Abstract–The life history and population dynamics of the finetooth shark (*Carcharhinus isodon*) in the northeastern Gulf of Mexico were studied by determining age, growth, size-at-maturity, natural mortality, productivity, and elasticity of vital rates of the population. The von Bertalanffy growth model was estimated as L_t=1559 mm TL $(1-e^{-0.24\,(t+2.07)})$ for females and L_t= 1337 mm TL $(1-e^{-0.41\,(t+1.39)})$ for males. For comparison, the Fabens growth equation was also fitted separately to observed size-at-age data, and the fits to the data were found to be similar. The oldest aged specimens were 8.0 and 8.1 yr, and theoretical longevity estimates were 14.4 and 8.5 yr for females and males, respectively. Median length at maturity was 1187 and 1230 mm TL, equivalent to 3.9 and 4.3 yr for males and females, respectively. Two scenarios, based on the results of the two equations used to describe growth, were considered for population modeling and the results were similar. Annual rates of survivorship estimated through five methods ranged from 0.850/yr to 0.607/ yr for scenario 1 and from 0.840/yr to 0.590/yr for scenario 2. Productivities were 0.041/yr for scenario 1 and 0.038/ yr for scenario 2 when the population level that produces maximum sustainable yield is assumed to occur at an instantaneous total mortality rate (Z) equaling 1.5 M, and were 0.071/yr and 0.067/yr, when Z=2 M for scenario 1 and 2, respectively. Mean generation time was 6.96 yr and 6.34 yr for scenarios 1 and 2, respectively. Elasticities calculated through simulation of Leslie matrices averaged 12.6% (12.1% for scenario 2) for fertility, 47.7% (46.2% for scenario 2) for juvenile survival, and 39.7% (41.6% for scenario 2) for adult survival. In all, the finetooth shark exhibits life-history and population characteristics intermediate to those of sharks in the small coastal complex and those from some large coastal species, such as the blacktip shark (*Carcharhinus limbatus*).

Life history and population dynamics of the finetooth shark (*Carcharhinus isodon*) in the northeastern Gulf of Mexico

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In 1993, a fishery management plan for sharks (NMFS, 1993) was developed for the management of shark populations in waters of the U.S. Atlantic and Gulf of Mexico. Because species-specific catch and life history information was limited, sharks were grouped and managed under three categories: large coastal, small coastal, and pelagic, based on known life history, habitat, market value, and fishery characteristics (NMFS, 1993). Sharks in the large coastal grouping included relatively large, slow-growing, and long-lived species, whereas the small coastal complex included relatively small, fast-growing, and short-lived species of sharks.

Generally, commercial fishermen target and harvest sharks in the large coastal complex (e.g. blacktip shark (*Carcharhinus limbatus*) and sandbar shark (*Carcharhinus plumbeus*)). Small coastal sharks are usually taken incidentally in numerous commercial fisheries and are commonly discarded or used for bait. More recently, with the reductions in commercial quotas for large coastal species since 1993 (NMFS, 1999), fishermen have been increasingly targeting small coastal sharks. Estimated commercial landings of small coastal sharks increased from 7 metric tons (t) dressed weight in 1994 to 305 t dressed weight in 1999. Estimated recreational catches of small coastal sharks reached a peak of 170,000 animals in 1998 (Cortés[1]). Given the importance of small coastal sharks as bycatch and their increasing value in directed commercial and recreational fisheries, it is important to obtain current and accurate information on their life history. This information can then be used in population models incorporating variation and uncertainty in estimates of life-history traits to predict the productivity of the stocks and ensure that they are harvested at sustainable levels.

The finetooth shark (*Carcharhinus isodon*) is a moderate-size species of the small coastal shark group found in coastal waters of the northwestern Atlantic Ocean from North Carolina to Florida, throughout the Caribbean Sea, and the Gulf of Mexico (Compagno, 1984; Castro, 1993). This species makes up a significant portion of a directed drift gillnet fishery operating off the southeast U.S. coast (Trent et al., 1997;

[1] Cortés, E. 2000. 2000 shark evaluation annual report. Sustainable Fisheries Division contribution no. SFD-00/01-119, 23 p. Southeast Fisheries Center, National Marine Fisheries Service, 3500 Delwood Beach Rd., Panama City, FL 32408.

Carlson[2]), with estimated commercial landings peaking at about 129.4 t dressed weight in 1999 (Cortés, unpubl. data). However, life-history information for this species is mostly restricted to some aspects of its reproduction and general biology (Branstetter, 1981; Castro, 1993). The purpose of the present study is to investigate the life history and population dynamics of the finetooth shark from the northeastern Gulf of Mexico. Specifically, we wish 1) to estimate age, growth, and natural mortality, 2) to determine size-at-maturity, and 3) to assess productivity and identify the vital rates to which population growth rates are most sensitive.

Materials and methods

Collection and laboratory processing

Finetooth sharks were collected from fishery-independent surveys in the northeastern Gulf of Mexico, from St. Andrew Bay to Apalachicola Bay, FL, during April–October from 1995 to 1999 (Carlson and Brusher, 1999). A 186-m long gill net consisting of panels of six different mesh sizes was used for sampling. Stretched mesh sizes ranged from 8.9 cm to 14.0 cm in steps of 1.27 cm, and an additional mesh size of 20.3 cm was used. Panel depths when fishing were 3.1 m. Webbing for all panels, except for that with 20.3-cm mesh size, was clear monofilament, double-knotted and double-selvaged. The 20.3-cm webbing was made of no. 28 multifilament nylon, single-knotted, and double-selvaged. When set, the nets were anchored at both ends. Generally, soak time ranged from 1.0 to 2.0 hours.

Precaudal (PC), fork (FL), total (TL), and stretched total (STL) length (mm), sex, and maturity state were determined for each shark. We developed several morphometric relationships to convert length measurements. Linear regression formulae were determined as FL=1.10(PC)+0.60; TL=1.23(FL)+20.34; and STL=1.10(TL)+11.25. All equations were highly significant (P<0.0001) and had coefficients of determination (r^2) between 0.97 and 0.99. Because most previous studies on small coastal species have summarized information in total length, i.e. the straight line from the tip of the snout to the tip of the tail in a natural position, our results are reported in natural TL to provide a direct comparison.

Maturity was assessed according to the guidelines of Castro (1993). Males were deemed mature if they possessed hardened claspers and the rhipidion opened freely. Females were considered mature if they were gravid, had oocytes larger than 26 mm in diameter, or if nidamental gland width was greater than 20 mm.

Vertebrae for age determination were collected from the column between the origin and termination of the first dorsal fin. Vertebral sections were placed on ice after collection

and were frozen upon arrival at the laboratory. Thawed vertebrae were cleaned of excess tissue and soaked in a 5% sodium hypochlorite solution for 5–30 min to remove remaining tissue. After cleaning, the vertebrae were soaked in distilled water for 30 min and stored in 95% isopropanol alcohol. Prior to examination, vertebrae were removed from alcohol, dried, and measured (length and width in mm).

Visual enhancement of growth bands

Various methods were tested to enhance visibility of growth bands. Sagittal sections were cut from the vertebral centrum at different thicknesses and stained with 0.01% crystal violet (Johnson, 1979; Schwartz, 1983), alizarin red (Gruber and Stout, 1983), or left unstained. Each section was mounted on a glass microscope slide with clear resin and examined under a dissecting microscope with transmitted light. Growth bands were found to be most apparent with the crystal violet stain on sagittal sections with a thickness of 0.35 mm (Fig. 1).

The distances from the centrum origin to the distal edge of each growth band and from the centrum origin to the centrum edge were measured by using the Image Tools, version 2 software package (UTHSCSA Image Tool, 1997). Each growth band included a broad light mark representing summer growth and a thin dark mark representing winter growth (Branstetter and Stiles, 1987). All three authors aged each specimen without knowledge of its length or sex. Two sets of independent age readings were made, the second set after consultation among the authors. The index of average percent error (APE; Beamish and Fournier, 1981) and the percentage of disagreements by $\pm i$ rings among authors were computed for the first set of age readings.

Determination of growth curves

Sex-specific relationships between total length (TL) and vertebral radius (VR) were calculated to determine the most appropriate method for back-calculation. Because no difference was found between sexes (ANCOVA: F=0.40, df=1, $P \geq 0.05$), they were combined to generate a linear relationship: TL= 153.75(VR) + 305.68 (P<0.0001; r^2=0.90; n=239). Because the intercept of the relationship did not pass through the origin, we applied a method proposed by Campana (1990), which is a modified Fraser-Lee equation that uses a biologically derived intercept:

$$L_a = L_c + \left((O_a - O_c) \times (L_c - L_0) / (O_c - O_0) \right),$$

where L_a = length at age a;
O_a = otolith distance from focus to annulus a;
O_c = otolith radius at capture;
L_c = length at capture;
L_0 = length at birth; and
O_0 = otolith radius at birth.

The biologically derived intercept corresponds to the size of the otolith (or analogous aging structure, i.e. vertebra)

[2] Carlson, J. K. 2000. Progress report on the directed shark gillnet fishery:right whale season, 2000. Sustainable Fisheries Division contribution no. SFD-99/00-90, 12 p. Southeast Fisheries Center, National Marine Fisheries Service, 3500 Delwood Beach Rd., Panama City, FL 32408.
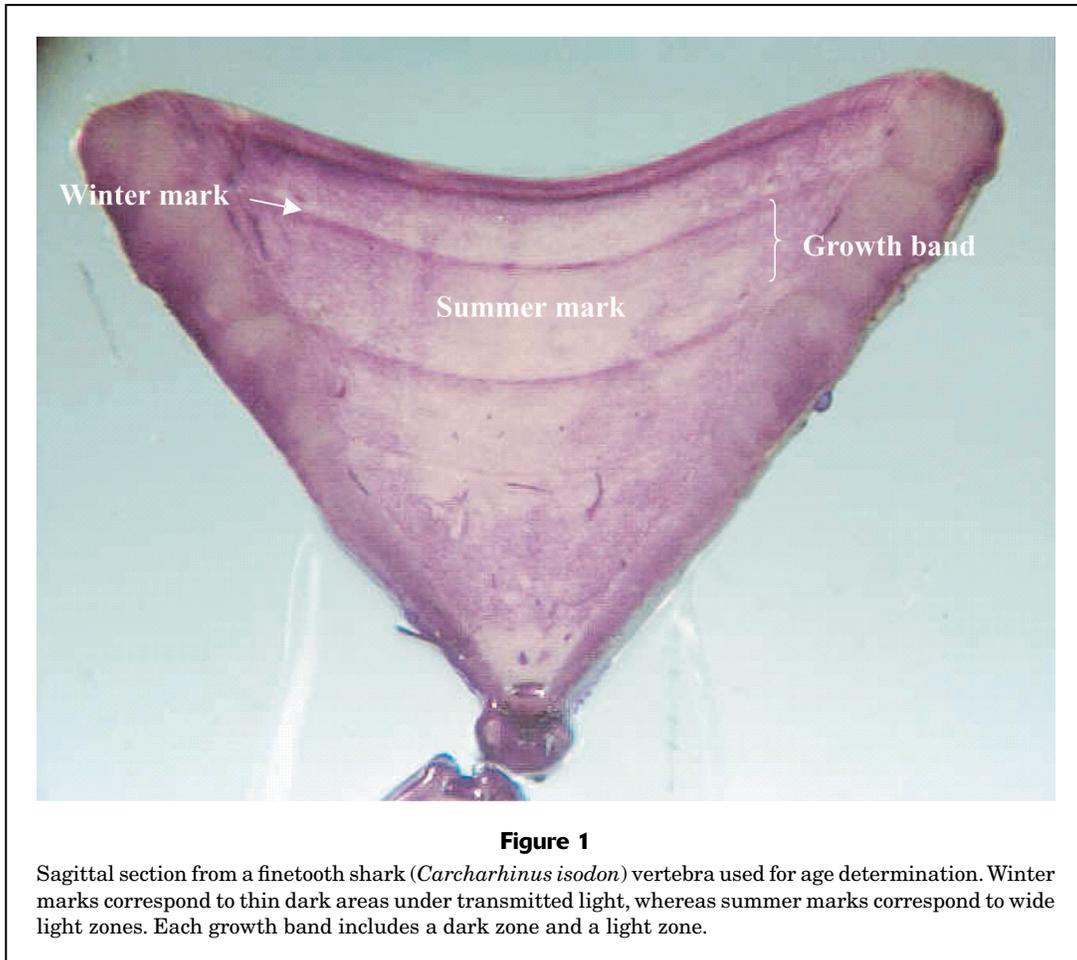
Figure 1

Sagittal section from a finetooth shark (*Carcharhinus isodon*) vertebra used for age determination. Winter marks correspond to thin dark areas under transmitted light, whereas summer marks correspond to wide light zones. Each growth band includes a dark zone and a light zone.

and fish at the time of hatching (Campana, 1990). For the finetooth shark, we used the estimated size at birth in the northeastern Gulf of Mexico (520 mm TL; Carlson, unpubl. data).

In developing theoretical growth models, we assumed that 1) the birth mark is the band associated with a pronounced change in angle in the intermedialia and is formed on an arbitrary birth date of 1 June, 2) growth bands are formed once a year, and 3) the narrow dark marks are deposited in winter on an arbitrary date of 1 January. Ages were calculated by using the algorithm: *age = the birth mark + number of winter marks −1.5, + the proportion of the year from winter mark deposition to the date of capture.* If only the birth mark was present, age was calculated as the time between birth and date of capture.

The von Bertalanffy growth model (Eq. 1; von Bertalanffy, 1938) was fitted separately to observed and back-calculated size-at-age data using the equation

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

where L_t = predicted length at time t;
L_∞ = theoretical asymptotic length;
K = growth coefficient; and
t_0 = theoretical age at zero length.

Growth model parameters were estimated by using least-squares nonlinear regression (SAS PROC NLIN; SAS, 1988).

For comparison, an alternate equation of the von Bertalanffy growth model (Eq. 2; Fabens, 1965) was also fitted separately to observed size at age data. This equation is described as

$$L_t = L_\infty (1 - b e^{-Kt}) = L_\infty - (L_\infty - L_0)e^{-Kt},$$

$$b = (L_\infty - L_0)/L_\infty = e^{Kt_0},$$

where L_t = predicted length at time t;
L_∞ = theoretical asymptotic length;
K = growth coefficient; and
L_0 = the length at birth.

Verification of the annual period of band formation was attempted by using the relative marginal increment analysis (Natanson et al., 1995):

$$MIR = (VR - R_n)/(R_n - R_{n-1}),$$

where MIR = the marginal increment ratio;
VR = the vertebral radius;

R_n = the last complete band; and
R_{n-1} = the next-to-last complete band.

Mean MIR was plotted against month to determine trends in band formation. A single factor analysis of variance was used to test for differences in MIR among months.

Chi-square tests of likelihood ratios (Kimura, 1980; Cerrato, 1990) implemented by using SAS code were used to determine whether there were differences between sexes. Theoretical longevity was estimated as the age at which 95% of L_∞ is reached (5(ln2)/K; Fabens, 1965; Cailliet et al., 1992).

Estimation of size at maturity

Median total length at maturity for male and female sharks was determined by fitting a logistic model, $Y=1/(1+e^{-(a+bX)})$, where Y=the binomial maturity data (immature=0, mature=1; Mollet et al., 2000) and X=total length (mm). Median total length at maturity was expressed as $MTL = -a/b$. The model was fitted using least squares nonlinear regression (S-Plus 2000, 2000).

Estimation of natural mortality, productivity, and elasticity

The instantaneous rate of natural mortality (M) was estimated by five indirect life-history methods described extensively elsewhere (see Cortés, 2002, and references therein). Four of the five methods (Pauly, 1980; Chen and Watanabe, 1989; and two methods by Jensen, 1996) use parameters estimated through the von Bertalanffy growth model. The fifth method (Peterson and Wroblewski, 1984) estimates M based on body mass. All required parameter estimates (age at maturity, maximum age, L_∞, K, t_0) were taken from the aging section of the present study. Mean annual water temperature (21.8°C), which is needed in the Pauly method, was taken from Brusher and Ogren (1976). Body mass of finetooth sharks at age was estimated by converting age into length through the growth model derived in the present study, and length into weight through the power relationship given in Castro (1993).

Population growth rates and productivity were estimated by two methods that complement each other. Productivity (i.e. rebound potential as defined in Smith et al., 1998) was calculated by a modified demographic technique that incorporates concepts of density dependence (Smith et al., 1998). In this method, rebound potentials or productivities (r_z) are calculated at the population level producing maximum sustainable yield (MSY), which is assumed to occur at $Z = 1.5\ M$ or, alternatively, at $Z = 2\ M$ (Z=total instantaneous mortality rate).

Two methods that assume density independence also were used. Life tables allowed calculation of mean generation times ($\overline{A}$), and Leslie matrix population models were used to estimate population growth rates ($\lambda=e^r$) and to calculate elasticities (proportional sensitivities; Caswell, 2001). Elasticities for fertility, juvenile survival, and adult survival were obtained by summation of matrix element elasticities across relevant age classes (e.g. fertility elastic-ity is the sum of all first-row elasticities) and sum to 1. The fertility term in matrix methodology includes survival to age-1 (see Cortés, 2002, for details).
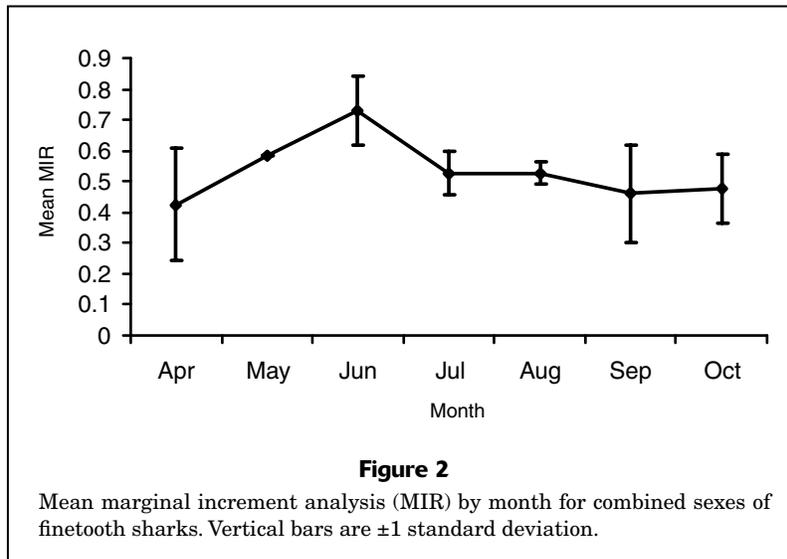
Probability density functions (pdfs) were developed to describe age at maturity, maximum age, M, survivorship at age ($S_x=e^{-M}$), and fecundity at age (m_x) for females, following in part the method and rationale in Cortés (2002). Two scenarios, based on the results of the two equations used to describe growth, were considered.

Scenario 1 Age at maturity was represented by a triangular distribution with 4.3 yr as the likeliest value and ±1 yr (3.3, 5.3 yr) as lower and upper bounds. Maximum age was represented by a linearly decreasing distribution scaled to a total relative probability of 1. The likeliest value corresponded to the age of the oldest animal aged in the age and growth study (8 yr) and the lower bound was the theoretical estimate of longevity (14.4 yr).

Natural mortality (M) for adults for the Smith et al. (1998) method was represented by a uniform distribution ranging from 0.162 (minimum) to 0.499 (maximum). Conversely, annual survivorship at age in the density-independent model was represented by a uniform distribution that ranged from the minimum estimate ($0.607=e^{-0.499}$) to a maximum, generally corresponding to the estimate derived through the weight-based method (which ranged from 0.722/yr at age 0 to 0.850/yr at age 15). Fecundity at age was assumed to follow a normal distribution with a mean of 4.036 and SD=0.793, with the lower and upper bounds of 2 and 6 reflecting the range of litter sizes reported for this species (Castro, 1993). We assumed a 1:1 male-to-female ratio, that 100% of females were reproductively active after reaching maturity, and a reproductive cycle of 2 yr. The percentage of mature females at age was estimated from the logistic model.

Scenario 2 The age-at-maturity and fecundity-at-age distributions were identical to those in scenario 1. The only difference in the pdf describing maximum age in this scenario compared to that used in scenario 1 was that the theoretical estimate of longevity (9.9 yr) was lower. Natural mortality for adults for the Smith et al. (1998) method was also represented by a uniform distribution ranging from a minimum of 0.174 to a maximum of 0.528. Survivorship at age in the density-independent model was represented by a uniform distribution that ranged from the minimum estimate ($0.590=e^{-0.528}$) to a maximum, generally corresponding to the estimate derived through the weight-based method (which ranged from 0.689/yr at age 0 to 0.840/yr at age 10).

The simulation and projection process involved randomly selecting a set of life-history traits from the pdfs describing each individual trait and calculating productivity (r_Z) in the modified demographic technique and population growth rates (λ), generation times ($\overline{A}$), and fertility, juvenile survival, and adult survival elasticities in the life table and matrix population model approach. This process was repeated 10,000 times, yielding frequency distributions, means, medians, and confidence intervals (calculated as the 2.5th and 97.5th percentiles) for parameter estimates. All

Figure 2

Mean marginal increment analysis (MIR) by month for combined sexes of finetooth sharks. Vertical bars are ±1 standard deviation.

simulations were run with Microsoft Excel spreadsheet software (Math Tools, Ltd., 1999) equipped with risk analysis and matrix algebra software and Microsoft Visual Basic for Applications (Crystal Ball, 2000).

Results

Age, growth, and maturity

The precision of band counts was high among the readers (authors). The first set of readings resulted in two or three out of three band count estimates agreeing in 97.7% of the cases, and an APE of 6.8%. Percent disagreement in band counts among the three readers was 42.9% within ±1 band, 5.6% within ±2 bands, and 0.4% within ±3 bands. After consultation, we reached agreement in 239 out of 247 (97%) vertebrae. Samples where counts had differed among the readers were discarded.

Although monthly changes in marginal increment analysis were found, peaks were not statistically different (single factor ANOVA; df=6, P=0.371). An increase in increment growth occurred from April until June, followed by a slow decrease and leveling until October (Fig. 2). The decrease in incremental growth from June through October was not large enough to indicate a double band formation (Natanson et al., 1995); thus bands were assumed to form once a year. A similar trend of increment growth was also reported for the blacknose shark (*Carcharhinus acronotus*) by Carlson et al. (1999).

The values of K (0.24/yr versus 0.35/yr for females, and 0.41/yr versus 0.49/yr for males) and L_∞ (1560 mm versus 1442/mm for females, and 1338/mm versus 1309/mm for males) obtained with the original von Bertalanffy (1938) growth equation (Eq. 1) and the modified equation of Fabens (1965) (Eq. 2) were somewhat different, but the fits to the observed data were similar (Table 1; Fig. 3). Because of the similarity between the models and the general and

ubiquitous use of equation 1 (von Bertalanffy, 1938), we present and compare further age and growth results using only the von Bertalanffy (1938) model.

Observed and back-calculated von Bertalanffy parameters and growth rates differed between males and females (Table 1 and Table 2). For both sexes, growth was rapid until age 4–5, slowing down for males thereafter, whereas the reduction in growth rate for females was not so accentuated (Fig. 3). Females had a lower growth coefficient (K=0.24/yr) than males (K=0.41/yr), and a higher theoretical maximum size (L_∞=1560 mm for females versus 1338 mm for males). Significant differences (log-likelihood ratio=14.46; P<0.001) between von Bertalanffy growth curves of males and females were found. Theoretical longevity estimates were 14.4 and 8.5 yr for scenario 1, and 9.9 and 7.2 yr for scenario 2, and the oldest aged sharks were 8.0 and 8.1 yr for females and males, respectively.

We found no significant differences (Kruskal-Wallis χ^2=0.101, P=0.751) in age distribution between sexes (Fig. 4). The most frequently occurring age classes were ages 4+, 3+, and 2+ for males, and ages 2+ and 3+ for females, each comprising between 19–22% and 18–24% of the samples for each sex, respectively. Young-of-the-year sharks (age 0+) made up 7.3% of all males and 11.1% of all females, whereas adults (ages 5–8) constituted 17.1% and 22.2%, respectively.

Back-calculated size at birth was estimated at 538 mm TL for both male and female sharks and matched well the known size at birth in the northeastern Gulf of Mexico (480–530 mm TL; Carlson, unpubl. data) (Table 2). Back-calculated mean lengths were smaller than observed lengths and when these were compared among older-aged sharks, Lee's phenomenon (Ricker, 1992) was apparent.

Median total length at maturity differed between males and females (Fig. 5). For males, the size at which 50% of the population reached maturity was 1187 mm TL, which corresponds to an age at maturity of ~3.9 yr. The smallest mature male found was 1000 mm TL and the largest

Table 1

Parameters of the von Bertalanffy growth models for male and female finetooth sharks. Estimates are provided for models developed with observed and back-calculated size at age. Equation 1 is the original von Bertalanffy growth model (von Bertalanffy, 1938) and Equation 2 is the modified von Bertalanffy growth model (Fabens, 1965). n = number of sharks in sample.

	Male	Asymptotic standard error	Lower 95% confidence limit	Upper 95% confidence limit	Female	Asymptotic standard error	Lower 95% confidence limit	Upper 95% confidence limit
Observed (Eq. 1)								
L_∞ (mm)	1337.8	27.9	1282.5	1393.2	1559.6	69.7	1421.6	1697.6
K (/yr)	0.412	0.043	0.327	0.496	0.244	0.036	0.173	0.315
t_0 (yr)	−1.390	0.178	−1.744	−1.037	−2.067	0.274	−2.610	−1.524
n	123				117			
Observed (Eq. 2)								
L_∞ (mm)	1309.3	20.657	1268.4	1350.2	1441.6	36.4	1369.5	1513.7
K (/yr)	0.487	0.033	0.422	0.551	0.352	0.029	0.295	0.409
n	123				117			
Back-calculated								
L_∞ (mm)	1347.1	19.3	1309.2	1385.0	1519.1	35.0	1450.3	1588.0
K (/yr)	0.383	0.019	0.347	0.419	0.282	0.018	0.247	0.318
t_0 (yr)	−1.135	0.054	−1.243	−1.209	−1.348	0.081	−1.490	−1.205
n	493				457			

Table 2

Back-calculated mean total length (mm) and observed mean total length (mm) at band formation for male (n=123) and female (n=117) finetooth sharks.
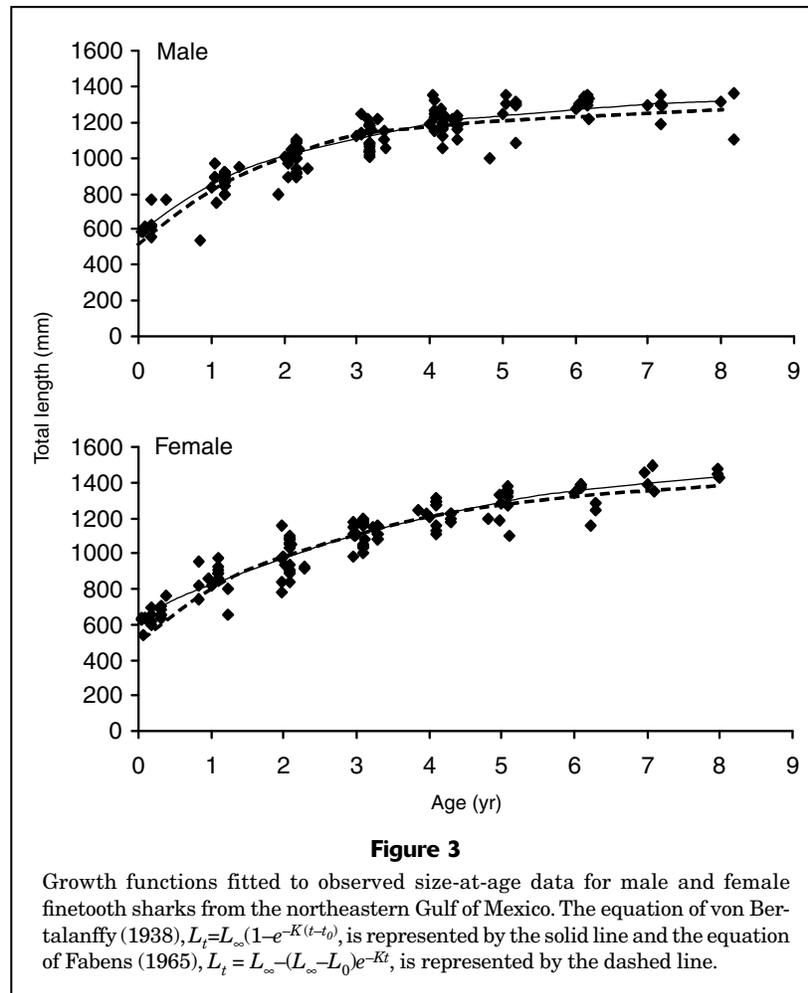
Band number	Birth	1	2	3	4	5	6	7	8
Male									
Back-calculated	538	758	963	1090	1173	1229	1252	1256	1220
SD	54.6	54.3	70.2	81.8	78.6	81.4	78.6	97.6	183.7
n	122	113	94	71	48	21	15	7	2
Observed	629	872	1006	1115	1201	1273	1307	1287	1230
SD	84.8	56.7	67.3	72.2	74.4	97.7	40.3	59.6	183.8
n	9	19	23	24	27	6	8	5	2
Female									
Back-calculated	538	751	950	1097	1199	1258	1317	1401	1445
SD	60.0	71.4	88.1	80.1	78.0	82.0	80.4	55.0	0.1
n	117	104	89	61	40	26	13	5	2
Observed	651	852	994	1109	1223	1287	1322	1434	1461
SD	53.9	79.3	96.7	62.7	63.1	82.6	85.8	30.4	21.3
n	13	15	28	21	14	13	8	3	2

immature male was 1298 mm TL. For females, the size at which 50% of the population was mature was 1230 mm TL, which is about 4.3 yr of age. The smallest mature female was 1187 mm TL and the largest immature female was 1240 mm TL.

Natural mortality, productivity, and elasticity

Scenario 1 Estimates of instantaneous rates of natural mortality for adults ranged from a minimum of 0.162 obtained through the Peterson and Wroblewski (1984) method to a maximum of 0.499 obtained through the Jensen (1996) method for an age at maturity of 3.3 yr or, when expressed as survivorship, from 0.850/yr to 0.607/yr. All other annual survivorship estimates for adults fell within that range: 0.671/yr for the Pauly (1980) method, 0.732/yr for the Jensen (1996) method based on an age at maturity of 5.3 yr, 0.694/yr for the Jensen (1996) method based on K, and 0.745–0.762/yr for the Chen and Watanabe (1989) method. Estimates of survivorship at age from the

Figure 3

Growth functions fitted to observed size-at-age data for male and female finetooth sharks from the northeastern Gulf of Mexico. The equation of von Bertalanffy (1938), $L_t = L_\infty(1 - e^{-K(t-t_0)})$, is represented by the solid line and the equation of Fabens (1965), $L_t = L_\infty - (L_\infty - L_0)e^{-Kt}$, is represented by the dashed line.

Peterson and Wroblewski (1984) method ranged from 0.722/yr for age-0 sharks to 0.850 for age-15 sharks.
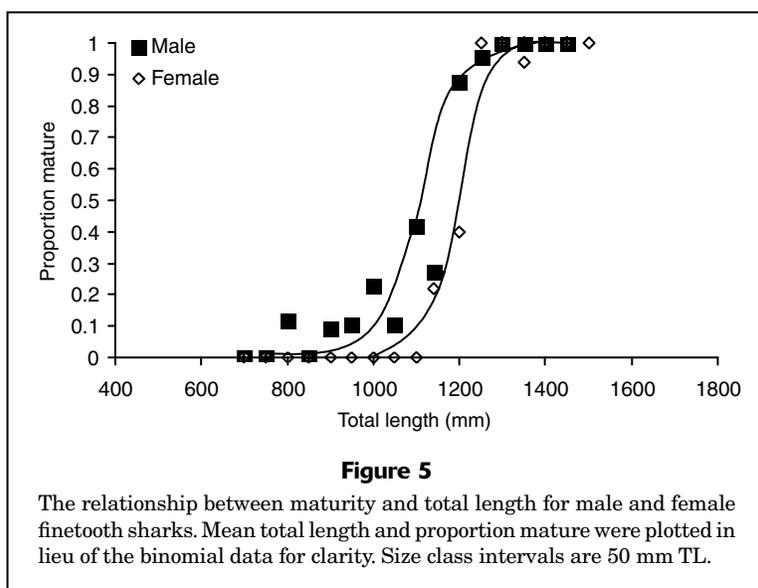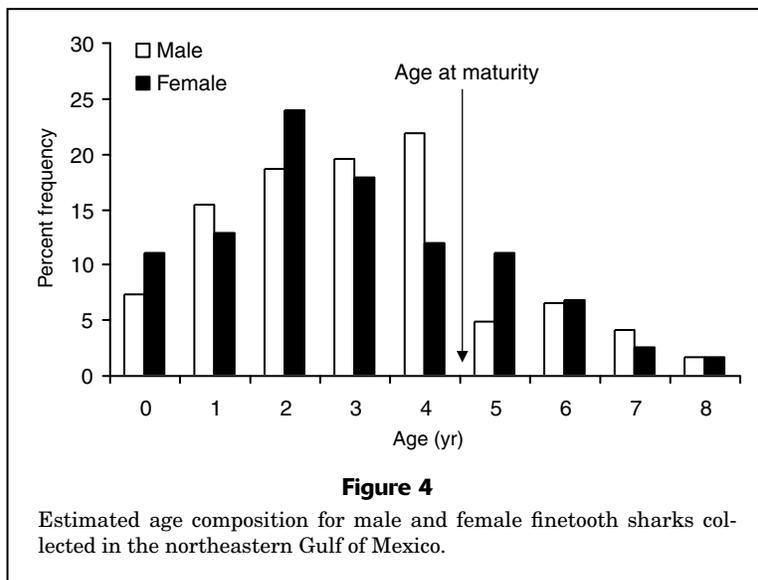
Productivities obtained through the density-dependent method averaged 0.041/yr, (median 0.042, 95% confidence limits: 0.024–0.054) for $Z=1.5$ M and 0.071/yr (0.073, 0.045–0.091) for $Z=2$ M (Fig. 6). Generation times obtained through life table simulation averaged 6.96 yr (6.90, 6.13–8.01). Expressed as a percentage, fertility elasticities averaged 12.6% (12.6, 11.1–14.0), elasticities of juvenile survival were 47.7% (48.9, 37.4–56.9), and those of adult survival totaled 39.7% (38.9, 31.5–50.2).

Scenario 2 Estimates of M for adults ranged from a minimum of 0.174 obtained through the Peterson and Wroblewski (1984) method to a maximum of 0.528 obtained through the Jensen (1996) method based on K or, when expressed as survivorship, from 0.840/yr to 0.590/yr. All other annual survivorship estimates for adults fell within that range: 0.596/yr for the Pauly (1980) method, and 0.607 and 0.732/yr for the Jensen (1996) method based on ages at maturity of 3.3 and 5.3 yr, respectively. Estimates of survivorship at age from the Peterson and Wroblewski (1984) method ranged from 0.689/yr for age-0 sharks to 0.840/yr for age-10 sharks.

Productivities from the density-dependent method averaged 0.038/yr (0.038, 0.023–0.052) for $Z=1.5$ M and 0.067/yr (0.068, 0.043–0.088) for $Z=2$ M (Fig. 6). Mean generation lengths from life tables averaged 6.34 yr (6.32, 5.75–7.04), fertility elasticities averaged 12.1% (12.3, 4.3–12.8), juvenile survival elasticities were 46.2% (48.9, 35.1–59.4), and adult survival elasticities totaled 41.6% (38.8, 28.6–53.2).

Discussion

Finetooth sharks exhibit age and growth characteristics intermediate to those of sharks in the small coastal complex (e.g. Atlantic sharpnose, blacknose, and bonnethead shark) and those of some large coastal sharks, such as the blacktip shark. For example, the bonnethead shark (*Sphyrna tiburo*) has been reported to have K values of 0.28–0.69/yr, age at maturity of 2.0–2.4 yr, and longevity of 6–12 yr (Parsons, 1993a; Carlson and Parsons, 1997). Finetooth sharks displayed lower K values (0.24–0.41/yr), and higher age at maturity (3.9–4.3 yr) and longevity (8–14 yr) estimates. These growth characteristics are closer to those exhibited by the blacktip shark (Branstetter, 1987;

Figure 4

Estimated age composition for male and female finetooth sharks collected in the northeastern Gulf of Mexico.

Figure 5

The relationship between maturity and total length for male and female finetooth sharks. Mean total length and proportion mature were plotted in lieu of the binomial data for clarity. Size class intervals are 50 mm TL.

Killam and Parsons, 1989) than to those from other small coastal species (Table 3).

The von Bertalanffy age and growth model based on observed data appears to provide a sound estimate for this population of finetooth sharks. The model was checked by comparing parameters from the observed model with those estimated by back calculation (Cailliet et al., 1986; Cailliet, 1990). For both methods, theoretical maximum length and growth coefficients (K) were similar. Theoretical maximum length (1587 mm TL for females and 1352 mm TL for males) matched well the empirical size of the largest sharks in the study area (1498 mm TL and 1360 mm for females and males, respectively). In addition, the average percent error in aging (APE=6.8%) was low and within the range of estimates provided in other studies that also used sagittal sections for aging (ranging from 3.0% for the

oceanic whitetip shark, *Carcharhinus longimanus* [Lessa et al., 1999] to 8.1% for the blacktip shark [Wintner and Cliff, 1995]). The fairly high precision is probably a result of good band readability and reader experience.

All age estimates from growth band counts were based on the hypothesis of annual growth band deposition. Although attempts were made to verify annual band deposition through marginal increment analysis, the pattern was inconclusive because of the lack of samples from November to March. However, the decrease in incremental growth from June through October was not large enough to indicate a double band formation (Natanson et al., 1995). Annual winter mark formation has also been assumed in other studies of subtropical species (Branstetter and Stiles, 1987; Natanson et al., 1995; Carlson et al., 1999) where the marginal increment analysis showed a pattern similar
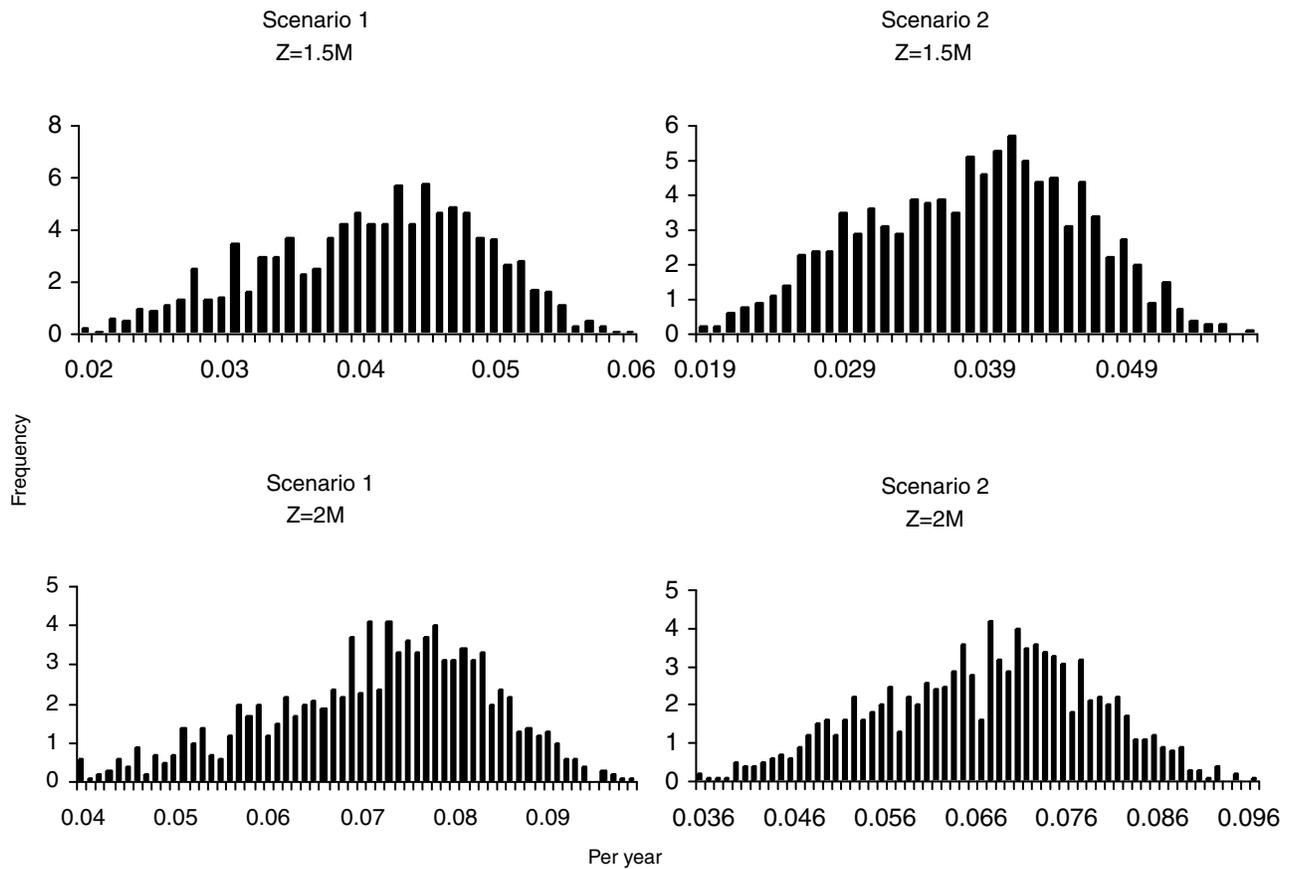
Figure 6

Frequency distributions of the results of 10,000 productivity simulations. Histograms are presented for runs simulating information from scenario 1 and scenario 2, at $Z=1.5\,M$ and $Z=2.0\,M$.

Table 3

A comparison of life-history characteristics and population parameter estimates for the finetooth shark with three other small and one large coastal shark species. Values reported are for females.

	Size at birth (cm) TL[1]	Maximum size (cm) TL[1]	K (/yr)[1]	Longevity (yr)[1,2]	Age at maturity (yr)[1]	Fecundity (/yr)[1]	$R_{Z=2M}$[3]	Generation time ($\bar{A}$; yr)[4]
Atlantic sharpnose	32	107	0.36–0.45	7 (10)	3	5	0.084	4.9
Bonnethead	30	104–124	0.28–0.69	7 (12)	2.2	9	0.105	3.9
Blacknose	42	130–154	0.21–0.48	5 (17)	3.5	2.5	—	4.2
Finetooth	53	160	0.24–0.41[5]	8 (14)[5]	4.3[5]	2	0.071[5]	6.9[5]
Blacktip	58	191–200	0.20–0.27	10 (18)	7	2.5	0.054	10

[1] From Appendix in Cortés (2000).

[2] Values in parentheses indicate theoretical estimates.

[3] From Smith et al. (1998).

[4] From Cortés (2002).

[5] From the present study, scenario 1.

to that found in the present study for the finetooth shark. However, future validation studies through chemical marking, tag-recapture, or bomb dating are needed to determine that growth bands are deposited annually for the finetooth shark as well as numerous other species.

Very few studies have applied the method of Fabens (1965) for estimating growth in sharks, but some have suggested that using an estimate of size at birth (L_0) rather than t_0 is a more robust technique (Goosen and Smale, 1997). In the present study, the estimates of K obtained with the Fabens (1965) method were slightly higher than those estimated with the original von Bertalanffy (1938) equation, probably because the former method forces the model through the y-intercept, making the initial part of the curve steeper (Fig. 3). Beyond age 1, both models were very similar for both sexes and in some cases overlapped in size at age. In addition, the estimates of productivity, generation time, and elasticities, where results from either model were used, were very close. The similarities in growth models with both techniques (Fabens and von Bertalanffy) are likely a reflection of adequate samples throughout all ages. The application of the Fabens (1965) method may be appropiate when there is an inadequate sample of very small individuals.

Differences in reproduction may exist between finetooth sharks from the Gulf of Mexico and northwestern Atlantic Ocean. Although not subjected to a quantitative analysis, Castro (1993) reported size at maturity to be about 1300 mm STL (1271 mm TL) for males and 1350 mm STL (1320 mm TL) for females off South Carolina. This is approximately 80–90 mm TL greater than the median size at maturity estimated for finetooth sharks from the Gulf of Mexico. There is growing evidence that differences in life-history traits between geographically separated populations of sharks are not unusual. To cite a few examples, Parsons (1993a, 1993b) and Carlson and Parsons (1997) found a clinal variation in reproduction and age and growth among populations of bonnethead sharks from the eastern Gulf of Mexico; Wintner and Cliff (1995) found that size at maturity differed greatly between blacktip sharks from South Africa and the Gulf of Mexico; and Mollet et al. (2000) found that the median length at maturity for female mako sharks (*Isurus oxyrinchus*) is greater in the western north Atlantic Ocean than in the southern hemisphere. Whether these deviations in life-history parameters are the result of phenotypic plasticity or genotype is yet to be determined.

Despite no known directed or indirect fishing mortality on the population of finetooth sharks from the northeastern Gulf of Mexico, younger age classes (ages 0 and 1) were not very important. Our sampling design incorporated a multiple-mesh gill net that was thought to capture all sizes of juvenile sharks (Carlson and Brusher, 1999). However, because selectivity functions have not been calculated for this species, we cannot ascertain whether these age groups are indeed naturally low in abundance in the areas sampled or whether this finding is an artifact due to sampling bias.

In addition to age and growth characteristics, the finetooth shark exhibits other life-history traits and population parameters that fall between those of the blacktip shark and those of other small coastal species (Table 3). Indeed, this species can be placed between the blacktip shark and the Atlantic sharpnose shark and bonnethead along the continuum of productivity estimates (r_z, with $Z=2\,M$) of Smith et al. (1998), and also between the blacktip shark and the Atlantic sharpnose shark, bonnethead, and blacknose shark in the "fast-slow" continuum of life-history traits and population parameters identified by Cortés (see his Fig. 2, 2002). Thus, the finetooth shark appears to be the "slowest" of the small coastal sharks studied so far, and to have moderate rebound potential and intermediate generation time. In addition, the probabilistic elasticity analysis indicated that population growth rates of finetooth sharks are much more sensitive to survival of the juvenile and adult stages than to survival of age-0 individuals or fecundity, as recently found for a suite of shark species (Cortés, 2002). This finding suggests that management actions should focus on protection of juveniles and adults rather than age-0 individuals, a recommendation that generally applies to sharks located towards the "fast" end of the life-history continuum. Minimum size limits could thus be effective measures to enhance juvenile survival and time-area closures could protect reproductive females, adult survival, and reproductive potential, should stocks of this species become overfished and management actions be required. Moreover, this study suggests that, when feasible, sharks should be managed on a species-specific basis, rather than by groupings of multiple species that may ignore marked differences in life-history traits.

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