Life history of the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) (Richardson, 1836) off the southeastern United States

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Abstract—The life history of the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) was described from 1093 specimens collected from Virginia to northern Florida between April 1997 and March 1999. Longitudinally sectioned vertebral centra were used to age each specimen, and the periodicity of circuli deposition was verified through marginal increment analysis and focus-to-increment frequency distributions. *Rhizoprionodon terraenovae* reached a maximum size of 828 mm precaudal length (PCL) and a maximum age of 11+ years. Mean back-calculated lengths-at-age ranged from 445 mm PCL at age one to 785 mm PCL at age ten for females, and 448 mm PCL at age one to 747 mm PCL at age nine for males. Observed length-at-age data (estimated to 0.1 year) yielded the following von Bertalanffy parameters estimates: L_∞= 749 mm PCL (SE=4.60), K = 0.49 (SE=0.020), and t_0=–0.94 (SE=0.046) for females; and L_∞=745 mm PCL (SE=5.93), K=0.50 (SE=0.024), and t_0=–0.91 (SE=0.052) for males. Sexual maturity was reached at age three and 611 mm PCL for females, and age three and 615 mm PCL for males. *Rhizoprionodon terraenovae* reproduced annually and had a gestation period of approximately 11 months. Litter size ranged from one to eight (mean=3.85) embyros, and increased with female PCL.

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The Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) is a small carcharhinid that inhabits the coastal waters of the western North Atlantic from the Bay of Fundy to the Yucatan (Castro, 1983). It is the most common small coastal species off the southeastern U.S. coast and the Gulf of Mexico (Branstetter, 1990). This species is frequently encountered by a variety of commercial fishing gear, including bottom longline, gill net, bandit reel (used by the snapper–grouper fishery), and shrimp trawl. *Rhizoprionodon terraenovae* is also a common catch in the recreational hook-and-line fishery.

The age and growth of this species has been described in the Gulf of Mexico by Parsons (1981, 1983a, 1985) and Branstetter (1981, 1986, 1987a). Although those studies provided significant information on the age and growth of *R. terraenovae*, data were collected from 1979 to 1984, a time in which fishing pressure on the *R. terraenovae* population was probably not as high as at present (Cortes, 1995). The previous studies dealt with fishes only from the northern Gulf of Mexico, and therefore may not represent the entire stock, although the stock structure for *R. terraenovae* in the northwestern Atlantic remains unclear (Heist et al., 1996). No published age and growth studies exist for specimens collected from the southeastern U.S. Atlantic coast. The reproductive biology of this species has been studied in both the Gulf of Mexico and off the southeastern U.S. coast (Parsons, 1983b; Castro, 1988, 1993; Castro and Wourms, 1993), but the lack of concurrent age and growth data off the southeastern United States limits the utility of these data for fishery management.

Considering the importance of accurate and timely age, growth, and reproductive information to fishery management, this study had two objectives: to describe age, growth, and reproduction in the southeastern U.S. population of *R. terraenovae*; and to compare these data to those of previous studies on the same species in the Gulf of Mexico.

Materials and methods

Rhizoprionodon terraenovae (n=1093) were collected throughout the year in coastal waters from April 1997 through March 1999. Collection sites ranged from Chesapeake Bay, Virginia, to Port Canaveral, Florida (Fig. 1). The majority of specimens were collected off the coast of South Carolina. A variety of sampling gears were employed for sample collection: bottom longline (47% of specimens), otter trawl (22%), port-sampling of commercial fishing

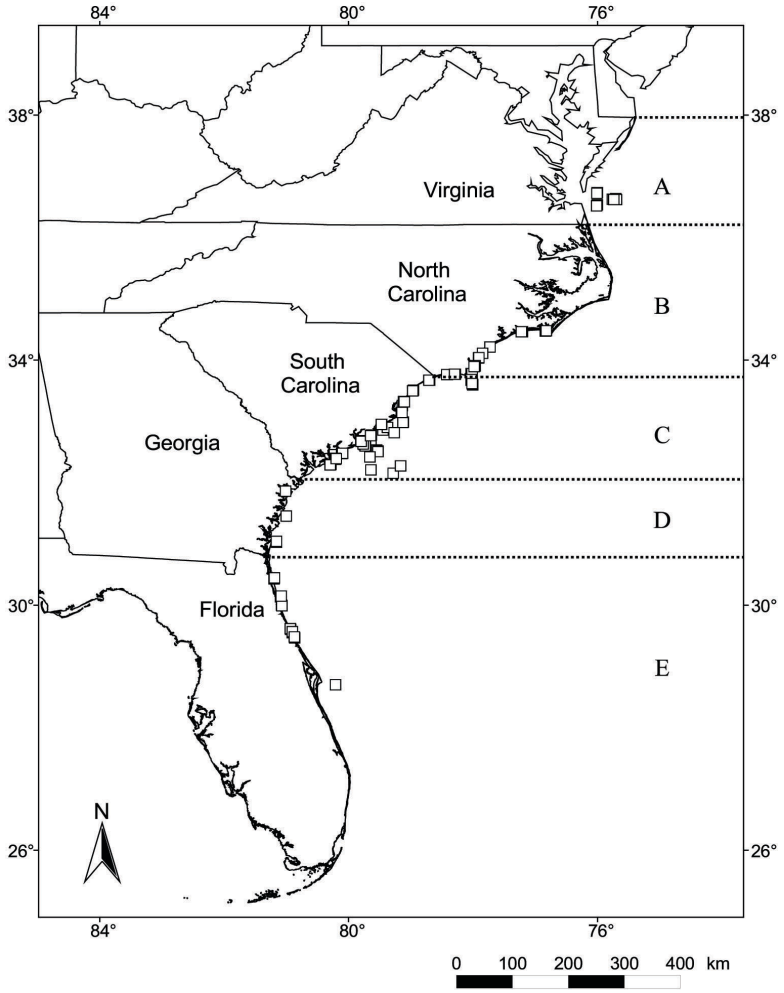

Figure 1

Sample collection sites and distribution by area (roughly equivalent to state borders) for *R. terraenovae* collected during this study, 1997–99. (□) represents locations where one or more *R. terraenovae* were captured. (**A**) = 13 males (694–793 mm PCL); (**B**) = 52 females (215–786 mm PCL), 51 males (200–765mm PCL); (**C**) = 497 females (197–813 mm PCL), 441 males (225–828 mm PCL); (**D**) = 8 females (302–763 mm PCL), 7 males (320–658 mm PCL); (**E**) = 6 females (335–738 mm PCL), 16 males (271–720 mm PCL).

vessels (16%), rod and reel (12%), gill net (3%), and other miscellaneous gear types (2%).

Following capture, the sex of each specimen was determined and the specimen was weighed (to the nearest 0.1 kg), evaluated for sexual maturity, and its body length was measured. Four body length measurements (to the nearest mm) were taken from each individual: precaudal length (PCL, measured from the tip of the snout to the anterior termination of the precaudal pit), fork length (FL), natural total length (NTL, measured with tail in a "natural" swimming position [Parsons, 1985]), and total length (TL, measured with dorsal portion of tail bent parallel to the body axis). Unless otherwise noted, precaudal lengths are used throughout this study. Regression relationships of TL, NTL, and FL on PCL were derived to facilitate comparison with other studies.

The claspers of males were measured from the clasper tip to the anterior termination of the vent. The siphon sac was measured from the base of the clasper fin (where the sac originates) to the anterior termination of the sac. The condition of the seminal vesicles was also recorded. Male maturity was indicated by calcification of the claspers and the presence of a fully formed siphon sac (Clark and von Schmidt, 1965; Parsons, 1983b). Gonadosomatic indices (GSIs, Parsons, 1983b) were calculated for male sharks with the formula

$$GSI = \textit{gonad weight}\ (\text{g})/\textit{body weight}\ (\text{g}) \times 100.$$

The ovaries and uteri of females were examined macroscopically for indicators of maturity, such as yolking eggs, embryos, or placental scars. Vitellogenic oocytes were easily identified by their bright yellow coloration in contrast to the pale white coloration of nonvitellogenic oocytes. If vitellogenic oocytes were present, the diameter of all vitellogenic oocytes in the ovary was measured (to the nearest 0.1 mm) with dial calipers. If maturing oocytes were not present, the most differentiated nonvitellogenic oocytes (which were noticeably larger that the rest of the oocytes in the ovary) were measured. Any embryos were removed from the uteri, counted, their sex determined, and measured (TL). Female maturity was determined by the presence of embryos, umbilical scars in the uterus from previous pregnancy, or the presence of large vitellogenic oocytes (greater than 15 mm diameter) nearing ovulation (Parsons, 1983b).

A segment of the vertebral column extending from the cervical region (dorsal to the branchial chamber) to the origin of the first dorsal fin was removed from each specimen and frozen. Vertebrae from the cervical portion of the spinal column were used for aging because of the shallow concavity of the intermedalia and the size similarity between adjacent centra in this region. The shallow concavity of the vertebrae facilitated processing and measurement during aging (Branstetter and McEachran, 1986). Age determination was attempted on 890 of the 1093 specimens collected during the study. Vertebrae selected for aging were separated from the frozen segment, defrosted, and soaked in 5% sodium hypochlorite for 5–30 min (depending on size) and were removed from the solution as soon as all excess connective tissue had been dissolved. A longitudinal section approximately 500 µm thick was cut from the center of each vertebrae with a Mark-V wafering saw and allowed to air-dry for at least 24 h. Dried sections were then attached to glass slides with Accu-mount 60 mounting medium and hand polished with wet 600-grit sandpaper to a thickness of approximately 350 µm. Several staining or ring elucidation techniques (e.g. Parsons, 1983a; Branstetter, 1986; Brown and Gruber, 1988; Hoenig and Brown, 1988) failed to significantly increase increment visibility; therefore all aging was performed with unstained vertebral sections.

Vertebral sections were read on a dissecting microscope with transmitted light and a polarizing filter at 20× magnification. Increment radii and marginal increments were measured through the center of the corpus calcareum (Fig. 2) with OPTIMAS image analysis software (Media Cybernetics, 1999). Precaudal length was regressed on centrum radius (CR) for males and females to test for an isometric relationship.

The increments observed in vertebral sections were narrow circuli similar to those described by Simpfendorfer (1993), as opposed to the growth bands described by Branstetter (1987a). All increment counts were made without knowledge of the size, sex, or collection date of the specimen. The primary reader (senior author) counted increments on all samples twice; each reading was separated by at least two months. Increment counts that were not in agreement were counted a third time. If the third count did not agree with one of the first two counts, the specimen was excluded from the analysis. The secondary reader (coauthor) counted increments from all specimens not eliminated by the primary reader's analysis. Between-reader disagreements were re-examined by both observers simultaneously. All specimens for which a consensus could not be reached were discarded. The index of average percentage error (IAPE; Beamish and Fournier, 1981) was used to estimate precision between the final readings of the primary reader and the initial readings of the secondary reader

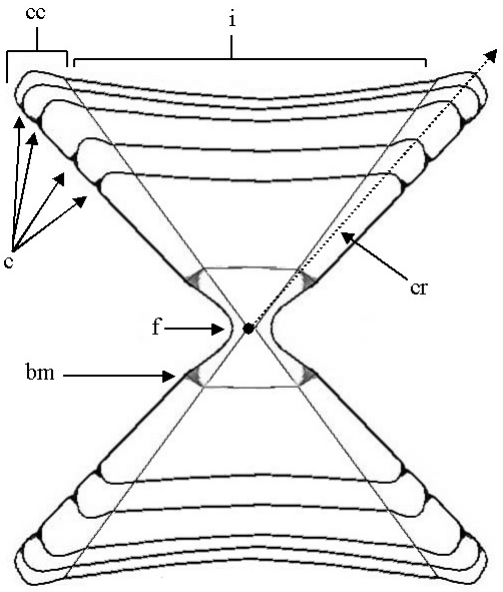

Figure 2

Diagrammatic representation of a vertebral section; bm = birth mark, c = circuli, cc = corpus calcareum, cr = line of centrum radii and annuli measurements, f = focus, i = intermedalia.

The annual periodicity of increment formation was verified through marginal increment analysis and focus-to-increment frequency distributions. Absolute marginal increment distances were converted to "relative" marginal increments by dividing the distance between the last increment and the edge of the centrum by the width of the last fully formed growth band (Skomal, 1990; Natanson, et al., 1995). This conversion compensated for differences in growth rates between age classes.

Back-calculated lengths at previous ages were estimated from vertebral measurements by using a modified Fraser-Lee equation proposed by Campana (1990):

$$L_a = L_c + [(C_a - C_c)\,(L_c - L_0)/(C_c - C_0)],$$

where L_a = length at age;
L_c = length at capture;
C_a = centrum radius from focus to increment a; and
C_c = centrum radius at capture.

L_0 and C_0 are biologically derived intercepts that represent the fish length and centrum radius, respectively, at which the proportionality between fish length and centrum growth are initiated. For the purposes of this study, mean body length and centrum radius at birth were used as the biologically derived constants (Sminkey and Musick, 1995).

The observed age-class data were used to estimate "actual ages" to 0.1 year. These were calculated by the number of circuli present plus growth since the formation of the last circulus. All specimens were given a 1 June birth date, which approximates the middle of the pupping season. This process corrected for growth since the last increment, preventing the potential overestimation of size-at-age that might result from analyzing the data by year class alone. All three types of length-at-age data (observed age class, observed actual age, and back-calculated age) were fitted to the von Bertalanffy growth equation (VBGE; von Bertalanffy, 1938):

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

where L_t = length at age t;
L_∞ = asymptotic length;
K = growth coefficient; and
T_0 = theoretical age at zero length.

Each of the three types were analyzed for sexes combined, as well as for each sex separately. The parameters for the VBGE were estimated through a stepwise Gauss-Newton iterative fitting process computed by JMP statistical analysis software (Anonymous, 1998).

Results

The sharpnose shark was abundant throughout the year in coastal waters within the sampling area. The ratio of males to females in the overall sample was not significantly different from a 1:1 ratio (chi-square test, n=1091, α=0.05, ν=1, χ^2=1.39, P=0.24).

Linear regression of TL, NTL, and FL on PCL resulted in the following equations:

$TL = 29.804 + 1.279PCL$ (n=1009, r^2=0.99, P<0.0001);
$NTL = 31.678 + 1.254PCL$ (n=493, r^2=0.99, P<0.0001);
$FL = 11.249 + 1.075PCL$ (n=1083, r^2=0.99, P<0.0001).

Reproduction and maturity

Size-at-maturity estimates were based on observations of 526 males and 564 females. The smallest fully mature male was 600 mm PCL, and the largest immature male was 615 mm PCL. All males greater than 615 mm PCL and 36% of males from 600 to 615 mm PCL were fully mature. The onset and completion of maturity in male *R. terraenovae* were demonstrated by the onset of development in the claspers and siphon sac (Fig. 3). Males began to mature at 500 mm PCL. The maturation of claspers and siphon sac reached completion approximately one year later, at 600 to 615 mm PCL.

The smallest maturing female was 509 mm PCL and contained one maturing oocyte five mm in diameter. The second smallest maturing female was 529 mm PCL. The smallest gravid female was 591 mm PCL. The largest immature female, based on lack of embryos or uterine scarring, was 611 mm PCL. Females from 591 to 611 mm PCL were either gravid (63%) or contained large (>10 mm diameter) maturing oocytes and were close to their first ovulation (37%). All females greater than 611 mm PCL were mature.

Mean GSI and mean ovarian egg diameter (MOD) both demonstrated prominent peaks during the calendar year. Male GSI values were highest in April and high values were also present in March and May (Fig. 4). However, the seminal vesicles remained turgid and full of semen for some time following the seasonal testicular degeneration which began in May. Female MOD values were highest in May and June. An increase in standard error along with a drop in mean value for the month of June (Fig. 4) demonstrated that ovulation began at that time. The extremely low MOD in July indicated the completion of ovulation.

Litter sizes ranged from one to eight, and generally increased with female PCL (Fig. 5). Mean litter size was 3.85 embryos, and significantly more embryos were found in the left uterus (mean=2.19) than in the right (mean=1.65; chi-square test, n=558, α=0.05, ν=4, χ^2=62.62, P<0.0001). Nonlinear regression of litter size on female PCL resulted in the following equation (n=278, r^2=0.51, P<0.0001):

$$Litter\ size = -11.07 + 0.021\ PCL + 1.37 \times 10^{-4}(PCL - 710.9)^2 .$$

Rhizoprionodon terraenovae were born at approximately 212 mm PCL. The smallest free-swimming neonate was 190 mm PCL, and the largest full-term embryo was 242 mm PCL. Most pupping occurred from mid-May to early June. However, a small number of neonates appeared as early as mid-April. Consequently, mean embryo total length was at a minimum in July and at a maximum in June (Fig. 6). The sexes of uterine embryos were not significantly different from the expected 1:1 ratio (chi-square test, n=844, α=0.05, ν=1, χ^2=0.076, P=0.78).

Age and growth

Separate linear regressions of PCL on centrum radius (CR) for males and females were not significantly different (ANCOVA, P=0.065) and were therefore combined (Fig. 7) to yield the following formula:

$PCL = 61.80 + 124.48CR$ (r^2=0.963, n=812, P<0.0001).

The regression line slightly overestimated centrum radius for the largest individuals (>700 mm PCL) of both sexes. Data transformation, as well as nonlinear regression, failed to increase the r^2 value, and only the largest specimens were affected.

Nonlinear regression of total body weight on length was significantly different between males and females (ANCOVA after log-transformation, P<0.001), and resulted in the following equations:

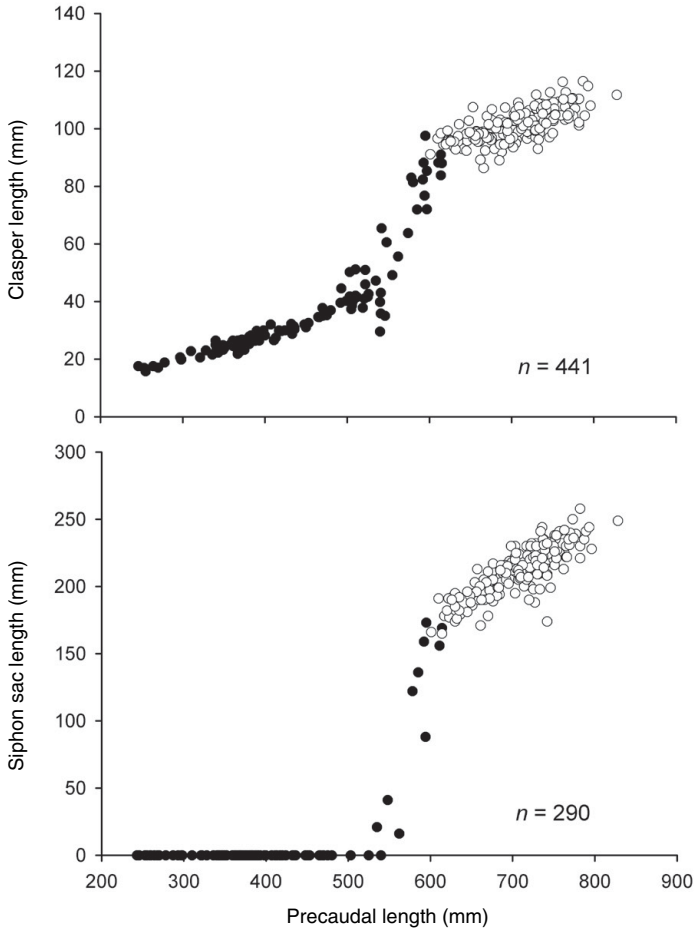

Figure 3

Relation of clasper and siphon sac length to precaudal length for male *R. terraenovae*; (●) represents individuals with uncalcified claspers; (○) represents individuals with fully calcified claspers.

Females: $W_t = e^{(-18.62)}PCL^{(3.04)}$ (r^2=0.99, P<0.0001, n=458);

Males: $W_t = e^{(-18.18)}PCL^{(2.96)}$ (r^2=0.99, P<0.0001, n=454),

where W_t = total body weight.

Aging was attempted on 890 specimens, 812 of which were aged without elimination. Agreement between the first and second counts conducted by the primary reader was 66%, with 91% within one increment, and 99% within two. Those sections that showed disagreement between the first and second reading (n=303) were counted a third time, and 96% agreed with one of the first two readings. The remaining 4% (12 specimens) were excluded from the analysis. Agreement between readers was 72%, with 95% within one increment and 99% within two. Vertebrae for which counts did not agree between readers (246 out of 878) were re-examined by both readers simultaneously. A concurrent age could not be reached on 66 vertebrae, which were eliminated from the study. The IAPE between the final readings of the primary reader and the initial readings of the secondary reader was 7.4%. Size-frequency distributions of the discarded individuals (data not shown) closely matched those of the raw data set and did not indicate the elimination of a large number of individuals from any age class during the aging process.

Mean relative marginal increments for age classes 1+ through 7+ combined demonstrated a minimum in July (Fig. 8). The 0+ age class was excluded from this analysis to ensure that growth from the birth mark did not affect the results. Frequency distributions of focus-to-increment measurements for ages 0+ through 7+ demonstrated single modes for all annuli in each age class for both males and females (Fig. 9).

Most *R. terraenovae* were found to have an increment in the intermedalia and an associated change in the angle of the corpus calcareum, which is similar to the birth mark

described by other authors (e.g. Casey et al., 1985; Branstetter, 1987b; Simpfendorfer, 1993). There were 239 young of the year *R. terraenovae* collected during this study, 88 of which contained no discernible birth mark. All young of the year lacking a birth mark were captured in June and July (Fig. 10), whereas all young of the year captured from August through April had a birth mark. Both marked and unmarked centra were noted in July and showed a readily apparent trend; individuals with a birth mark were significantly larger than those without a birthmark (*t*-test, df=96, t=–7.138, P<0.0001).

Back-calculated lengths-at-age were similar to observed lengths-at-age in all cases, although observed values were slightly higher for all age classes (Table 1). There was no evidence of Lee's phenomenon in the older age classes. Back-calculated size at the birth mark overestimated size at birth as determined by observations of neonates and full-term embryos.

The VBGE estimates calculated by age class, actual age, and back-calculated age demonstrated little variation either within or among data types (Table 2). The VBGE parameters from all data types corresponded well with known life history parameters for size at birth and maximum size. Unless otherwise noted, all comparisons throughout the remainder of this study were based on VBGE estimates derived from the "actual age" data type.

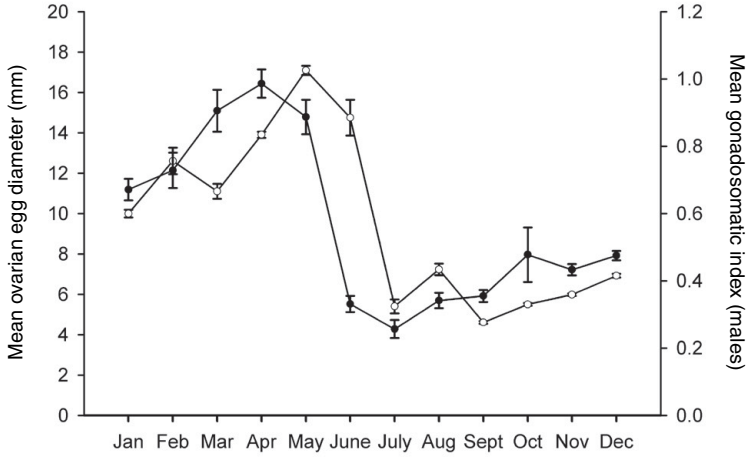

Figure 4

Mean gonadosomatic index and mean ovarian egg diameter by month for female *R. terraenovae*. Open circles indicate females (n=275), closed circles indicate males (n=214). Error bars represent mean ± one standard error.

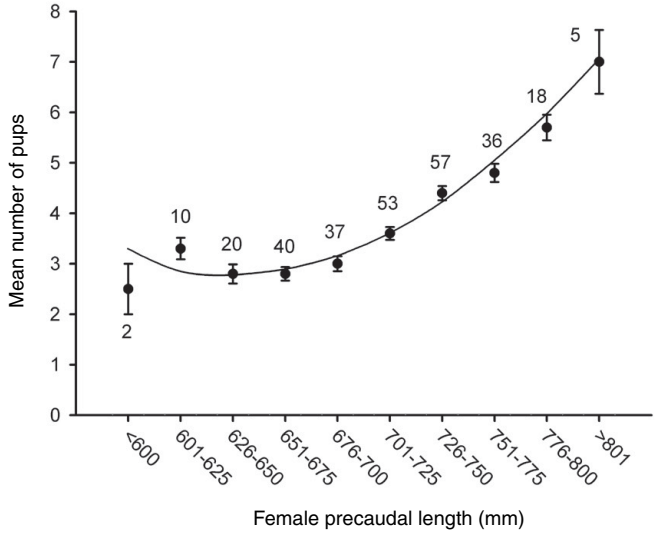

Figure 5

Mean litter size on female size class. Solid line represents best-fit quadratic equation. Numbers indicate sample size for each data point. Error bars represent mean ± one standard error.

Discussion

Reproduction

Length-at-maturity estimates for male *R. terraenovae* were similar among the three published studies. Parsons (1983b) estimated male maturity at ~610 to 653 mm PCL (lengths from other studies were converted to PCL by using the formulae derived from the current study) and Branstetter (1987a) estimated the same at 600 mm PCL. We determined that males reach full maturity at ~600 to 615 mm PCL. The three studies failed to agree on length at maturity for female *R. terraenovae*. Branstetter (1987a) and Parsons (1983b) approximated the size of females at maturity at 660 mm PCL and from 650 to 690 mm PCL, respectively. We found, however, that females mature at a smaller size, from 590 to 610 mm PCL.

The reproductive seasonality of *R. terraenovae* in our study appeared to lack synchrony; males reached their reproductive peak in April and females in May and June. Mature males dissected in late May and June had visibly atrophied testes compared to those collected in April and early May. However, their seminal vesicles were still highly swollen and contained large amounts of semen. This condition indicated that male *R. terraenovae* were still capable of mating during May and June, when female MOD values were highest. Therefore, the mating season of *R. terraenovae* off the southeastern U.S. coast appeared to last from mid May to early July. Simpfendorfer (1992) noted a similar misalignment of peaks in reproductive seasonality between the sexes in *R. taylori*.

The largest litters noted in our study contained eight pups (n=4). This increases the maximum litter size reported for *R. terraenovae* in the northwestern Atlantic

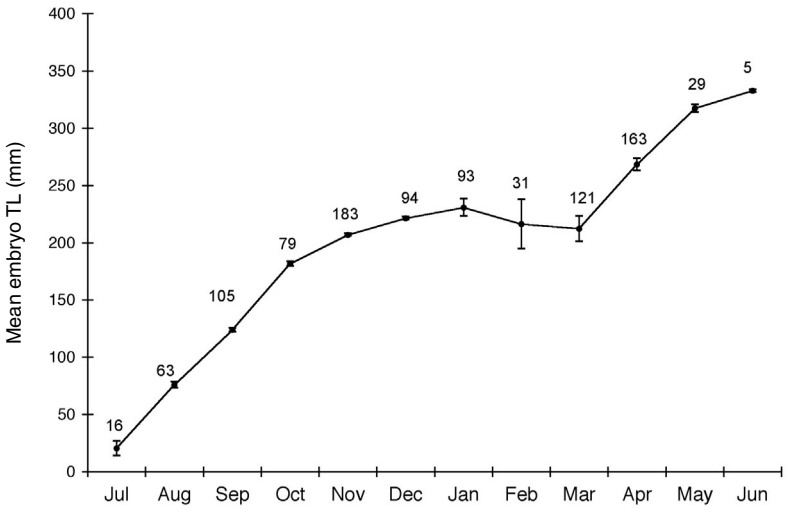

Figure 6

Mean total length by month for embryos collected from April 1997 through March 1999. Numbers indicate sample size for each data point. Error bars represent mean ± one standard error.

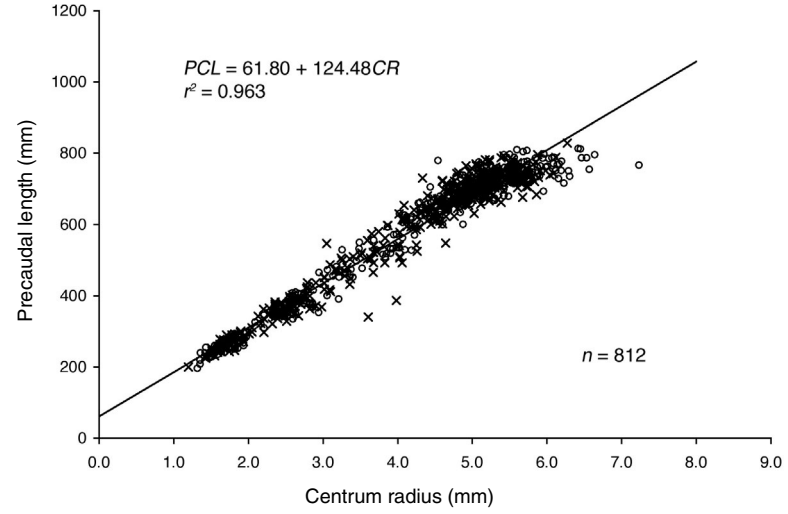

Figure 7

Linear regression of precaudal length (mm) on centrum radius (mm) for *R. terraenovae*; (X) represents males, (○) represents females.

(Parsons, 1983b; Castro and Wourms, 1993). Early reports of up to 12 pups in sharpnose sharks collected from Cuban waters (Bigelow and Schroeder, 1948) were likely the result of misidentification (Castro and Wourms, 1993).

Age and growth

The PCL-CR regression line slightly overestimated centrum radius for large individuals. This trend has also been noted in large female *Carcharhinus obscurus* (Natanson et al., 1995) and appears to result from a change in the slope of the linear relationship as growth becomes asymptotic near the maximum length of the species. This phenomenon was deemed to have a minimal effect on the linear regression formula used in this study. Although the linear relationship appears to undergo an immediate change in slope at about 700 mm PCL, there are not enough data following this change (that is, the animal does not increase substan-

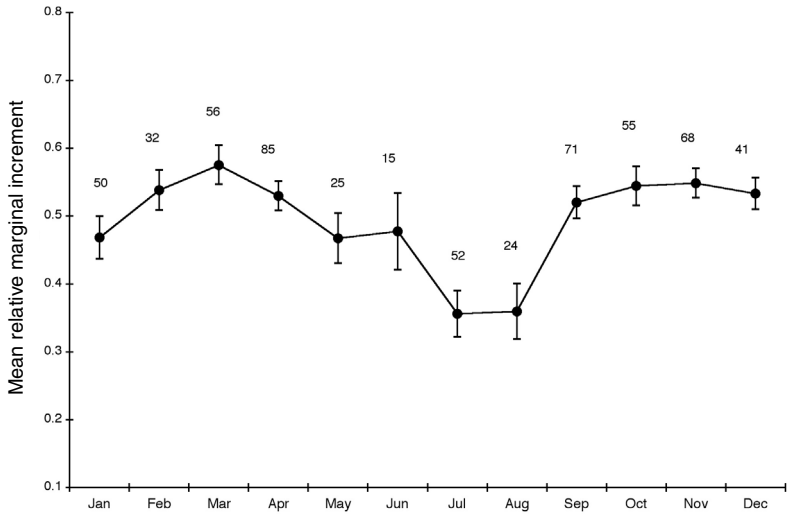

Figure 8

Mean relative marginal increment (mm) by month for age classes 1+ through 7+. Numbers indicate sample size for each data point. Error bars represent mean ± one standard error.

Table 1

Mean, minimum, and maximum lengths-at-age (mm) and statistics for observed actual and back-calculated ages (0–10+ years).

	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+
Females											
Back-calculated											
mean	249	452	556	619	665	698	722	740	754	775	777.9
minimum	189	307	422	521	563	600	627	673	711	754	
maximum	301	573	646	742	764	795	795	800	785	804	
SD	19	32	35	36	35	34	29	28	22	19	
n	379	305	273	232	186	137	90	42	13	5	1
Observed											
mean	320	513	629	676	700	717	741	755	762	788	787.0
minimum	197	391	469	606	615	345	663	688	726	764	
maximum	465	624	707	780	765	805	812	810	796	813	
SD	63	51	49	33	30	66	26	31	23	20	
n	123	32	42	46	50	47	48	29	8	4	1
Males											
Back-calculated											
mean	247	452	564	634	675	695	708	717	728	715	
minimum	191	310	372	519	582	625	651	690	706		
maximum	317	553	681	760	778	809	753	764	743		
SD	21	36	45	40	38	32	24	21	16		
n	337	260	225	191	159	102	49	15	4	1	
Observed											
mean	323	509	600	676	716	722	722	732	743	720	
minimum	200	340	387	578	623	653	661	699	729		
maximum	466	602	730	777	796	828	763	773	757		
SD	63	59	69	46	39	34	24	21	14		
n	116	35	34	32	57	53	35	10	3	1	

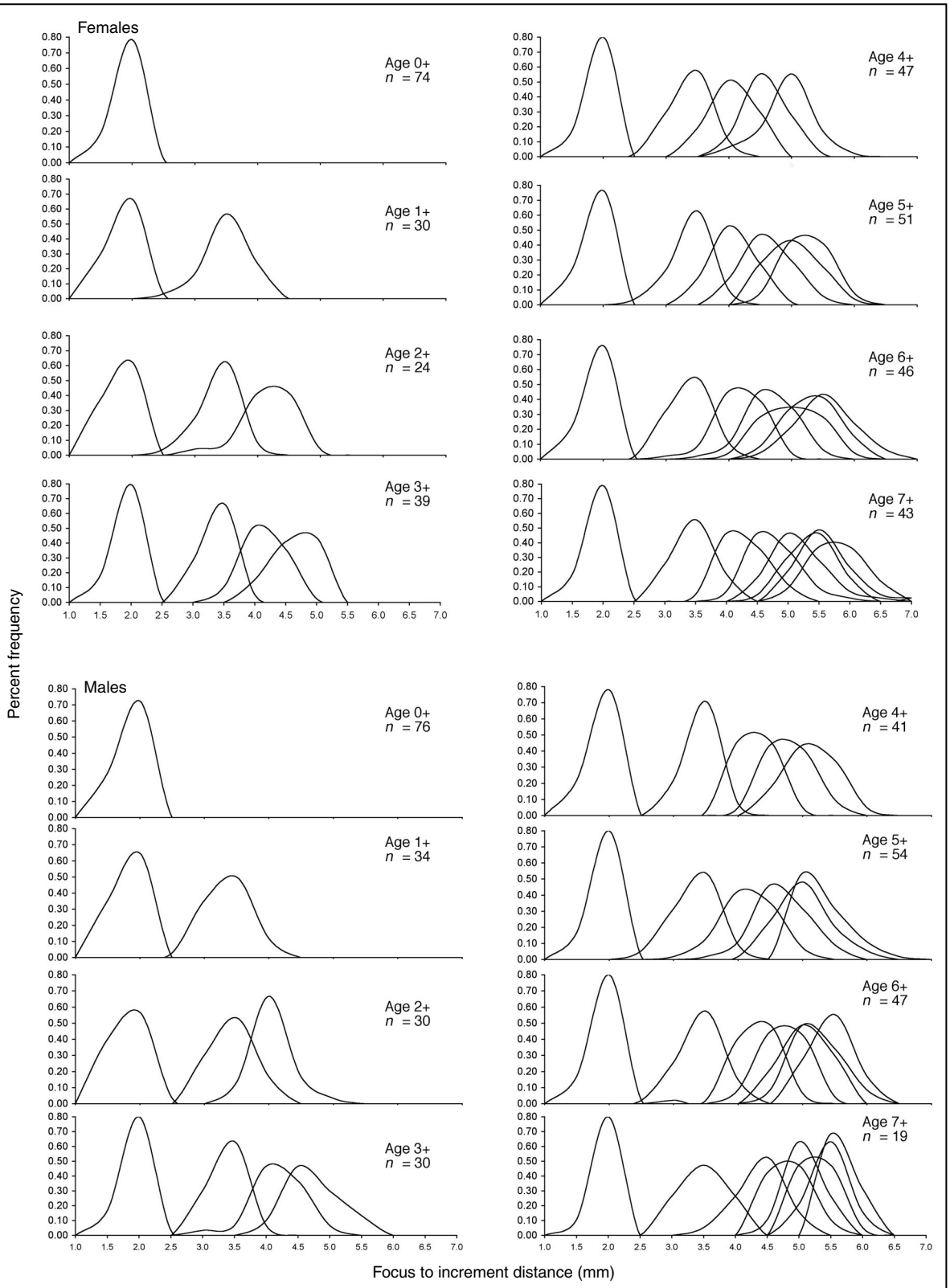

Figure 9

Focus to increment distance (mm) frequency distributions for males and females age 1+ to 7+. The first distribution represents the birth mark in all cases, subsequent distributions represent (from left to right) measurements to the first, second, third, fourth, fifth, sixth, and seventh increments, respectively.

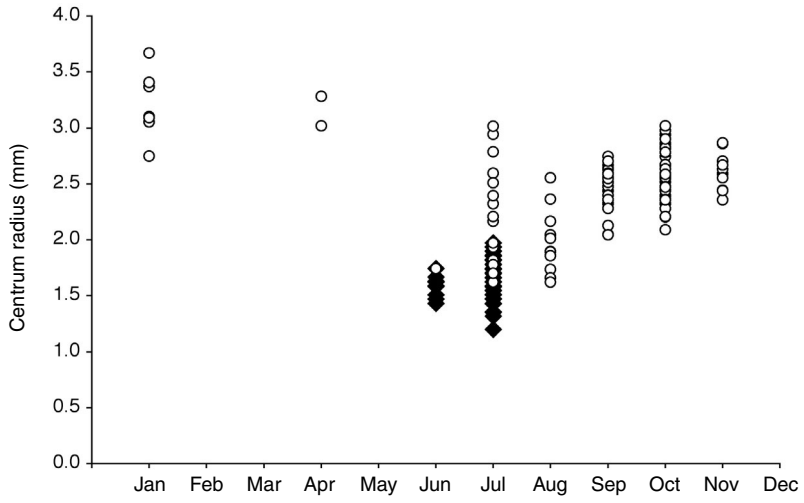

Figure 10

Centrum radius of age 0+ *R. terraenovae,* by month. (♦) represents individuals without a birth mark, (○) represents individuals with a birth mark.

Table 2

Von Bertalanffy growth parameters of *Rhizoprionodon terrraenovae* from the southeastern coast of the United States. Von Bertalanffy growth parameters from previous studies in the northern Gulf of Mexico are included for comparison.

	Von Bertanalanffy growth parameters								
Sex	L_∞ (mm PCL)	K	t_0	SE of L_∞	SE of K	SE of t_0	n	Data type	Study
Females	752	0.52	–1.07	5.33	0.025	0.052	433	age class	current
Males	746	0.53	–1.07	6.83	0.030	0.059	379		
Sexes combined	750	0.52	–1.07	4.23	0.019	0.039	812		
Females	749	0.49	–0.94	4.60	0.020	0.046	433	estimated actual age	current
Males	745	0.50	–0.91	5.93	0.024	0.052	379		
Sexes combined	748	0.50	–0.92	3.65	0.015	0.034	812		
Females	738	0.46	–0.90	2.64	0.006	0.015	1856	back-calculation	current
Males	726	0.53	–0.79	3.14	0.009	0.016	1447		
Sexes combined	732	0.49	–0.85	2.02	0.006	0.011	3303		
Sexes combined	820	0.36	–0.99	—	—	—	20	estimated actual age	Branstetter (1987a)
Males	709	0.39 to 0.53	–2.01	—	—	—	15	age class	Parsons(1985)

tially in length following the shift) to reliably fit a second regression line. The back-calculation equation used in our study does not employ the linear regression in its calculations and was minimally affected by the negative bias that this phenomenon had on the slope of the regression.

Marginal increment analysis in the present study indicated that growth increments form in summer. This finding is contrary to that of earlier studies on *R. terraenovae*, which indicated winter deposition (Parsons, 1985; Branstetter and McEachran, 1986; Branstetter 1987a). However, other species in this genus have been shown to deposit increments during the summer months. Simpfendorfer (1993) demonstrated summer (February) increment deposition in *R. taylori* in Australian waters. He cited stress during the breeding season as a possible cause because hepatosomatic index and condition factor in both sexes were low during the mating season, an indication of probable stress. Furthermore, growth increments in elasmobranchs may reflect periods of slow calcareous accretion that have been compressed by increased growth (Gelsleichter, 1998). This pattern of deposition may result in increments from periods of slow growth not becoming

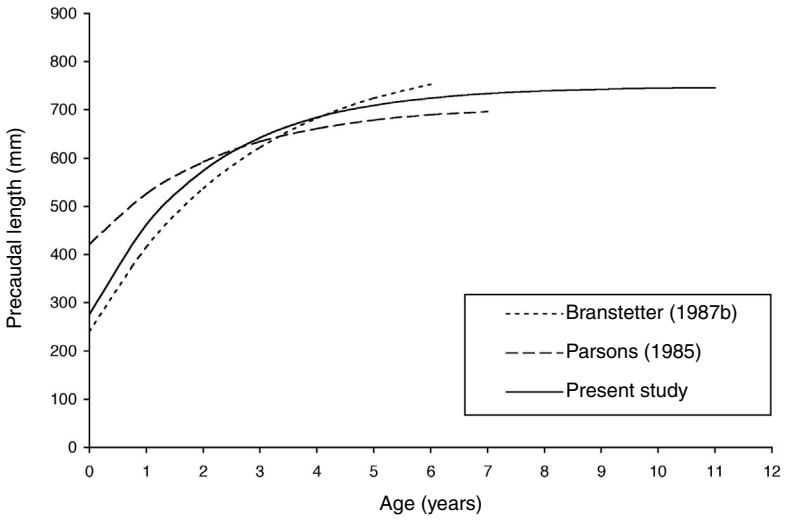

Figure 11

A comparison of growth curves for *R. terraenovae* from the present study with those from previous works by other authors. Growth curve from the present study is based on estimated actual ages for both sexes (parameter values are presented in Table 2).

visible for some time after their actual formation until enough new tissue has grown distally to provide the compression and contrast necessary for reliable identification. In other words, the increments observed in our study first became visible in July, but may have actually formed one to several months earlier. It should be noted that the methods of vertebrae processing and examination followed during our study were more similar to those of Simpfendorfer (1993) than to those of Parsons (1985) or Branstetter (1987a). These methods may have contributed to the close similarity found in both the physical appearance (i.e. that of "check marks" as opposed to pairs of growth bands) and temporal deposition of increments between our study and that of Simpfendorfer (1993).

We found young of the year *R. terraenova*e with and without a birth mark. This is unusual in that most studies that have documented the presence of a birth mark have found one present in all specimens examined (e.g. Casey et al., 1985; Branstetter, 1987b; Simpfendorfer, 1993). Simpfendorfer (1993) suggested that the "birth" mark in *R. taylori* was probably laid down sometime after birth because he observed the same overestimation of size at birth by back-calculations noted previously in our study. No temporal estimation of the lag between birth and the formation of a birth mark has been published. The young-of-the-year *R. terraenovae* examined during our study demonstrated a distinct temporal transition from the lack of a birth mark to the presence of a birth mark (Fig. 10). The data suggest that the birth mark is not actually laid down at birth in June, but approximately one month later in July. This time lag may explain the overestimation of size at birth by back-calculation. It is possible that the mechanism for the formation of the birth mark lies in the switch from embryonic to normal somatic growth, which may not occur immediately following parturition.

The von Bertalanffy growth parameters derived for our study demonstrated differences from those derived for previous studies (Fig. 11). Parsons (1985) estimated an L_∞ of 709 mm PCL, and Branstetter (1987a) 820 mm PCL. L_∞ for our study was 745 mm PCL for males, and 749 mm PCL for females. The t_0 value produced by Parsons was low at –2.01 yr, whereas the values produced by Branstetter (–0.99 yr) and our study (–0.90 yr for males and –0.94 yr for females) agreed well with the known gestation period of approximately 11 months. Parsons (1985) estimated K by several methods, resulting in values ranging from 0.39 to 0.53. The higher values agreed well with the estimates of our study (0.49 for females and 0.50 for males). Branstetter's (1987a) estimate of K was 0.36, lower than that of the current study.

Yearly growth rate estimates by Parsons (1983b) and Branstetter (1987a) revealed an increase of 133 to 211 mm PCL during the first year of life, 94 mm during the second year, 55 mm during the third year, and 16 to 32 mm growth after maturity. We found similar, though slightly higher growth rates: 198 to 202 mm PCL during the first year, 100 to 108 mm during the second, 63 to 69 mm during the third, and from 0 to 46 mm thereafter.

Parsons (1985) determined age at maturity by three methods: extrapolation of growth rates to size at maturity, the VBGE, and Holden's method (Holden, 1974). The estimates produced by these methods ranged from 2.0 to 3.5 for males, and 2.4 to 3.9 for females. Branstetter (1987a) compared his von Bertalanffy-derived estimates to those of Parsons (1985), and found his results in general agreement with Parsons' higher estimates. Branstetter (1987a)

thus concluded that males mature in three years and females in four. In our study, males reached full maturity at 2.4 to 2.6 years of age, making them functionally mature at the third breeding season following birth. Females were found to mature at 2.2 to 2.5 years, which would also result in full maturity just prior to the third postnatal breeding season. Although it was noted in both previously cited studies that males matured six months to one year earlier than females, no such discrepancy in age at maturity between the sexes was apparent in our study.

Differences between studies

The differences between this and previous studies on *R. terraenovae* are likely a combination of many contributing factors. These studies were conducted in different regions at separate times and may reflect clinal or temporal differences (or both) between Gulf of Mexico and northwestern Atlantic *R. terraenovae* populations. However, there are other contributing factors that must be considered as well, most notably differences in data collection and analysis techniques.

Parsons' (1985) growth curves were based on males and were grouped into age classes (not assigned actual ages). His von Bertalanffy parameters were then derived by using the Ford and Walford plot method (Parsons, 1985), requiring the use of mean lengths of each age class. This age class grouping does not take into account growth since the deposition of the last increment, and may therefore bias the Ford and Walford plot by pulling the data to a faster asymptote (Branstetter and McEachran, 1986; Branstetter, 1987a;). This bias produced a low L_∞ (706 mm PCL) and t_0 (–2.01 years) in Parsons' estimates (Branstetter and McEachran, 1986; Branstetter, 1987a). This phenomenon was not evident in VBGE estimates based on age classes in our study, which were very similar to estimates based on actual ages (Table 2), and was probably due to the fact that iterative fitting of age data to the VBGE by computer software (an option unavailable to Parsons at the time of his study) is less sensitive to unaddressed growth than the graphically based Ford and Walford plot method.

Although the aging technique used by Branstetter (1987a) was similar to that of our study (counts on longitudinal sections of cervical centra), Parsons' (1985) aging technique took ring counts from the face of centra that had been removed from a more posterior region of the vertebral column than the region chosen in our study. It has been stated by several authors (Branstetter and McEachran, 1986; Martin and Cailliet, 1988; Kusher et al., 1992) that increment counts made from sections of vertebral centra are generally preferable to those taken from the face of unsectioned centra. Sectioned centra allow for better documentation of the increment structure near the edge because the increments become narrower and more difficult to delineate with increasing age (Branstetter and McEachran, 1986; Martin and Cailliet, 1988; Kusher et al., 1992). This distinction is critical when the potential consequences of age underestimation (including overestimation of K, growth rate, and maximum sustainable yield) are considered.

Based on comparison of our work to that of previous studies (Branstetter, 1981, 1987a; Parsons, 1983a, 1983b, 1985), there may be differences between the Gulf of Mexico and southeastern U.S. Atlantic populations of Atlantic sharpnose sharks. The question then becomes whether these differences are clinal or temporal in nature. Clinal variation, for instance, may explain the differences noted in size and age at maturity in female *R. terraenovae*. Simpfendorfer (1993) noted differences in size at maturity between populations of *R. taylori* in Australia, as did Parsons (1993) and Carlson et al. (1999) between populations of *Sphyrna tiburo* and *Carcharhinus acronotus*, respectively, off the Gulf coast of Florida. However, the extended time frame between the current and previous studies (15 to 20 years), also opens the possibility that the differences are related to a temporal change in population structure of the species across the entire Gulf and Western Atlantic region. In the earlier studies, data were collected during a time when fishing pressure (both directed and indirected) on *R. terraenovae* was lower than at present, and fisheries were shown to have dramatic effects on shark populations in less time (Anonymous[1]). The differences noted between the studies may thus be a manifestation of temporal changes in population structure of the species as a whole over the last two decades. A more current study on Gulf of Mexico *R. terraenovae* is needed to properly address these potential population differences.

Conclusion

Small shark species such as *R. terraenovae* tend to show rapid growth in the first few years of life and a dramatically slower growth rate once maturity is reached. This aspect of their growth complicates age estimation by vertebral increments because the most recent marks in older specimens are so closely spaced that accurate counting and measurement become problematic. The overlapping of increments in these older specimens or the lack of identifiable increment formation altogether due to asymptotic growth may lead to an underestimation of ages in large adults. Althhough the maximum age demonstrated in our study was 11+ years, the actual life span of *R. terraenovae* may be longer.

The life history parameter estimates that have been presented in our study are based on one of the largest short-term samples collected for any study of elasmobranch life history to date. The most significant aspect of this study is the documentation of differences in size and age at maturity between female *R. terraenovae* in the Gulf of Mexico and females off the southeastern U.S. coast. A difference in age of maturity of one year in an animal with a relatively short life span, such as *R. terraenovae,* can have a dramatic effect on the outcome of population models (see Cortes, 1995). Although the documentation of age at maturity differences by different researchers may be highly susceptible

[1] Anonymous. 1993. Fishery management plan for sharks of the Atlantic Ocean, 167 p. U.S. Dep. Commerce., NOAA, NMFS, Silver Spring, MD 20910.

to analytical bias during the aging process, the documentation of differences in size at maturity is unmistakable.

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