

## Age and growth of *Carcharhinus leucas* in the northern Gulf of Mexico: incorporating variability in size at birth

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Age and growth rates of bull shark *Carcharhinus leucas* [ $n = 255$ ; 555–2230 mm fork length ( $L_F$ )] from the northern Gulf of Mexico were estimated from ring counts on vertebral sections collected from fishery-dependent and -independent surveys. Two growth models were fitted to observed data: the von Bertalanffy growth model (VBGM) with  $t_0$  as the third parameter and a modified version of the VBGM using a fixed size-at-birth intercept as the third parameter. To address the variability in size-at-birth, a Monte Carlo simulation was incorporated into the size-at-birth intercept. The sex-specific growth models were not significantly different, allowing a sexes combined model to be generated. The traditional VBGM predicted a theoretical maximum size ( $L_\infty$ ) of 3007·1 mm  $L_F$ , a growth coefficient ( $K$ ) of 0·042 year<sup>-1</sup> and a theoretical age at zero length ( $t_0$ ) of -6·844 years. The modified VBGM with a fixed size-at-birth intercept of 565 mm  $L_F$  predicted an  $L_\infty$  of 2289·2 mm  $L_F$  and a  $K$  value of 0·089 year<sup>-1</sup>. When comparing model estimates to previously published information, the traditional VBGM predicted a significantly lower theoretical maximum size and a higher growth coefficient than those produced using data collected during the 1980s. Overall, results obtained using the VBGM with a fixed size-at-birth produced more biologically realistic parameters than that of the VBGM with  $t_0$ . The Monte-Carlo simulation incorporating variability in size-at-birth produced similar results to the VBGM using a fixed size-at-birth. This study provides the first attempt to incorporate variability at size-at-birth and provide measurements of variability around the individual parameter estimates for an elasmobranch. © 2005 The Fisheries Society of the British Isles

Key words: age and growth; bull shark; *Carcharhinus leucas*; life history; parameter estimation; Monte-Carlo simulation.

## INTRODUCTION

An understanding of the age structure and growth dynamics of a population is important for effective conservation and management (Cortés, 2004). Age and growth information is often utilized for determination of natural mortality and longevity and, ultimately for calculation of vital rates in demographic models (Goldman, 2004). Moreover, successful fisheries management requires precise and accurate age information in order to make informed decisions because

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inaccurate age estimates can lead to serious errors in stock assessments and possibly overexploitation (Campana, 2001).

In order for models to be considered accurate regarding the growth dynamics of a species, multiple models or various formulations of the same model may be required to determine which most accurately describes the growth of that species (Mollet *et al.*, 2002; Carlson & Baremore, 2005). Historically, the von Bertalanffy growth model (VBGM; von Bertalanffy, 1938) with a  $t_0$  parameter has been the model mostly applied for elasmobranchs (Cailliet & Goldman, 2004). More recently, some studies have begun to apply modified versions of the von Bertalanffy growth model (Mollet *et al.*, 2002; Carlson *et al.*, 2003). An alternate model introduced by Fabens (1965) reparameterizes the VBGM by removing the  $t_0$  parameter and forcing the model through the  $y$ -intercept (*e.g.* hypothesized size-at-birth; Van Dykhuizen & Mollet, 1992; Goosen & Smale, 1997; Carlson *et al.*, 2003). While this model may be more applicable when there is an inadequate sample of very small individuals (Carlson *et al.*, 2003), the model still relies on one estimate of size-at-birth when, in reality, size-at-birth varies. No attempt has been made to incorporate the variability in size-at-birth into those parameter estimates.

The bull shark *Carcharhinus leucas* (Valenciennes) is a cosmopolitan species found in the Indian, Pacific and Atlantic Oceans and one of the few euryhaline sharks (Compagno, 1984). The bull shark is a common coastal shark in the northern Gulf of Mexico (Springer, 1938) and has a large nursery area in coastal and inland waters of Louisiana (Blackburn *et al.*, in press). Bull sharks are taken commercially and recreationally as part of the large coastal shark fishery complex in the Gulf of Mexico and the north-west Atlantic Ocean, which is currently regarded to be overfished (Cortés *et al.*, 2002).

A previous study examined the life history of the bull shark in the northern Gulf of Mexico (Branstetter & Stiles, 1987). That study, however, contained a low sample size ( $n = 59$ ) and had little age information from the early life stages. The purpose of the present study was to re-examine the age and growth dynamics of the bull shark in the Gulf of Mexico. Two forms of the von Bertalanffy growth model were compared to determine the model that best describes the growth data of the bull shark. In addition, a simple method for incorporating variability in size-at-birth into model parameter estimates was developed.

## METHODS

### COLLECTION AND LABORATORY PROCESSING

Bull sharks were collected from both fishery-independent and fishery-dependent sources in the Gulf of Mexico from July 1995 to February 2003. Details of the fishery-independent sources can be found in Neer *et al.* (in press) and Carlson & Brusher (1999). Information regarding the fishery-dependent sources can be found in Trent *et al.* (1997). Additional fishery-dependent samples were obtained from the Commercial Shark Fishery Observer Program (CSFOP; G. Burgess, pers. data).

Precaudal ( $L_{PC}$ ), fork ( $L_F$ ), total ( $L_T$ , straight line measurement from the tip of the snout to the end of the tail, with the tail held in the natural position) and stretched total ( $L_{ST}$ , straight line measurement from the tip of the snout to the end of the tail, with the

tail fully extended in line with the main axis of the body) length (mm), sex and maturity state were determined for each bull shark when possible. Maturity state determinations were made following Neer *et al.* (in press) and Branstetter & Stiles (1987). For comparison with previous studies, morphometric relationships were determined from the current data to convert length measurements as follows:  $L_F = 1.09L_{PC} + 16.77$  ( $n = 161$ ;  $r^2 = 0.99$ );  $L_F = 0.83L_T + 13.84$  ( $n = 192$ ;  $r^2 = 0.99$ );  $L_T = 1.21L_F + 13.84$  ( $n = 192$ ;  $r^2 = 0.99$ ).

Vertebrae for age determination were collected either from under the first dorsal fin (fishery-independent samples) or the cervical region dorsal to the branchial chamber (fishery-dependent samples). Branstetter & Stiles (1987) indicated that there were no differences in age estimates between the two regions. Vertebrae were prepared for sectioning following techniques outlined in Neer & Cailliet (2001) and were either stored dry or in 95% isopropanol alcohol. Prior to examination, vertebrae were removed from alcohol and dried, if necessary, and the centrum diameter measured in mm. Sex-specific regressions between  $L_F$  and centrum diameter ( $D_C$ ) were calculated to assess the appropriateness of using vertebrae as an ageing structure. ANCOVA was conducted to examine how the relationship of  $L_F$  and  $D_C$  differed between sexes.

Sagittal vertebral sections 0.3 mm in thickness were cut from the vertebrae using a Buhler Isomet low speed saw. Sections were stained with a 0.01% crystal violet solution following Carlson *et al.* (2003). Each section was mounted on a glass microscope slide with clear resin and ring estimates were determined by examining the sections under a dissecting microscope with transmitted light (Fig. 1).

## AGE DETERMINATION AND VERIFICATION

Each specimen was aged by two readers without knowledge of its length or sex. Each growth cycle included a broad band representing summer growth and a narrow band

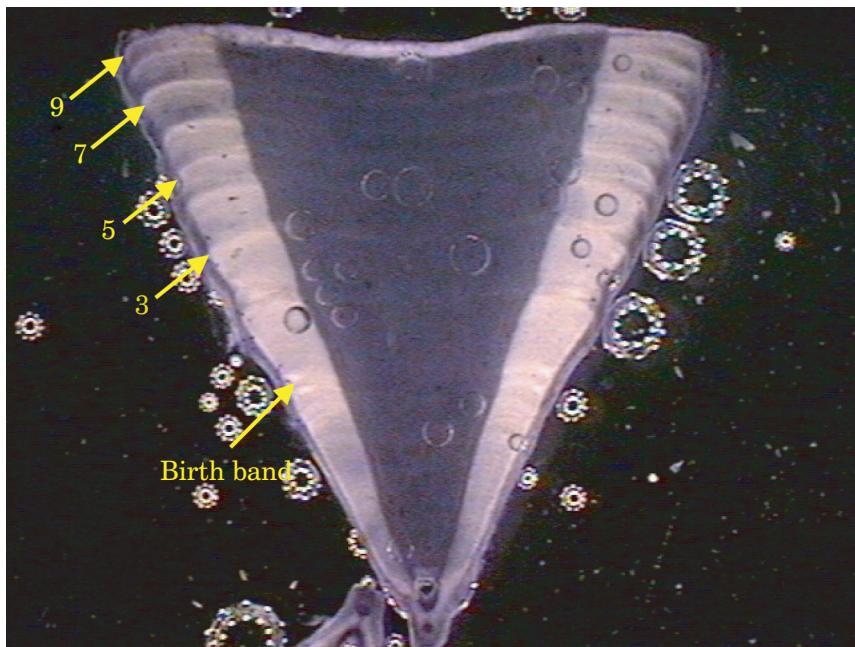


FIG. 1. Sagittal vertebral section used for age determination from a male 1150 mm fork length bull shark. This fish was estimated to be 8+ years old.

representing winter growth (Branstetter & Stiles, 1987; Cailliet & Goldman, 2004). The narrow bands, hereafter referred to as 'rings', were counted for age determination. If the estimates did not agree, the specimen was aged a second time after consultation to reach a consensus with one of the previous age estimates. If no consensus was reached, the sample was discarded. An index of average per cent error (APE; Beamish & Fournier, 1981) and percentage of agreements by  $\pm i$  rings (Cailliet, 1990) between readers were computed for the first set of 'ring' counts. Per cent agreement was computed for all samples and by 100 mm  $L_F$  size categories (Goldman, 2004). Ageing precision was examined using a test of symmetry as described in Hoenig *et al.* (1995).

To examine the annual periodicity of the ring formation, verification was attempted using the relative marginal increment analysis following Natanson *et al.* (1995):  $I_M = (V_R - R_n)(R_n - R_{n-1})^{-1}$ , where  $I_M$  = the marginal increment ratio,  $V_R$  = the vertebral radius,  $R_n$  = the last complete ring and  $R_{n-1}$  = the next-to-last complete ring. The distances from the centrum origin to the distal edge of the last two growth rings and from the centrum origin to the centrum edge were measured using the Image Tools Version 3 Software Package (Department of Dental Diagnostics Science, University of Texas Health Center, Austin, TX, U.S.A.) Mean  $I_M$  was plotted against month and season (spring = March to May; summer = June to August; autumn = September to November; winter = December to February) to examine trends in 'ring' formation. A one-way ANOVA was used on the arcsin-transformed  $I_M$  data to examine differences between month and season (Zar, 1984). This analysis was completed for bull sharks of all size classes combined and for bull sharks displaying only two rings in the vertebral section because potential differences in  $I_M$  can be found by conducting the analysis over all age classes or restricting it to a single age (Campana, 2001).

## DETERMINATION OF GROWTH CURVES

In using theoretical growth models, it was assumed that: (1) the birth mark is the ring associated with a pronounced change in angle in the intermedia and (2) growth rings are deposited annually (Branstetter & Stiles, 1987). Age estimates were calculated as age = the birth ring + number of narrow rings - 1. If only the birth ring was present, the bull shark was considered a 0+ year old individual.

The traditional von Bertalanffy growth model (VBGM with  $t_0$ ) was fitted separately to sex-specific observed size-at-age data using the equation:  $L_t = L_\infty(1 - e^{-K(t-t_0)})$ , where  $L_t$  = predicted length at time  $t$ ,  $L_\infty$  = theoretical asymptotic length,  $K$  = growth coefficient and  $t_0$  = theoretical age at zero length. Likelihood ratio tests (Kimura, 1980; Cerrato, 1990) were used to determine whether growth models differed between sexes (Haddon, 2001). Theoretical longevity was estimated as the age at which 95% of  $L_\infty$  is reached ( $5 \times \ln 2 K^{-1}$ ; Fabens, 1965; Cailliet *et al.*, 1992). Growth model parameters were estimated using least-squares nonlinear regression in the statistical software package Systat 9.0.

A modified form of the von Bertalanffy growth model was also fitted to observed size-at-age data (Fabens, 1965). This form expresses the three-parameter model with two unknown parameters ( $L_\infty$  and  $K$ ) and known size at birth ( $L_o$ ). This equation (VBGM with  $L_o$ ) is described as:  $L_t = L_\infty(1 - be^{-Kt}) = L_\infty - (L_\infty - L_o)e^{-Kt}$ ,  $b = (L_\infty - L_o)L_\infty^{-1} = e^{Kt_0}$ , where  $L_t$  = predicted length at time  $t$ ,  $L_\infty$  = theoretical asymptotic length,  $K$  = growth coefficient and  $L_o$  is the length at birth.

In order to incorporate variability in size-at-birth into the model, a Monte-Carlo simulation was employed where 1000 estimates of size-at-birth were randomly generated from a normal distribution with a mean of 570 mm  $L_F$  and a s.d. of 79 mm. This mean and s.d. were derived from length information from four neonates with open umbilical scars observed during this study, and information on two additional neonates obtained from the Coastal Fisheries Institute, Louisiana State University and the Louisiana Department of Wildlife and Fisheries. Size-at-birth was truncated at a minimum size of 450 mm  $L_F$  and a maximum size of 650 mm  $L_F$  to prevent the inclusion of biologically unrealistic birth sizes. For each generated size at birth, a VBGM growth model was fit to

the observed data, sexes combined, and the parameters  $L_\infty$  and  $K$  were recorded. The mean and 95% CI were determined for the parameters  $K$  and  $L_\infty$  from these 1000 simulations. All simulations were run with Microsoft Excel spreadsheet software using a Visual Basic macro, equipped with add-in simulation software (Crystal Ball 2000, Decisioneering, Inc., Denver, CO, U.S.A.).

The results were compared with previous work on bull sharks in the northern Gulf of Mexico by Branstetter & Stiles (1987). The traditional VBGM was re-fitted to their original observed sex-combined size-at-age data and the resulting growth models compared to those of the current study using a likelihood ratio test (Kimura, 1980; Cerrato, 1990). Prior to fitting the model,  $L_T$  measurements from Branstetter & Stiles (1987) were converted to  $L_F$  using regression equations derived in this study.

## RESULTS

### COLLECTION AND LABORATORY PROCESSING

A total of 268 bull shark specimens were collected during this study. Females ranged from 600 to 2230 mm  $L_F$ , while males ranged from 624 to 2020 mm  $L_F$  (Fig. 2). Bull sharks were collected from all months except April, October and December, although not from all months every year. Samples covered all maturity stages for both sexes.

A linear relationship was determined between  $L_F$  and  $D_C$  indicating that vertebrae appear useful for age estimation. As no difference was found between sexes (ANCOVA, d.f. = 1,  $P = 0.826$ ), data were combined to generate a single linear relationship:  $L_F = 67.41(D_C) + 128.63$  ( $P < 0.0001$ ;  $r^2 = 0.98$ ;  $n = 264$ ).

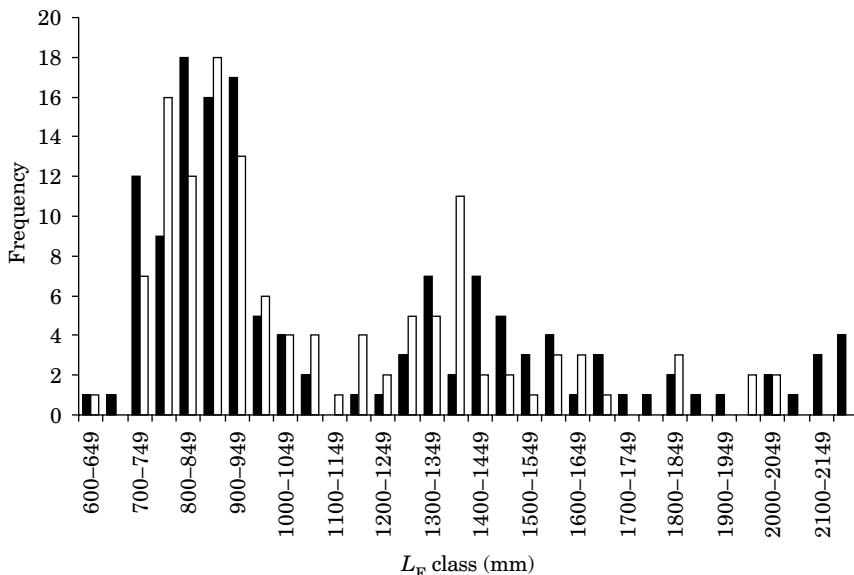


FIG. 2. Length-frequency histogram for male (□;  $n = 128$ ) and female (■;  $n = 139$ ) bull sharks encountered during this study. The sex of one individual was unknown.

## AGE DETERMINATION AND VERIFICATION

Age estimates were determined for 255 of the 268 specimens processed for age determination. Age estimates ranged from 0+ to 29+ years for females ( $n = 130$ ) and from 0+ to 25+ years for males ( $n = 124$ ). Sex was not available for one specimen. The precision of ring counts was high between readers, resulting in an APE of 3·40%. Per cent agreement between readers was 76·1% total agreement, 93·4% within one ring, and 98·5% within two rings. Per cent agreement by size category also indicated good precision over most size classes. (Table I). The test of symmetry between readers did not indicate any systematic differences in age estimates ( $\chi^2$ , d.f. = 29,  $P > 0\cdot05$ ).

Significant differences were found in the marginal increment analysis between seasons for bull shark age classes combined (single factor ANOVA by season:  $F_{3,187}$ ,  $P < 0\cdot001$ ; Fig. 3). *Post hoc* pair-wise comparisons found winter was significantly different from spring and summer (Bonferroni pair-wise *post hoc* test:  $P < 0\cdot001$ ). Autumn was significantly different from spring ( $P < 0\cdot005$ ), and spring was significantly different from summer ( $P < 0\cdot001$ ). Significant differences were also found in the analysis by month for all bull shark age classes combined (single factor ANOVA by month:  $F_{8,182}$ ,  $P < 0\cdot001$ ; Fig. 3). Most monthly pair-wise comparisons were not different; January and August were significantly different for four of the pair-wise comparisons.

Although monthly and seasonal changes in marginal increment analysis observed in bull sharks with only two bands followed a similar trend as all age classes combined, peaks were not statistically different (single factor ANOVA by

TABLE I. Per cent agreement (PA) and PA  $+/- 1$  year, for age estimates determined for bull sharks when placed into 100 mm fork length groups

$L_F$ Group (mm)	$n$	Agree	Agree $+/- 1$	PA	PA $+/- 1$
600–699	3	3	3	100	100
700–799	42	33	42	79	100
800–899	57	50	57	88	100
900–999	39	31	36	79	92
1000–1099	12	8	11	67	92
1100–1199	6	4	5	67	83
1200–1299	11	9	10	82	91
1300–1399	26	19	24	73	92
1400–1499	16	12	15	75	94
1500–1599	11	7	11	64	100
1600–1699	8	6	8	75	100
1700–1799	2	2	2	100	100
1800–1899	6	4	5	67	83
1900–1999	3	2	3	67	100
2000–2099	5	1	2	20	40
2100–2199	7	3	3	43	43
2200–2299	1	0	1	0	100
$N$	255	194	238		
Average per cent agreement				67·3	88·9

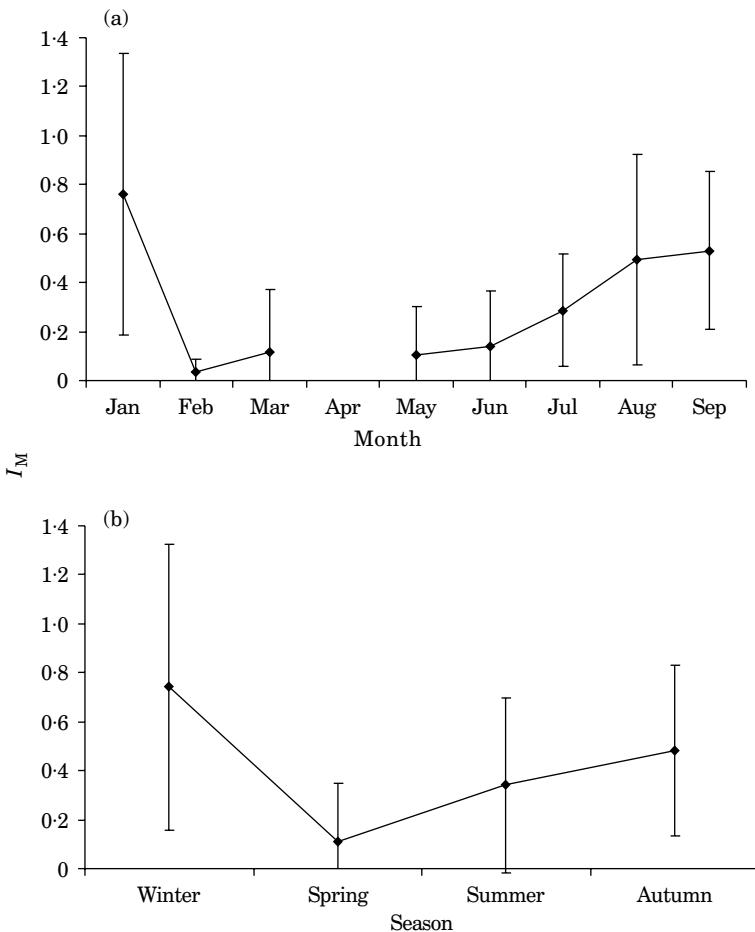


FIG. 3. Mean  $\pm$  s.d. marginal increment ( $I_M$ ) analysis for bull sharks ( $n = 169$ ) by (a) month and (b) season.

month:  $F_{6,32}$ ,  $P > 0.10$ ; by season:  $F_{2,36}$ ,  $P > 0.10$ ; Fig. 4). This lack of significance may be due to the small sample size available for analysis ( $n = 39$ ).

#### DETERMINATION OF GROWTH CURVES

Both growth models fit the observed data well: traditional VBGM with  $t_0$  (corrected  $r^2 = 0.914$ ) and VBGM with  $L_o$  (corrected  $r^2 = 0.842$ ), and were highly significant ( $P < 0.001$ ; Fig. 5). Likelihood ratio tests indicate the growth model parameters were not different between sexes, thus the data were combined ( $\chi^2$ , d.f. = 3,  $P > 0.05$ ). The traditional VBGM with  $t_0$  for sexes combined predicted a  $L_\infty$  of 3007.1 mm  $L_F$ , a  $K$  value of 0.042 year $^{-1}$  and a  $t_0$  of -6.844 years. The VBGM with  $L_o$  of 565 mm  $L_F$  predicted a  $L_\infty$  of 2289.2 mm  $L_F$  and a  $K$  value of 0.089 year $^{-1}$  (Table II). Theoretical longevity was determined to be

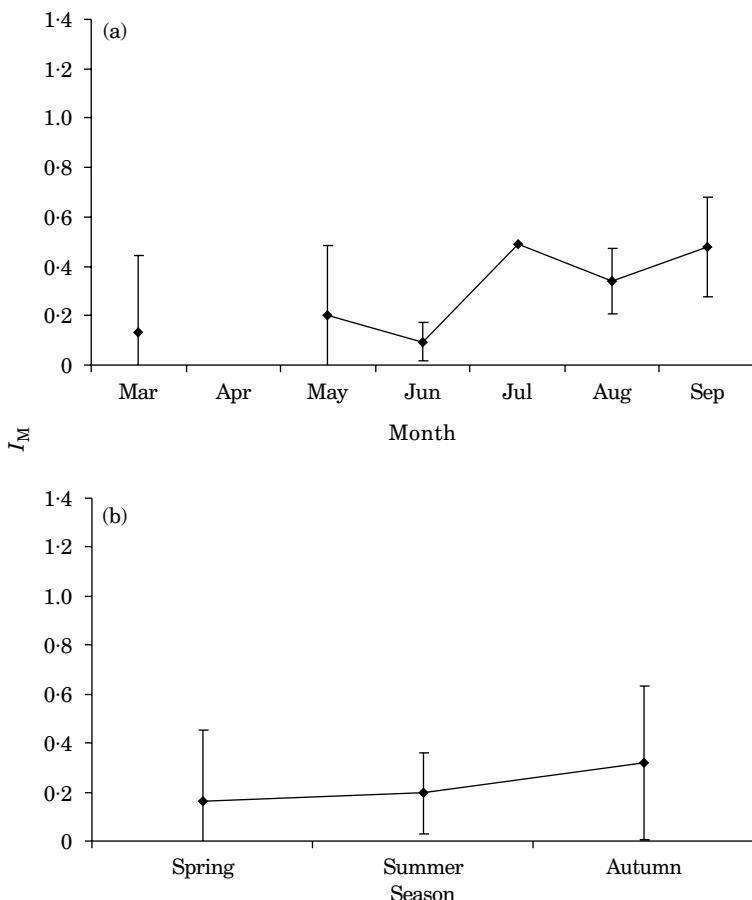


FIG. 4. Mean  $\pm$  s.d. marginal increment ( $I_M$ ) analysis for bull sharks determined to have only two rings in their vertebrae ( $n = 39$ ) by (a) month and (b) season.

38.6 years for the VBGM with  $L_o$  while the VBGM with  $t_0$  produced a theoretical longevity of 82.5 years.

The Monte-Carlo simulation incorporating variability in size-at-birth produced similar results to the VBGM with  $L_o$  using a fixed size-at-birth. Predicted mean  $L_\infty$  was 2299.2 mm  $L_F$  and mean  $K$  was  $0.089 \text{ year}^{-1}$ , with a mean size-at-birth of 565.7 mm  $L_F$  (Table III). Theoretical longevity was determined to be 38.6 years, s.d. and 95% CL from the simulation for these parameters are listed in Table III.

The traditional VBGM with  $t_0$  for combined sexes using the original size-at-age data from Branstetter & Stiles (1987) predicted a  $L_\infty$  of 3771.8 mm  $L_F$ , a  $K$  value of  $0.024 \text{ year}^{-1}$  and a  $t_0$  of  $-10.351$  years. Theoretical longevity was estimated to be 144.2 years. Significant differences were found between growth model parameter estimates from the current study and the Branstetter & Stiles (1987) data ( $\chi^2$ , d.f. = 3,  $P < 0.001$ ).

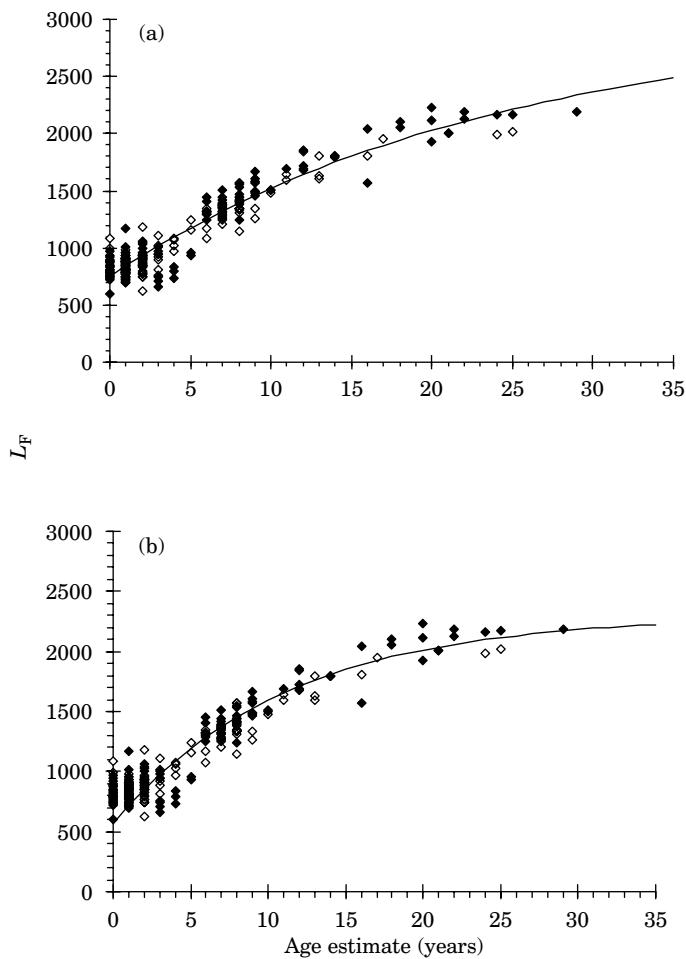


FIG. 5. Growth functions fitted to the combined sexes [ $\diamond$ , males ( $n = 124$ );  $\blacklozenge$ , females ( $n = 130$ )] observed size-at-age data for bull sharks. (a) The von Bertalanffy growth function with the  $t_0$  parameter [ $L_t = L_\infty(1 - e^{-K(t-t_0)})$ ] and (b) the Fabens' (1965) modified von Bertalanffy growth function with a fixed size-at-birth intercept [ $L_\infty - (L_\infty - L_0)e^{-Kt}$ ] (see Table II for model parameters).

## DISCUSSION

The VBGM with  $L_o$  produced the more biologically realistic parameter estimates than the traditional VBGM with  $t_0$  for the bull shark (Tables II and III). The VBGM with  $L_o$  predicted a  $L_\infty$  of 2299.2 mm  $L_F$  while the VBGM with  $t_0$  estimated a  $L_\infty$  of 3007.1 mm  $L_F$ , much larger than the largest bull shark observed in this study (2230 mm  $L_F$ ) or the largest previously reported bull shark from the Gulf of Mexico (2234 mm  $L_F$ ; Branstritter & Stiles, 1987). Although an adequate number and range of samples were available throughout all ages, the failure of the VBGM with  $t_0$  to reach an asymptote through the middle and upper data points probably resulted in the inflated estimate of theoretical maximum size. Branstritter & Stiles (1987) also encountered this problem in their

TABLE II. Von Bertalanffy growth parameters for the bull shark, sexes combined. Parameters are given in fork length. Value in parentheses is the asymptotic s.e. for that parameter. The lower and upper 95% CL are also provided. Von Bertalanffy growth model with fixed size-at-birth was not computed for the Branstetter & Stiles (1987) data

	VBGM with $t_0$			VBGM with fixed size-at-birth intercept		
	$L_\infty$ (mm)	$K$ (year $^{-1}$ )	$t_0$ (year)	$n$	$L_\infty$ (mm)	$K$ (year $^{-1}$ )
Current study						
Parameter value	3007.1 (218.3)	0.042 (0.006)	-6.844 (0.483)	254	2289.2 (80.7)	0.089 (0.007)
s.e.						
95% CL	2577.2–3436.9	0.031–0.053	-7.80–−5.89		2130.2–2448.2	0.075–0.103
Branstetter & Stiles (1987) data						
Parameter value	3771.8 (777.3)	0.024 (0.009)	-10.351 (2.144)	59	NA	NA
s.e.					NA	NA
95% CL	2214.7–5328.9	0.006–0.043	-14.65–−6.06		NA	NA

NA, not applicable.

TABLE III. Von Bertalanffy growth model parameters incorporating variability in size-at-birth for the bull shark, sexes combined. Parameters are given in fork length. Value in parentheses is the standard deviation for that parameter. The 95% CL are also provided

	$L_\infty$ (mm)	$K$ (year $^{-1}$ )	$L_F$ at birth (mm)	$n$
Parameter value	2299·2	0·089	656·678	254
s.d.	(108·9)	(0·014)	(48·450)	
$\pm 95\%$ CL	6·8	0·0009	3·007	

study of bull shark and derived their estimates of the VBGM by hand-fitting a curve through the upper data points. The estimates of longevity produced using the parameter estimates of  $K$  from the two models also indicate that the VBGM with  $L_o$  is more biologically realistic. The traditional VBGM with  $t_0$  predicated a  $K = 0·042$ , which translates into a theoretical longevity estimate of 82·5 years. The VBGM with  $L_o$  estimated  $K$  to be 0·089, producing a theoretical longevity estimate of 38·6 years. The oldest animal aged in this study was a 29+ year old female. While it is possible that older animals may exist, it seems doubtful that this species lives to 82 years based on the data currently available.

Bull sharks have been documented to have a wide range in size-at-birth. Cliff & Dudley (1991) reported a size-at-birth of c. 620 mm  $L_F$  for bull sharks collected off South Africa based on free-swimming neonates, while Sadowsky (1971) reported size-at-birth ranging from 635 to 680 mm  $L_F$  for bull sharks in Brazilian waters. In the Gulf of Mexico, Clark & von Schmidt (1965) reported a range of 510–676 mm  $L_F$  for bull sharks collected off Florida while data on bull sharks off Louisiana indicate they are born between 555 and 660 mm  $L_F$  (J.A. Neer, unpubl. data). Attempts were made to account for this variability in size-at-birth by using the Monte-Carlo simulation. Both simulations, however, produced comparable results. Identical estimates of  $K$  were obtained (0·089), while the theoretical estimates of maximum size varied only slightly ( $L_\infty = 2299·2$  mm  $L_F$  for the Monte-Carlo simulation with variability in size-at-birth v. 2289·2 mm  $L_F$  for the VBGM with  $L_o$ ). While the difference in the parameter estimates in this example was small, this may not be the case for all species.

The  $I_M$  results provide verification of the assumption that ring formation is annual in the bull shark. Branstetter & Stiles (1987) also concluded annual ring formation for bull shark based on  $I_M$  analysis, while Wintner *et al.* (2002) concluded annual increment formation for bull sharks in South African waters using ‘mark-recapture’ methods on captive animals. Despite this corroboration, further validation of the annual periodicity of the ring pattern observed in the bull shark is necessary through techniques such as chemical marking, bomb carbon dating or tag-recapture studies.

While the results support annual ring deposition, the timing of deposition of the thin mineralized dark ring needs further study. The  $I_M$  analysis indicates these marks form annually in spring months. These results are contrary to what the majority of studies employing  $I_M$  analysis on elasmobranchs have reported (Cailliet & Goldman, 2004). Studies by Loefer & Sedberry (2003) and Simpfendorfer (1993), however, demonstrated summer deposition of the thin mineralized dark ring for two species of sharpnose sharks, *Rhizoprionodon*

*terraenovae* (Richardson) and *Rhizoprionodon taylori* (Ogilby) respectively. Simpfendorfer (1993) proposed that stress during the breeding season was a possible explanation for the formation of mark, while Loefer & Sedberry (2003) indicated that the observed pattern may reflect 'periods of slow calcareous accretion that have been compressed by increased growth', as hypothesized by Gelsleichter (1998). While many species of sharks in the Gulf of Mexico have winter dark ring deposition, they also have summer breeding cycles (Carlson *et al.*, 1999, 2003). Neonate bull sharks were observed from March to May (J.A. Neer, unpubl. data), indicating that ring deposition in this species may be related to a spring pupping season. The underlying mechanisms governing ring deposition in elasmobranchs, however, still need to be determined.

Sample size and missing samples for many age classes probably caused the observed differences in the traditional VBGM with  $t_0$  between this study and the Branstritter & Stiles (1987) study. Estimates of  $L_\infty$  for the current study (3007 mm  $L_F$ ) and  $K$  ( $0.042 \text{ year}^{-1}$ ) were considerably lower than that obtained using the data from Branstritter & Stiles ( $L_\infty = 3771.8 \text{ mm } L_F$ ,  $K = 0.024 \text{ year}^{-1}$ ) and were significantly different using the log-likelihood ratio test. Although the oldest bull sharks in both studies were similar (24 and 29+ years old), the Branstritter & Stiles (1987) data contained very little size-at-age information for the youngest size classes (only one 1 year-old and one 3 year-old with the remaining animals all 6 years or older). The lack of very young or old individuals has been reported to greatly affect growth model estimates (Cailliet & Goldman, 2004).

The analysis of the age and growth of the bull shark clearly demonstrates the potential value of using models other than the traditional VBGM. Asymptotic values and growth coefficients estimated from that model suggest unrealistic biological characteristics for this species. Although few studies on elasmobranch age and growth have fit alternate models, some recent studies have illustrated that other growth models (*e.g.* Gompertz) provide better fits and more accurately describe growth other than the VBGM (Mollet *et al.*, 2002; Carlson & Baremore, 2005; Neer & Thompson, 2005). Because demographic models require accurate measurements of the growth coefficient, inaccurate life history information can seriously affect any resulting population models. Additionally, the inclusion of variability around growth parameter estimates, such as those determined using the Monte-Carlo simulation, may prove useful for population modelling and stock assessments.

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