific natality, and S=0.657. In scenario 1, first year natural mortality was arbitrarily doubled (M=0.42 × 2=0.84) or S_0=0.432. In scenario 2, a value of S_0=0.512 was obtained from the Leslie matrix algorithm by assuming an equilibrium (or stationary) population (Vaughan and Saila, 1976). Thus, the following equation was solved for S_0 after assuming r=0:

$$S_o = \frac{e^r}{m_1 + \sum_{i=1}^{I-1}\left[\left(m_{i+1}e^{-ir}\right)\left(\prod_{j=1}^{i} S_j\right)\right]},$$

where m_i is fecundity at age, I is the oldest age group in the population (10 years), and S_j is survival from age j to j+1. In scenario 3, (referred to as the best case scenario), S_0 was assumed to be equal to survivorship in the following years (S_0=S=0.657=$e^{-0.42}$). For this best case scenario, the stable age distribution (C_x) was calculated according to Krebs (1985) and plotted.

In a second set of analyses, the input biological or life history parameters (t_{mat}, t_{max}, m_x, S, S_0) were varied to test the sensitivity of the resultant demographic parameters (R_0, G, r, and $t_{\times 2}$). These sensitivity analyses measured the percentage change of the output de-

mographic parameter of interest relative to the best case scenario. In the case of t_{x2}, sensitivity was assessed by calculating a multiplication factor that measures the number of times the population doubling time changes relative to the best case scenario (example: if t_{x2}=15.7 in the best case scenario and 4.1 in the altered state, then the multiplication factor [mf]=15.7/4.1=3.8, i.e. t_{x2} has been shortened 3.8 times in the altered state).

Based on the results from the initial set of analyses (scenarios 1 through 3), the existing knowledge of life history traits in *R. terraenovae*, and the results from the FMP (e^r=1.91), input parameter values were manipulated in the direction that would be favorable to population increase and should thus be regarded as optimistic scenarios. The following variations, relative to the best case scenario, were applied: doubling m_x (m_x=2; scenario 4); reducing t_{mat} by 1 year (t_{mat}=3; scenario 5) and by 2 years (t_{mat}=2; scenario 6); reducing t_{mat} by 1 year and doubling m_x (t_{mat}=3, m_x=2; scenario 7); reducing t_{mat} by 2 years and doubling m_x (t_{mat}=2, m_x=2; scenario 8); increasing S_0 by 10% (S_0=0.723; scenario 9) and by up to 50% (S_0=0.985; scenario 10); increasing S by 10% (S=0.723; scenario 11) and by up to 50% (S=0.985; scenario 12); doubling t_{max} (t_{max}=20 [note that S and S_0 will also vary, since they depend on t_{max}]; scenario 13); and an extreme manipulation that was undertaken to approximate the FMP value of e^r=1.91 (equivalent to an r of 0.647), where t_{mat} was reduced by 1 year, m_x was doubled, and S and S_0 set at 95% (t_{mat}=3, m_x=2, S=S_0=0.95; scenario 14).

A third set of simulations was run incorporating the estimated mean instantaneous fishing mortality rate from 1986 to 1989 (F=0.428), as used in the stock assessment of small coastal species (Parrack[2]) on which the FMP for sharks of the Atlantic Ocean is based, to demonstrate the effect of exploitation and various age-at-first-entry scenarios. Fishing mortality (F) was added to natural mortality (M) in the survivorship function $l_x = N_0(e^{-(M+F)x})$, with F initially starting at age 0, then sequentially up to age 9. A_{rep}, the minimum age at which individuals can first enter the fishery and still allow the population to replace itself ($r \geq 0$) was calculated by noting the age at which the intrinsic rate of increase (r) becomes zero or positive. These simulations were run first under scenarios 1 through 3, and then under scenarios 4 through 14.

Results

The initial set of life history tables yielded net reproductive rates per generation (R_0), ranging from 0.844 to 1.284, a generation length (G) of 5.8 years, and intrinsic rates of population change (r), ranging from –0.029 to 0.044 (Table 1) depending on the value of first year survivorship (S_0) used. In scenario 1 (S_0=0.432), the results indicated that the population would decrease at a rate of 2.9% per year and would halve about every 24 years. Halving times are indicated by negative values in the t_{x2} column. In scenario 2 (S_0=0.512), r is equal to 0 by definition. Under the best case scenario (scenario 3; S_0=0.657), the

[2] Parrack, M. L. 1990. A preliminary study of shark exploitation during 1986–1989 in the U.S. FCZ. Contrib. MIA-90-493, NOAA, NMFS, SEFC, Miami, FL 33149, 23 p.

Table 1

Simulations of the Gulf of Mexico population of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, under three scenarios that use input parameter values representing the best biological information available. Only natural mortality is included in these analyses. First year survival rates (S_0) were obtained as follows: S_0=0.432 (scenario 1) was obtained by doubling the natural mortality value computed from Hoenig's (1983) relationship between mortality rate and maximum age; S_0=0.512 (scenario 2) was computed from the Leslie matrix algorithm (see text) assuming an equilibrium population (Vaughan and Saila, 1976). The third line (in italics) represents the best case scenario (scenario 3; S_0=S=0.657).

	Input parameter values[1]					Computed parameter values[2]				
Scenario	t_{mat}	t_{max}	m_x	S	S_0	R_0	G	r	e^r	t_{x2}
1	4	10	1[3]	0.657	0.432	0.844	5.762	–0.029	0.971	–23.9
2	4	10	1	0.657	0.512	1.000	5.762	0.	1.000	—
3	*4*	*10*	*1*	*0.657*	*0.657*	*1.284*	*5.762*	*0.044*	*1.045*	*15.7*

[1] t_{mat}=age at maturity; t_{max}=maximum age; m_x=age-specific natality; S=survivorship after the first year of life; S_0=survivorship for the first year of life.

[2] R_0=net reproductive rate per generation; G=generation length, in years; r=intrinsic rate of population change refined through the Euler equation (see text); e^r=finite rate of population change; t_{x2}=theoretical doubling (positive values) or halving (negative values) time in years assuming a stable age distribution.

[3] "1" indicates baseline age-specific natality.

population increased at 4.5% per year and doubled about every 16 years.

The predicted stable age distribution (C_x) for the best case scenario (Fig. 1) suggested that about 80% of the population was composed of immature individuals. Because of the lack of data on sizes and ages at first capture in the recreational and commercial fisheries, the actual proportion of the population subject to fishing is unknown. Likewise, no size or age composition of this population is available from surveys, precluding any comparisons with the theoretical C_x.

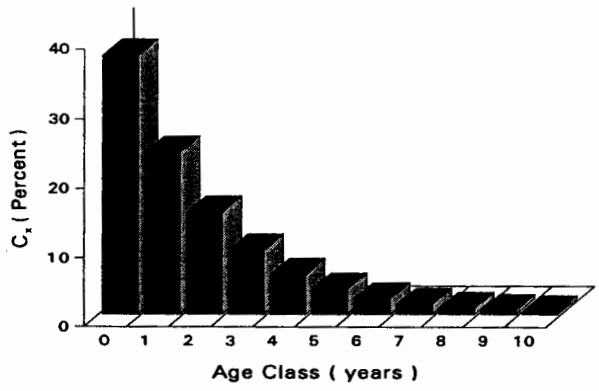

Figure 1

Predicted stable age distribution of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, under the best case scenario presented in Table 1, assuming geometric growth (with r=0.044) and constant age-specific mortality and fertility rates.

Results of the sensitivity analyses indicated that doubling age-specific natality, m_x, had a distinct effect (a 286% increase) on the population's rate of increase, r (scenario 4), and would allow the population to double in only 4.1 years or 3.8 times faster than in the best case scenario (Table 2). Generation length, G, remained the same, while net reproductive rate per generation, R_0, increased 100% (Table 3).

Decreasing age at maturity, t_{mat}, by one year (scenario 5) produced a smaller change in r, $t_{\times 2}$, and R_0 (Tables 2 and 3) than doubling m_x, but decreased G by 12% (Table 3). Further decreasing t_{mat} by another year (scenario 6) produced almost the same values of r and $t_{\times 2}$ as those obtained in scenario 4 (Table 2), although R_0 increased only 5% and G decreased by 20%. The combined effect of decreasing t_{mat} and doubling m_x together (scenarios 7 and 8) produced increases in r up to near 700% and $t_{\times 2}$ values up to 8 times shorter than in the best case scenario (Table 2). Under scenarios 7 and 8, R_0 also increased by up to more than 200%, while G decreased by up to 20%.

Increasing first year survivorship, S_0, by 10% (scenario 9) yielded a value of r 39% higher and a value of $t_{\times 2}$ 1.4 times shorter than in the best case scenario (Table 2), affected R_0 very little (a 10% increase only), and had no effect on G (Table 3). A further increase

Table 2

Simulations of the Gulf of Mexico population of *Rhizoprionodon terraenovae* to test the sensitivity of computed population rate of increase and doubling time to input biological parameter values. Input values were manipulated in scenarios 4 through 14; the best case scenario (BC; top row) is shown in italics to facilitate comparison. All other symbols are as defined in Table 1.

	Input parameter values					Computed parameter values			
Scenario	t_{mat}	t_{max}	m_x	S	S_0	r	% change of r[1]	$t_{\times 2}$	mf[2]
BC	*4*	*10*	*1*	*0.657*	*0.657*	*0.044*	—	*15.7*	—
4	4	10	2[3]	0.657	0.657	0.170	286	4.1	3.8
5	3	10	1	0.657	0.657	0.111	152	6.2	2.5
6	2	10	1	0.657	0.657	0.168	282	4.1	3.8
7	3	10	2	0.657	0.657	0.265	502	2.6	6.0
8	2	10	2	0.657	0.657	0.356	709	1.9	8.3
9	4	10	1	0.657	0.723	0.061	39	11.4	1.4
10	4	10	1	0.657	0.985	0.117	166	5.9	2.7
11	4	10	1	0.723	0.657	0.123	179	5.6	2.8
12	4	10	1	0.985	0.657	0.378	759	1.8	8.7
13	4	20	1	0.811	0.658	0.228	418	3.0	5.2
14	3	10	2	0.950	0.950	0.634	1,341	1.1	14.3

[1] % change of r relative to the best case scenario.

[2] Multiplication factor indicating the number of times $t_{\times 2}$ has been shortened relative to the best case scenario.

[3] "2" indicates baseline age-specific natality values have been doubled.

Table 3

Simulations of the Gulf of Mexico population of *Rhizoprionodon terraenovae* to test the sensitivity of computed net reproductive rate per generation and generation length to input biological parameter values. Input values were manipulated in scenarios 4 through 14; the best case scenario (BC; top row) is shown in italics to facilitate comparison. All other symbols are as defined in Table 1.

	Input parameter values					Computed parameter values			
Scenario	t_{mat}	t_{max}	m_x	S	S_0	R_0	% change of R_0[1]	G	% change of G[1]
BC	*4*	*10*	*1*	*0.657*	*0.657*	*1.28*	—	*5.76*	—
4	4	10	2[2]	0.657	0.657	2.57	100	5.76	0
5	3	10	1	0.657	0.657	1.72	34	5.06	–12
6	2	10	1	0.657	0.657	1.34	5	4.58	–20
7	3	10	2	0.657	0.657	3.43	168	5.06	–12
8	2	10	2	0.657	0.657	4.08	219	4.58	–20
9	4	10	1	0.657	0.723	1.41	10	5.76	0
10	4	10	1	0.657	0.985	1.92	50	5.76	0
11	4	10	1	0.723	0.657	2.05	60	6.06	5
12	4	10	1	0.985	0.657	11.66	809	7.20	25
13	4	20	1	0.811	0.658	4.99	290	8.30	44
14	3	10	2	0.950	0.950	29.6	2,212	6.7	16.3

[1] % change of R_0 and G relative to the best case scenario.
[2] "2" indicates baseline age-specific natality values have been doubled.

in S_0 up to 50% (scenario 10) had a more distinct effect on r (166% increase), $t_{\times 2}$ (2.7 times shorter), and R_0 (50% increase), but did not affect G (Tables 2 and 3). Increasing age 1+ survivorship (S) by 10% (scenario 11) had a similar effect on all the demographic parameters to increasing S_0 by 50% (scenario 10; Tables 2 and 3), whereas increasing S by 50% (scenario 12) had a very profound effect on all the demographic parameters, increasing r by 759%, shortening $t_{\times 2}$ by almost 9 times (similar to scenario 8), increasing R_0 by over 800% and lengthening G by 25% (Tables 2 and 3).

Doubling longevity (t_{max}) to 20 years (scenario 13) also markedly affected r (418% increase), $t_{\times 2}$ (5 times shorter), and R_0 (290% increase), and produced the largest value of G (8.3 or a 44% increase) in all scenarios (Tables 2 and 3).

Finally, the extreme manipulations of scenario 14 (reducing t_{mat} to 3 years, doubling m_x, increasing S and S_0 to 95%, with a t_{max} of 10 years) produced a 13-fold increase in r, a value of $t_{\times 2}$ more than 14 times shorter, a 22-fold increase in R_0 and only a 16.3% increase in G (Tables 2 and 3).

For all simulations, population doubling time ($t_{\times 2}$) was lessened and generation length (G) was the demographic parameter less sensitive to changes in input biological parameter values.

With the estimated mean fishing mortality from 1986 to 1989 (F=0.428) added to natural mortality starting at each age interval from 9 to 0, R_0 and r were progressively reduced as F was progressively started closer to age-0 (Table 4). In scenarios 1 (S_0=0.432) and 2 (S_0=0.512), r was always negative and became increasingly so as simulated fishing started earlier in the life of *R. terraenovae*. Only by using best case scenario (scenario 3) values could the population be made to replace itself or grow by manipulating age at first capture. When fishing pressure was applied between 6 and 5 years of age or about 97 cm total length (TL) the population was able to replace itself. Generation length remained the same under the three scenarios but progressively decreased as fishing mortality included progressively earlier ages. Theoretical halving time also progressively shortened as fishing started at younger ages, whereas in the best case scenario doubling time increased as age at first capture dropped from 9 to 6 years.

The effect of added fishing mortality on survivorship can be identified as a progressive decrease in percentage survival as fishing starts progressively earlier in the lifespan of the shark (Fig. 2). Age-specific reproduction also decreases significantly as fishing mortality is applied at progressively earlier ages (Fig. 3).

When the estimated mean fishing mortality from 1986 to 1989 (F=0.428) was added to natural mortality in scenarios 4 through 14 (Table 5), A_{rep}, the earliest age at which sharks can first be captured to

Figure 2

Survivorship curves for *Rhizoprionodon terraenovae* under the survival conditions presented in Table 1 for the best case scenario (S=S_o=0.657) and fishing mortality as in Table 4 (F=0.428), starting at three different ages (1, 5, and 8 years).

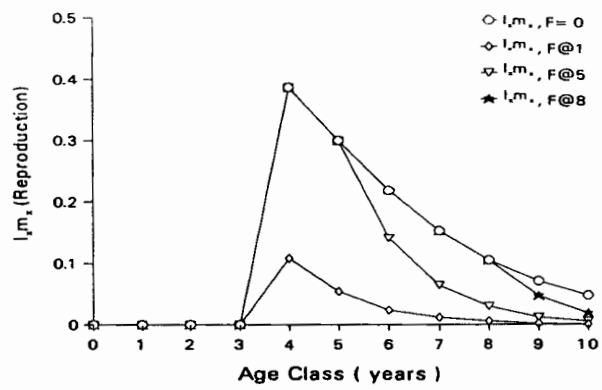

Figure 3

Age-specific reproduction for *Rhizoprionodon terraenovae* under the survival conditions presented in Table 1 for the best case scenario (S=S_o=0.657) and fishing mortality as in Table 4 (F=0.428), starting at three different ages (1, 5, and 8 years).

Table 4

Simulations of the Gulf of Mexico population of *Rhizoprionodon terraenovae* under the three same scenarios as in Table 1 but with estimated mean fishing mortality from 1986 to 1989 (F=0.428 [Parrack[2]]) added to natural mortality starting at different ages. All symbols are as defined in Table 1. Computations based on the following first year survival rates: scenario 1 (S_o=0.432); scenario 2 (S_o=0.512); and scenario 3 (best case, S_o=0.657).

Demographic parameter	Age at first capture									
	9	8	7	6	5	4	3	2	1	0
Scenario 1										
R_o	0.83	0.81	0.77	0.71	0.62	0.49	0.32	0.21	0.14	0.09
G	5.70	5.60	5.45	5.27	5.06	4.86	4.86	4.86	4.86	4.86
r	–0.03	–0.04	–0.05	–0.07	–0.09	–0.14	–0.23	–0.31	–0.38	–0.46
e^r	0.97	0.96	0.95	0.94	0.91	0.87	0.80	0.74	0.68	0.63
t_{x2}	–21.7	–18.2	–14.4	–10.7	–7.4	–4.9	–3.1	–2.3	–1.8	–1.5
Scenario 2										
R_o	0.99	0.96	0.91	0.84	0.73	0.58	0.38	0.25	0.16	0.10
G	5.71	5.60	5.45	5.27	5.06	4.86	4.86	4.86	4.86	4.86
r	–0.00	–0.01	–0.02	–0.03	–0.06	–0.11	–0.19	–0.27	–0.35	–0.43
e^r	1.00	0.99	0.98	0.97	0.94	0.90	0.82	0.76	0.70	0.65
t_{x2}	–346.6	–99.0	–40.8	–21.0	–11.4	–6.3	–3.6	–2.5	–2.0	–1.6
Scenario 3 (best case)										
R_o	1.27	1.23	1.17	1.08	0.94	0.75	0.49	0.32	0.21	0.13
G	5.71	5.60	5.45	5.27	5.06	4.86	4.86	4.86	4.86	4.86
r	0.04	0.04	0.03	0.01	–0.01	–0.06	–0.14	–0.22	–0.31	–0.38
e^r	1.04	1.04	1.03	1.01	0.99	0.94	0.86	0.80	0.73	0.68
t_{x2}	16.5	18.7	23.9	49.5	–57.8	–11.7	–4.8	–3.0	–2.2	–1.8
size[1]	105	103.7	101.9	99.2	95.4	90	82.2	71.0	55.0	32.3

[1] Total length, in cm, obtained from the von Bertalanffy growth equation relating age to length (see text).

Table 5

Simulations of the Gulf of Mexico population of *Rhizoprionodon terraenovae* under several scenarios (4 through 14) using different input biological parameter values and with fishing mortality (F=0.428) as in Table 4. The best case scenario (BC; top row) is included in italics to facilitate comparison. All other symbols are as defined in Table 1; A_{rep} is the age at which sharks can first enter the fishery and still allow the population to replace itself.

	Input parameter values					Computed parameter values					
Scenario	t_{mat}	t_{max}	m_x	S	S_0	A_{rep}	R_0	G	r	e^r	$t_{\times 2}$
BC	*4*	*10*	*1*	*0.657*	*0.657*	*6*[1]	*1.08*	*5.27*	*0.010*	*1.010*	*49.5*
4	4	10	2[2]	0.657	0.657	4	1.50	4.87	0.084	1.088	8.2
5	3	10	1	0.657	0.657	4	1.18	4.18	0.040	1.041	17.3
6	2	10	1	0.657	0.657	3	1.25	3.47	0.064	1.066	10.8
7	3	10	2	0.657	0.657	2	1.20	3.99	0.046	1.047	15.1
8	2	10	2	0.657	0.657	1	1.20	3.29	0.057	1.059	12.2
9	4	10	1	0.657	0.723	5	1.04	5.06	0.007	1.007	99.0
10	4	10	1	0.657	0.985	4	1.12	4.86	0.024	1.024	28.9
11	4	10	1	0.723	0.657	4	1.09	5.01	0.017	1.017	40.8
12	4	10	1	0.985	0.657	1	1.15	5.70	0.025	1.025	27.7
13	4	20	1	0.811	0.658	3	1.16	5.33	0.028	1.028	24.7
14	3	10	2	0.950	0.950	0	2.56	4.86	0.206	1.229	3.4

[1] Under this scenario, sharks can enter the fishery at age 6 and above with a fishing mortality rate of F=0.428 (F=0 for all sharks ages 5 and below) added to the natural mortality rate and still allow the population to replace itself ($r \geq 0$).

[2] "2" indicates baseline age-specific natality values have been doubled.

allow for full population replacement ($r \geq 0$) given the fishing mortality, became progressively smaller as the value of r increased (see Table 2 for reference). Increasing S_0 by 10% (scenario 9) allowed for an age at first capture of 5 years, while doubling m_x (scenario 4), reducing t_{mat} to 3 years of age (scenario 5), increasing S_0 by 50% (scenario 10), or increasing S by 10% (scenario 11) all had the same effect of allowing for an age at first capture of 4 years (90 cm TL) compared with 6 years (99 cm TL) under the best case scenario. Reducing t_{mat} by 2 years (scenario 6) or increasing t_{max} to 20 years (scenario 13) both allowed for an A_{rep} of 3 years (82 cm TL), while reducing t_{mat} by 1 year and doubling m_x (scenario 7) allowed an A_{rep} of 2 years. Under the most extreme manipulations, which included reducing t_{mat} by 2 years and doubling m_x (scenario 8), increasing S by 50% (scenario 12), and reducing t_{mat} to 3 years, doubling m_x, and setting S and S_0 at 95% (scenario 14), an age at first capture of 1 year (55 cm TL; scenarios 8 and 12) and of 0 years (32 cm TL) could be applied in a given year.

Discussion

These demographic analyses using the best available information indicate that the Gulf of Mexico population of *R. terraenovae* may be very vulnerable to fishing pressure. Results showed that, based on known life history parameters, the population's intrinsic rate of increase was, at best, only r=0.044, equating to a finite rate of e^r=1.045, which is much lower than the rate estimated for "small coastal" species in the stock assessment used to develop the FMP for sharks of the Atlantic Ocean (e^r=1.91). Furthermore, comparable rates to the FMP values were only obtained after extreme manipulations of the input life history parameters, which diverged too widely from observed life history parameters to be realistic. For example, one of the possible scenarios that would yield an estimate of e^r of 1.91 implies that age at maturity has to be decreased from 4 to 3 years, fertility doubled, and survivorship increased by almost 50% relative to the most optimistic initial scenario, i.e. the best case scenario, resulting in estimates of 29.6 for R_0, 6.7 for G, and 1.1 for $t_{\times 2}$. This means that, in the absence of fishing, the population would almost double every year.

Rhizoprionodon terraenovae is the main species caught in the Texas recreational shark fishery and is also caught by the headboat and other recreational fisheries in the Gulf of Mexico. More importantly, it represents a significant bycatch in the shrimp trawl fishery operating in the Gulf of Mexico and to a lesser extent in the longline reef fish and shark fisheries, and in the gillnet fishery in the same area. The lack of data on the age and size at which individuals of *R.*

terraenovae first enter these fisheries, as well as the relative proportions of each age and size group represented, preclude a more detailed analysis at this time. However, the demographic analysis representing the best case scenario indicated that under the present fishing level *R. terraenovae* should not enter the fishery until individuals reach about 97 cm TL or almost 6 years of age if the population was managed to just replace itself. There is evidence that smaller animals are being caught in the various fisheries, but the proportions of each age class are unknown.

The biological parameters incorporated in scenarios 1 through 3 represent the best, most reliable information available. Data on age and growth were taken from a tetracycline-validated laboratory study (Branstetter, 1987) which indicated that females mature entering their fifth year of life (age-4) and that maximum age is between 8 and 10 years. In another study (Parsons, 1985), female maturity was estimated at between 2.4 to 3.9 years. However, this study used only males and mean lengths for age classes, which, as pointed out by Branstetter (1987), affected the von Bertalanffy parameters. The possibility of earlier female age at maturity and even longer lifespan was incorporated in several of the demographic analyses (scenarios 5, 6, 7, 8, 13, and 14), which evidently yielded more liberal results on which more risk-prone management decisions could be based.

The unpublished information on fertility at age was derived from a study on the reproductive biology of *R. terraenovae* (Parsons, 1983) and relates female total length to number of uterine eggs or embryos for 78 specimens. Parsons (1983) also noted that tropical populations of *R. terraenovae* had been reported to have as many as 12 embryos. This possibility was taken into account by doubling fertility at age in several analyses (scenarios 4, 7, 8, and 14), which again produced more optimistic estimates of population parameters.

The age, growth, and reproduction information used in this study was based on animals collected in the northern central and western Gulf of Mexico. The extent to which this information is applicable to the entire population or whether there are different stocks in the Gulf with different age, growth, and reproductive capabilities is not known. For example, I recently examined an 82-cm-TL pregnant female with 3 embryos, measurements which fit nicely the regression equation of Parsons (1983), but which would result in a back-calculated age of 3 years with the von Bertalanffy growth function, although the female could have been older, e.g. age 4, owing to variability in size at age, which is not uncommon in sharks (Kusher et al., 1992, and references therein).

The most important and also the most difficult parameter to estimate is natural mortality (M). The value of M used in this study was taken from Hoenig's (1983) relationship between longevity and total mortality for virgin or lightly exploited stocks. The assumption that Z could be approximated to M, or that no fishing mortality occurred during the period for which growth parameters for this species were derived, may have been violated. However, the possibility of lower natural mortality values was incorporated in several analyses (scenarios 9 through 14). While Hoenig's equation represents a shortcut and obvious simplification of reality, the lack of catch and effort data, or age or size composition for stocks of this species precludes calculation of any other estimates of M at this time. Lack or inappropriateness of both fishery and biological data may explain why several other researchers have used the same approach to estimate natural mortality in shark population studies. Except for age-0 *Negaprion brevirostris* (Manire and Gruber, 1993), no actual age-specific estimates of natural mortality are available for any shark species.

The value derived for M (0.42) in this study is equivalent to an annual survivorship of 0.66, which is low when compared with survival estimates for other species of sharks. Values derived from Hoenig's (1983) regression equation include 0.82 for the angel shark, *Squatina californica*, (Cailliet et al., 1992); 0.85 for *N. brevirostris* (Hoenig and Gruber, 1990); 0.87 for *Triakis semifasciata* (Smith and Abramson, 1990; Cailliet, 1992); and 0.90 for *Carcharhinus plumbeus* (Hoff, 1990). Grant et al. (1979) derived a value of 0.90 for the Australian school shark, *Galeorhinus australis*, using cohort analysis, and Walker (1992) used a value of 0.82 in a dynamic pool fishery simulation model of the gummy shark, *Mustelus antarcticus*, which was also obtained through cohort analysis. The lower survivorship value for *R. terraenovae* may be due to the smaller size of this species which would make it more susceptible to predation by other sharks, especially at early ages, since pups are born at about only 30 cm TL in coastal waters about 10 m deep (Castro, 1993).

The very high estimate of F (0.428) used in this study was derived from a shark stock assessment that is the basis for the recently implemented (26 April 1993) FMP for sharks of the Atlantic Ocean. However, the accuracy of this estimate, based on a 4-year catch-and-effort time series, is uncertain, and the demographic analyses undertaken in this study indicate that *R. terraenovae* is vulnerable to high removal levels in the early years of life.

It is also possible that the age, growth, and reproductive data used in this study are only representative of the population at a time when fishing pressure was not as high as it is at present. Potential

Table 6

Life history parameters for several species of sharks compared to the best case scenario for *Rhizoprionodon terraenovae* in the Gulf of Mexico.

Species	R_0	G	r	e^r	t_{x2}	Study
Triakis semifasciata	4.47	22.35	0.067	1.069	10.3	Cailliet, 1992
Negaprion brevirostris	1.27	16.23	0.015	1.015	46.7	Hoenig and Gruber, 1990
Squalus acanthias	3.05	49.63	0.023	1.023	30.1	Jones and Geen, 1977[1]
Carcharhinus plumbeus	1.48	21.5	0.018	1.018	38.5	Hoff, 1990
Squatina californica	2.25	14.5	0.056	1.057	12.4	Cailliet et al., 1992
Rhizoprionodon terraenovae	1.28	5.78	0.044	1.045	15.7	This study

[1] Modified by Eguchi and Cailliet (Gregor Cailliet, Moss Landing Marine Laboratories, Moss Landing, CA 95039-0450. Personal commun., 1994).

compensatory mechanisms countering stock depletion may include increased growth with corresponding earlier age at maturity, earlier size at maturity, higher fecundity, immigration of stocks from other areas, and increased survival rates through density-dependent regulation (Walker, 1992).

The estimates of demographic parameters derived under the best case scenario in this study are within the range of values derived for other species of sharks (Table 6). The estimate of R_0 (1.28) for *R. terraenovae* is almost identical to that derived by Hoenig and Gruber (1990) for *N. brevirostris* (1.27), probably owing to the similar fecundity in the two species. Generation length (G) is considerably shorter in *R. terraenovae* than in any other species because of its shorter lifespan. The estimates of r and e^r fall between those for other species. These relatively low values in a fast-growing, short-lived species such as *R. terraenovae* can be explained mainly by low fecundity and high mortality levels as the demographic analyses showed. Theoretical doubling time (t_{x2}) also lies between estimates for other species of sharks.

In the light of the incomplete yet reasonable biological information available, it seems sound to conclude that *R. terraenovae*, as perhaps some of the other small coastal species included in the FMP, is a species vulnerable to fishing. This becomes especially relevant with the recent implementation of the shark FMP which has set quotas and trip limits and has provided for fisheries closures for larger coastal species while allowing the unrestricted capture of small coastal sharks, of which *R. terraenovae* is the most representative species. Increased fishing pressure on *R. terraenovae*, especially on younger animals, would certainly deplete the stocks of this species.

The present study raises some serious concerns about the use of surplus production models utilizing very short series of catch and effort data and not taking into account the biological characteristics of a species. In the particular case of *R. terraenovae*, it can lead to policies that in turn lead to overfishing and stock depletion. It is advised that bycatch of *R. terraenovae* in the shrimp fishery and other fisheries in the Gulf of Mexico, as well as in the eventual development of a directed fishery for this species, be closely monitored in the near future. Development of stock identification techniques are also needed to determine stock structure and the degree of mixing and immigration of this species into fishing areas. Updated, more complete fisheries statistics combined with improved biological information should be used to re-assess the status of *R. terraenovae* in the small coastal species group of the shark FMP for future sound management actions.

Acknowledgments

This study was made possible by the work on age and growth of *R. terraenovae* by S. Branstetter and G. Parsons and by the studies on reproduction by G. Parsons, who also kindly made available the relationship between fecundity and female total length. I particularly thank Gregor Cailliet and an anonymous referee for their constructive review of this manuscript. This work was supported by a postdoctoral research fellowship from the Ministry of Education and Science of Spain to the author.

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