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Age and growth of the great hammerhead shark, *Sphyrna mokarran*, in the north-western Atlantic Ocean and Gulf of Mexico

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Abstract. The great hammerhead shark, *Sphyrna mokarran*, is a cosmopolitan species that is caught in a variety of fisheries throughout much of its range. The apparent decline of great hammerhead shark populations has reinforced the need for accurate biological data to enhance fishery management plans. To this end, age and growth estimates for the great hammerhead were determined from sharks ($n = 216$) ranging in size from 54- to 315-cm fork length (FL), captured in the Gulf of Mexico and north-western Atlantic Ocean. Growth curves were fitted using multiple models and evaluated using Akaike's information criterion. The von Bertalanffy growth model was the best fitting model, with resulting growth parameters of $L_\infty = 264.2$-cm FL, $k = 0.16$ year^{-1}, $t_0 = -1.99$ year for males, and $L_\infty = 307.8$-cm FL, $k = 0.11$ year^{-1}, $t_0 = -2.86$ year for females. Annual band pair deposition was confirmed through marginal-increment analysis and a concurrent bomb radiocarbon validation study. Great hammerheads have one of the oldest reported ages for any elasmobranch (44 years) but grow at relatively similar rates (on the basis of von Bertalanffy k value) to other large hammerhead species from this region. The present study is the first to provide vertebral ages for great hammerheads.

Additional keyword: von Bertalanffy.

Introduction

The great hammerhead shark, *Sphyrna mokarran* Rüppell, 1837, is a cosmopolitan circum-tropical species found in both coastal and pelagic seas (Compagno 1984). Great hammerhead sharks are caught in a variety of fisheries, including artisanal and small-scale commercial fisheries, bottom longlines as well as offshore pelagic longlines (Compagno 1984; Camhi 1998). Great hammerhead sharks are generally not a target species, but are valuable incidental catch because of their large fins which are prized in Hong Kong fish markets (Abercrombie *et al*. 2005). According to Clarke *et al*. (2004), hammerheads (*Sphyrna* spp.) are the second-most abundant species group in the international trade in fins.

Because detailed catch and life-history information is limited, species-specific assessments for the great hammerhead shark are generally lacking, although some studies have reported large declines in relative abundance. Species-specific catch information from beach nets set off of Kwa-Zulu Natal during 1978–2003 have shown an approximate 79% decline for the great hammerhead shark (Dudley and Simpfendorfer 2006). A recent assessment for a hammerhead complex (i.e. *S. lewini*, scalloped hammerhead; *S. mokarran*; *S. zygaena*, smooth hammerhead) in the north-western Atlantic Ocean found about a 70% decline in abundance since 1981 (Jiao *et al*. 2009). In the Mediterranean Sea, meta-analysis of abundance indices indicated that Sphyrnidae (including the aforementioned species) had declined by an estimated 99% since the early 19th century (Ferretti *et al*. 2008). The most recent IUCN Red List assessment lists great hammerheads as endangered globally (Camhi *et al*. 2009). In the present study, we focused on populations of this species found in the north-western Atlantic and the Gulf of Mexico because of their apparent decline (see above) and the availability of samples through institutional sampling programs.

Whereas accounts of behaviour (e.g. Strong *et al*. 1990), occurrence (e.g. Sadowsky 1971) and general biology of great hammerheads (e.g. Stevens and Lyle 1989) have been published, no study has provided any age and growth data for the species in any part of its range. Knowledge of the age structure and growth rate of a population is a basic component of life history. Accurate life-history information is a critical input to population models that are used to predict the productivity of the stock and ensure that it is harvested at sustainable levels (Cortés 2000). To this end, the purpose of the present study was to determine a vertebral-based age and growth model for populations of great hammerheads in the north-western Atlantic Ocean and the Gulf of Mexico.

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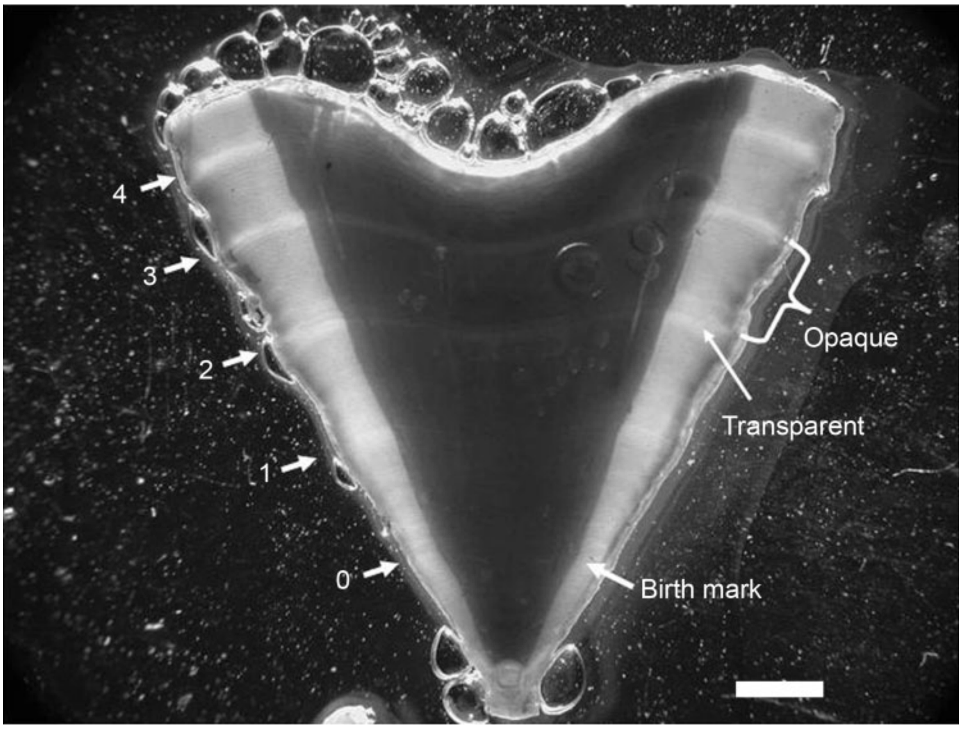

Fig. 1. Sagittal vertebral section from a 4-year-old great hammerhead (*Sphyrna mokarran*), illustrating the banding pattern and annuli used to assign age. Scale bar = 2 mm.

Materials and methods

Animal collection

From 2003 to 2009, vertebral samples were obtained from sharks captured through fishery-independent (research fishing) surveys (Grace and Henwood 1998; Carlson and Brusher 1999; Hueter and Tyminski 2007; NSRC 2007), recreational fishing tournaments (J. P. Tyminski, pers. comm.) and from observer programs in two directed shark fisheries (Trent *et al.* 1997; Hale *et al.* 2009; Morgan *et al.* 2009). Depending on the collection source, precaudal (PCL), fork (FL), total (TL) and/or stretched total (STL) length (cm), sex, and maturity state were determined for each shark.

Age and growth

Depending on the source, vertebrae for age determination were sampled from the column between the origin and termination of the first dorsal fin or above the branchial chamber. Vertebrae from both locations were utilised in the study, because growth-increment counts were shown not to differ between them (A. N. Piercy, unpubl. data). Vertebrae were placed on ice after collection, and frozen on return to the laboratory. Thawed vertebrae were manually cleaned of excess tissue and soaked in 5% sodium hypochlorite solution for 5–30 min to remove the remaining tissue. After cleaning, the vertebrae were rinsed in running tap water and stored in 70% ethanol.

Prior to examination, one vertebra was randomly removed from alcohol and dried. The vertebra was fixed to a clear glass slide with resin (Crystalbond 509 or thermoplastic cement, Electron Microscopy Sciences, Hatfield, PA, USA) and sectioned with a Buehler 82 Isomet low-speed saw (Buehler, Lake Bluff, IL, USA). Each section was mounted on a glass microscope slide with clear resin (Cytoseal 60, Fisher Scientific, Pittsburg, PA, USA) and examined using a dissecting microscope under transmitted light. To achieve the most appropriate technique for enhancing 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) or left unstained. Growth bands were found to be most easily viewed on crystal violet-stained sagittal sections with a thickness of 0.6 mm.

Opaque bands and narrow translucent bands were identified following the description and terminology detailed in Cailliet and Goldman (2004) (Fig. 1). Verification of the annual period of band formation was performed using relative marginal increment analysis (Conrath *et al.* 2002; Piercy *et al.* 2007), as follows:

$$\mathrm{MIR} = R_{\mathrm{n}}/R_{\mathrm{n}-1}, \qquad (1)$$

where MIR = the marginal increment ratio, R_{n} = the distance to the outer edge of the last complete band, and $R_{\mathrm{n}-1}$ = the distance between the penultimate and the last band. Mean MIR was plotted against month to determine trends in band formation. A Kruskal–Wallis one-way analysis of variance on ranks was used to test for differences in MIR by month.

Two readers (A. Piercy and J. Carlson) randomly read vertebral sections independently and without knowledge of sex or length of specimens. Vertebral-age estimates for which there was disagreement were re-read simultaneously by both readers using a Meiji Techno R2 Dissecting Microscope (Meiji Techno America, Santa Clara, CA, USA) equipped with a Hitachi KP-D50 Digital Camera and software (Hitachi Kokusai Electric America Ltd, Woodbury, NY, USA). If no agreement was reached, samples were discarded. Several methods were used to evaluate precision and bias among age determinations, following the recommendations of Cailliet and Goldman (2004). Percentage agreement ((PA = number agreed/number read) × 100) and percentage agreement plus or minus 1 year were calculated for 10-cm (e.g. 50–59-cm FL) length intervals to evaluate precision (Goldman 2002). The index of average percentage error (IAPE; Beamish and Fournier 1981) was calculated to compare the average deviation of readings from the means of all readings for each vertebral section, as follows:

$$\text{IAPE} = \frac{1}{N}\sum_{j=1}^{N}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{|x_{ij} - x_j|}{x_j}\right], \qquad (2)$$

where N = the number of sharks aged, R = the number of readings; x_{ij} = the ith age estimation of the jth shark at the ith reading, and x_j = the mean age calculated for the jth shark. Bowker's test of symmetry following Hoenig *et al.* (1995) was used to determine whether differences between readers were systematic or a result of a random error.

Following Carlson and Baremore (2005), several models were fitted to sex-specific observed size-at-age data to estimate the age and growth. The von Bertalanffy growth model (von Bertalanffy 1938) was described using the equation

$$L_t = L_\infty(1 - e^{-k(t-t_0)}), \qquad (3)$$

where L_t = the mean fork length at time t, L_∞ = theoretical asymptotic length, k = growth coefficient, and t_0 = theoretical age at zero length.

A modified equation of the von Bertalanffy growth model, with a size-at-birth intercept rather than the t_0 parameter (Van Dykhuizen and Mollet 1992; Goosen and Smale 1997; Carlson *et al.* 2003) was described as

$$L_t = L_\infty(1 - be^{-kt}), \qquad (4)$$

where $b = (L_\infty - L_0)/L_\infty$ and L_0 = the length at birth. Estimated length at birth for the great hammerhead shark is 50-cm FL (A. T. Nguyen and A. N. Piercy, unpubl. data).

We also used a modified form of the Gompertz growth model (Ricker 1975). This model was expressed following Mollet *et al.* (2002) as

$$L_t = L_o(e^{G(1-e(-kt))}), \qquad (5)$$

where $G = \ln(L_o/L_\infty)$.

All growth-model parameters were estimated using Marquardt least-squares non-linear regression on SAS statistical software PROC NONLIN (SAS Institute, Inc., Cary, NC, USA). Akaike's information criterion (AIC) was used to determine the model that provided the best fit to the length-at-age data (Burnham and Anderson 2002).

$$\text{AIC} = n \times \ln(\hat{\sigma}^2) + 2p, \qquad (6)$$

where n = the sample size, $\hat{\sigma}$ = the residual sum of squares divided by n, and p = the number of parameters.

In developing theoretical growth models, we assumed that (1) the birth mark is the band associated with a pronounced change in the angle in the intermedialia, and we assigned an arbitrary birth date of 1 July, on the basis of the occurrence of near-term embryos in specimens caught in late June (A. T. Nguyen and A. N. Piercy, unpubl. data), and (2) subsequent narrow translucent growth bands occur annually thereafter. Thus, ages (y) were calculated as age = birth mark + (number of translucent bands − 1). If only the birth mark was present, the age was 0+ years. All age estimates from growth-band counts were assumed to represent annual growth-band deposition on the basis of bomb radiocarbon analysis (Passerotti *et al.* 2010). Chi-square tests of likelihood ratios (Kimura 1980) were used to determine whether growth rate differed between sexes. Theoretical longevity was estimated as the age at which 95% of L_∞ is reached (5(ln 2)/K; Fabens 1965; Cailliet *et al.* 1992).

Results

Of the original 224 samples, only six (2.6%) were considered unreadable and were discarded. The first set of band counts resulted in an index of average percentage error of 2.1%. When grouped by 10-cm length intervals, agreement for combined sexes was reached for an average of 87% and 99% ± 1 band for sharks <200-cm FL (available as an Accessory Publication to this paper). For sharks >200-cm FL, agreement was reached for 64% and 84% ± 1 band of samples initially read. Bowker's test of symmetry (Hoenig *et al.* 1995) indicated no systematic disagreement between readers ($\chi^2_{\text{d.f.}=32} = 46$, $P = 0.62$).

Sharks with outer growth bands that were too closely spaced to accurately measure the band distance were not included in the relative marginal-increment analysis. Marginal-increment ratios were calculated for 106 sharks, spanning 10 months and most size classes (range = 89–299-cm FL). No suitable samples were collected in June and December. Marginal increments were significantly different among months (Kruskal–Wallis $H_{\text{d.f.}=9} = 31.23$, $P < 0.001$), with a trend of increasing monthly increment growth that peaked in November, remained constant until March and declined to May (Fig. 2). These results suggest that a single transparent band is formed annually on vertebrae.

Under the statistical criteria defined by Carlson and Baremore (2005), all growth models fitted the data well. Although all models were highly significant ($P < 0.001$), AIC values were lowest for von Bertalanffy growth models (Table 1). The values of k and L_∞ from all equations varied slightly, although fits to the observed data were better for the sex-specific von Bertalanffy models (Table 2). Observed von Bertalanffy parameters and growth rates differed between males and females (likelihood ratio: $\chi^2_{\text{d.f.}=3} = 147.4$, $P < 0.001$). For both sexes, growth was rapid until the age 10, slowing down considerably for males thereafter, whereas the reduction in growth rate for

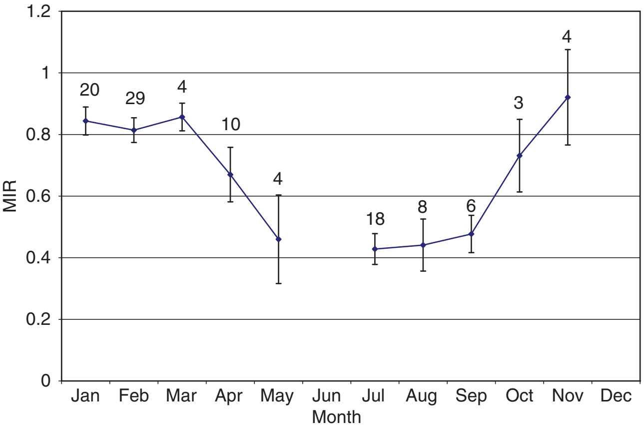

Fig. 2. Mean marginal-increment analysis by month for combined sexes of great hammerhead sharks (*Sphyrna mokarran*) ranging in size from 89- to 299-cm fork length (FL). Vertical bars are ± the standard error of the mean. Numbers above the line represent the monthly sample size.

females was not as accentuated (Fig. 3). However, females exhibited a greater variability in size-at-age than males after age 10. Females had a lower growth coefficient ($k = 0.11$ year^{-1}) than did males ($k = 0.16$ year^{-1}), and a larger asymptotic size, 307.8-cm FL and 264.2-cm FL respectively. Theoretical longevity estimates were 31.4 years for females and 21.6 years for males. Observed size-at-age was relatively similar between the sexes for younger animals (ages 0–5, FL 69–175 cm). A smaller sample size from older age classes hinders direct comparison of size-at-age in older ages. However, similar sizes of maximum observed ages were noted, with the oldest aged female shark being 44 years, with a FL of 315 cm, and the oldest male shark being 42 years, with a FL of 300 cm. To facilitate comparisons with other studies, FL of this species can be converted to TL by using the following equation ($r^2 = 0.98$; $N = 24$):

$$\mathrm{TL} = 1.2533(\mathrm{FL}) + 3.472. \tag{7}$$

Discussion

Despite the great hammerhead being a cosmopolitan species, the present study is the first to provide age and growth estimates for any part of its range. Thus, no inter-regional or temporal comparisons of growth parameters are possible. Comparisons with sympatric congeners suggest that great hammerheads grow at a similar rate (on the basis of the von Bertalanffy k value) to scalloped hammerheads ($k = 0.09$–0.13 year^{-1}) in the north-western Atlantic Ocean (Piercy *et al*. 2007) and smooth hammerhead sharks ($k = 0.13$ year^{-1}) from the eastern Pacific Ocean (Garza Gisholt 2004) (Table 3). However, among all studies on hammerheads, great hammerheads reached the oldest observed maximum age (44 years). Maximum observed age for scalloped hammerheads was 30.5 years (Piercy *et al*. 2007) and 18 years for *S. zaygaena* (Garza Gisholt 2004). Although both of these studies assumed annual band formation, in agreement with our study, it is possible that differences in the observed maximum age are due to the method of interpreting band formation and/or sample size.

Table 1. Akaike's information criterion (AIC) values for fitted growth models for *Sphyrna mokarran*

Δ-AIC, the difference between the AIC of the best fit model and those of the other models tested

Model	AIC	Parameter	Δ-AIC	Akaike weight
Male				
Gompertz	483.15	3	10.60	0.005
Gompertz (modified)	481.15	2	8.60	0.013
von Bertalanffy	472.54	3	0.00	0.981
von Bertalanffy (modified)	488.90	2	16.30	0.001
Female				
Gompertz	558.25	3	3.31	0.112
Gompertz (modified)	556.25	2	1.31	0.304
von Bertalanffy	554.94	3	0.00	0.584
von Bertalanffy (modified)	574.33	2	19.39	0.001
Combined sexes				
Gompertz	601.80	3	6.06	0.041
Gompertz (modified)	599.80	2	4.06	0.111
von Bertalanffy	595.74	3	0.00	0.847
von Bertalanffy (modified)	613.58	2	17.84	0.001

Maximum size

The great hammerhead shark is one of the larger species of Carcharhiniformes and individuals up to 600-cm TL have been reported (Compagno 1984). For example, off northern Australia, great hammerheads of up to 445-cm TL (352-cm FL; values in italics are derived from a length conversion equation) have been recorded (Stevens and Lyle 1989), whereas off South Africa in the Indian Ocean, individuals of up to 326-cm PCL (~*400*-cm TL; ~*316*-cm FL) have been reported caught in protective beach gill-nets (Cliff 1995). In the north-western Atlantic Ocean and the Gulf of Mexico, Clark and von Schmidt (1965) documented a 414-cm-TL (*327*-cm-FL) female and Springer (1963) measured a specimen of up to ~548-cm TL (*434*-cm FL). In our study, the largest individual captured was of 320-cm FL (415-cm TL), which is similar to the theoretical maximum size from the von Bertalanffy model and to that reported by Clark and von Schmidt (1965). However, despite utilising multiple sources (e.g. commercial longlines, recreational fishing tournaments) for capturing individuals, great hammerheads approaching sizes of up to 600-cm TL could not be collected. While Stevens and Lyle (1989) indicated that individuals >400-cm TL (*316*-cm FL) appear to be rare, great hammerhead populations have suffered considerable declines worldwide from commercial and recreational harvest (Camhi *et al*. 2009) and growth overfishing may be occurring.

Assessment of error

The degree of clarity of growth bands present on vertebrae of this species was very high. The relative ease of counting the growth bands resulted in a low IAPE of ageing (2.1%) and a high percentage agreement for most age classes. Although not directly comparable among studies, our IAPE value is one of the lowest reported in the elasmobranch age and growth literature. Additionally, no systematic bias in band enumeration was detected using Bowker's chi-square tests of symmetry

Table 2. Estimates of growth and goodness-of-fit from the best fit von Bertalanffy growth model for male, female and sexes combined in *Sphyrna mokarran*

Values in parentheses are standard errors. FL, fork length; AIC, Akaike's information criterion

Sex	Asymptotic size (cm, FL)	Growth coefficient (year^{-1})	t_0 (year)	F	P	r^2	AIC	s.d. of residuals
Male	264.2 (± 5.61)	0.16 (± 0.01)	−1.99 (± 0.20)	599.00	<0.001	0.92	472.54	16.11
Female	307.8 (± 11.23)	0.11 (± 0.01)	−2.86 (± 0.44)	311.51	<0.001	0.85	554.94	25.06
Combined	286.9 (± 5.99)	0.13 (± 0.01)	−2.51 (± 0.15)	778.27	<0.001	0.89	595.74	21.44

(Hoenig *et al.* 1995). These results suggest that our ageing method produced a consistent age estimate for *S. mokarran*.

Periodicity of growth band deposition

The trend in marginal-increment analysis indicated that growth-band formation occurs annually. Although many shark age and growth studies have reported a transparent band forming in the winter (e.g. Carlson and Baremore 2005), the observed pattern in *S. mokarran* of this band forming in the summer has been previously seen in other sharks (e.g. *Carcharhinus plumbeus*, sandbar shark; Sminkey and Musick 1995). Annual band formation has been reported in most shark age and growth studies, with the exception of two scalloped hammerhead studies in the Pacific Ocean (Chen *et al.* 1990; Tolentino and Mendoza 2001) and an early study on shortfin makos (*Isurus oxyrinchus*) (Pratt and Casey 1983). Chen *et al.* (1990) and Tolentino and Mendoza (2001) reported semi-annual growth-band formation. However, these studies on scalloped hammerheads suffered from high variability in MIR values and low sample sizes. Also, a more recent study on shortfin makos reported annual growth-band deposition on the basis of bomb radiocarbon methods (Campana *et al.* 2002). Furthermore, bomb radiocarbon analysis of vertebrae by Passerotti *et al.* (2010) validated annual growth-band formation in great hammerheads in the Gulf of Mexico and north-western Atlantic Ocean.

Longevity

Theoretical longevity estimates calculated by the method of Fabens (1965) for both male and female great hammerhead sharks were lower than the observed maximum ages. These differences are common in age and growth studies focused on elasmobranchs and are likely to be related to the above-mentioned difficulty in obtaining large sample sizes of the older age classes used in the model estimation. Although many sharks are long-lived (Cortés 2000), the maximum observed age of great hammerheads (44 years) is one of the oldest reported ages for any elasmobranch and is the oldest seen for any in a temperate or tropical environment. However, accurate determination of the maximum age of long-lived elasmobranchs can be hindered by the clarity of the bands deposited late in life. Crowding (small inter-band spacing) of these later bands can increase the counting error and can lead to underestimation of ages (e.g. Francis *et al.* 2007). Francis *et al.* (2007), using bomb radiocarbon analysis, hypothesised that vertebral age estimates for porbeagle sharks (*Lamna nasus*) may be 50% lower than the actual ages. Even though crowding of later growth bands in older sharks was observed in the present study, the clarity of the bands present in vertebrae allowed for accurate counts even in the later ages. Furthermore, vertebral ages from band counts were in agreement with those from the bomb radiocarbon analysis for two older specimens (Passerotti *et al.* 2010).

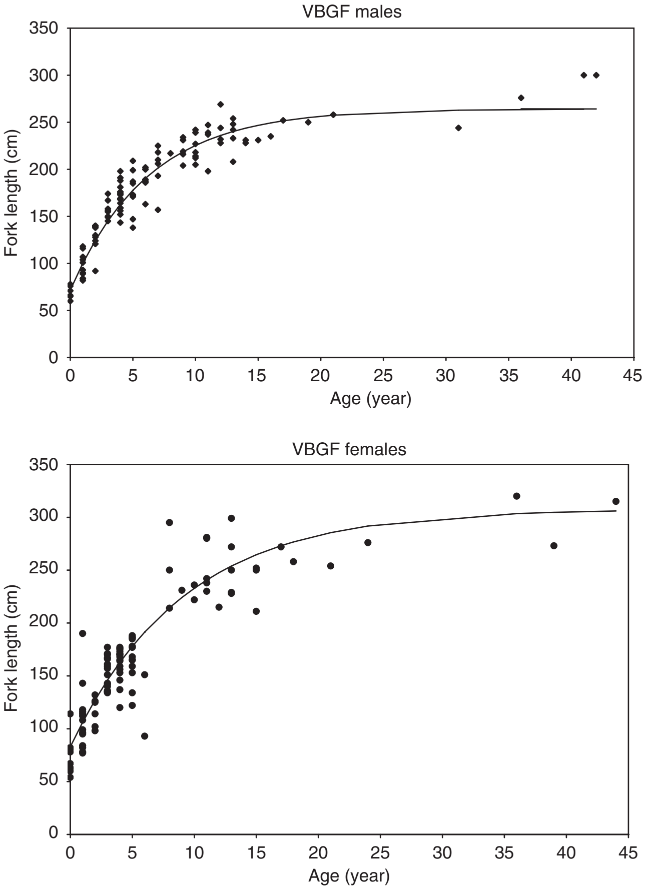

Fig. 3. The best fit von Bertalanffy growth model for male and female great hammerhead sharks (*Sphyrna mokarran*) collected in the north-western Atlantic Ocean and the eastern Gulf of Mexico.

Male great hammerhead sharks were shown to grow slightly faster and reach a smaller asymptotic size than was the case for female sharks. This sex-specific variation in growth parameters is commonly seen in juvenile age classes of elasmobranch species (e.g. sand tiger, *Carcharias taurus*, Branstetter and Musick 1994; blue shark, *Prionace glauca*, Skomal and Natanson 2003; spinner shark, *Carcharhinus brevipinna*, Carlson and Baremore 2005) and may be related to differences

Table 3. Comparison of von Bertalanffy growth parameters in *Sphyrna mokarran*, *S. zygaena* and *S. lewini*

Species	Sex	*n*	Maximum observed age (years)	Asymptotic size (cm, FL)	Growth coefficient (year^{-1})	t_0 (year)	Study
S. lewini	Male	191	30.5	214.8	0.13	−1.62	Piercy *et al.* (2007)
	Female	116	30.5	233.1	0.09	−2.22	
S. mokarran	Male	111	42.0	264.2	0.16	−1.99	Present study
	Female	105	44.0	307.8	0.11	−2.86	
S. zygaena	Combined	39	18.0	301.6	0.14	−2.45	Garza Gisholt (2004)

in energy allocation from somatic growth to reproductive development.

Conclusions

Examination of only age and growth parameters and maximum age for great hammerheads would suggest this species exhibits characteristics typical of other large, slow-growing, less productive elasmobranchs (Cortés 2000). However, back-transforming median length-at-maturity data of A. T. Nguyen and A. N. Piercy (unpubl. data; 187-cm male; 224-cm female) by using growth parameters determined in the present study suggests that the median age-at-maturity for this species is between 5 and 6 years. This age-at-maturity is similar to that of a more productive large coastal species, such as the blacktip shark, *Carcharhinus limbatus* (Carlson *et al.* 2006), in contrast to the dusky shark, *Carcharhinus obscurus*, which reaches a maximum observed age of 37 years and matures at 21 years of age (Natanson *et al.* 1995). Litter sizes of the great hammerhead shark are also large (mean = 15–23; Cortés 2000; A. T. Nguyen and A. N. Piercy, unpubl. data) when compared with those of the dusky shark and sandbar shark (Sminkey and Musick 1995). Despite large documented declines in abundance (Camhi *et al.* 2009), great hammerheads may therefore have a greater ability to recover from population depletion than do other large sharks. Full demographic and productivity models incorporating various levels of fishing mortality could be utilised to test this hypothesis. Demographic models utilising the age and growth data presented in the present study will also allow for better assessments of current fishery management policies and provide a means to forecast stock-rebuilding time. Future studies should explore this work.

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References

Abercrombie, D. L., Clarke, S. C., and Shivji, M. S. (2005). Global-scale genetic identification of hammerhead sharks: application to assessment of the international fin trade and law enforcement. *Conservation Genetics* **6**, 775–788. doi:10.1007/S10592-005-9036-2

Beamish, R. J., and Fournier, D. A. (1981). A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 982–983. doi:10.1139/F81-132

Branstetter, S., and Musick, J. (1994). Age and growth estimates for the sand tiger in the northwestern Atlantic Ocean. *Transactions of the American Fisheries Society* **123**, 242–254. doi:10.1577/1548-8659(1994)123<0242:AAGEFT>2.3.CO;2

Burnham, K. P., and Anderson, D. R. (2002). 'Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach.' 2nd edn. (Springer: New York.)

Cailliet, G. M., and Goldman, K. J. (2004). Age determination and validation in chondrichthyan fishes. In 'The Biology of Sharks and Their Relatives'. (Eds J. Carrier, J. A. Musick and M. Heithaus.) pp. 399–447. (CRC Press: Boca Raton, FA.)

Cailliet, G. M., Mollet, H. F., Pittenger, G. G., Bedford, D., and Natanson, L. J. (1992). Growth and demography of the Pacific angel shark (*Squatina californica*), based on tag returns off California. *Australian Journal of Marine and Freshwater Research* **43**, 1313–1330. doi:10.1071/MF9921313

Camhi, M. D. (1998). 'Sharks on the Line: A State-by-State Analysis of Sharks and Their Fisheries.' (National Audubon Society: New York.)

Camhi, M. D., Valenti, S. V., Fordham, S. V., Fowler, S. L., and Gibson, C. (2009). 'The Conservation Status of Pelagic Sharks and Rays: Report of the IUCN Shark Specialist Group Pelagic Shark Red List Workshop.' (IUCN Species Survival Commission Shark Specialist Group: Newbury, UK.)

Campana, S. E., Natanson, L. J., and Myklevoll, S. (2002). Bomb dating and age determination of large pelagic sharks. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 450–455. doi:10.1139/F02-027

Carlson, J. K., and Baremore, I. E. (2005). Growth dynamics of the spinner shark (*Carcharhinus brevipinna*) off the United States southeast and Gulf of Mexico coast: a comparison of methods. *Fishery Bulletin* **103**, 280–291.

Carlson, J. K., and Brusher, J. H. (1999). An index of abundance for juvenile coastal species of sharks from the northeast Gulf of Mexico. *Marine Fisheries Review* **61**, 37–45.

Carlson, J. K., Cortés, E., and Bethea, D. M. (2003). Life history and population dynamics of the finetooth shark, *Carcharhinus isodon*, in the northeastern Gulf of Mexico. *Fishery Bulletin* **101**, 281–292.

Carlson, J. K., Sulikowski, J. R., and Baremore, I. E. (2006). Do differences in life history traits exist for blacktip sharks, *Carcharhinus limbatus*, from the United States South Atlantic Bight and Eastern Gulf of Mexico? *Environmental Biology of Fishes* **77**, 279–292. doi:10.1007/S10641-006-9129-X

Chen, C. T., Leu, T. C., Joung, S. J., and Lo, N. C. H. (1990). Age and growth of the scalloped hammerhead, *Sphyrna lewini*, in northeastern Taiwan waters. *Pacific Science* **44**, 156–170.

Clark, E., and von Schmidt, K. (1965). Sharks of the Central Gulf Coast of Florida. *Bulletin of Marine Science* **15**, 13–83.

Clarke, S., McAllister, M. K., and Michielsens, C. G. J. (2004). Estimates of shark species composition and numbers associated with the shark fin trade based on Hong Kong auction data. *Journal of Northwest Atlantic Fishery Science* **35**, 453–465. doi:10.2960/J.V35.M488

Cliff, G. (1995). Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 8. The great hammerhead shark *Sphyrna mokarran* (Rueppel). *South African Journal of Marine Science* **15**, 105–114.

Compagno, L. J. V. (1984). FAO species catalogue. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2: Carcharhiniformes. FAO Fisheries Synopsis No. 125, Vol. 4, Part 2. FAO, Rome.

Conrath, C. C., Gelsleichter, J. J., and Musick, J. A. (2002). Age and growth of the smooth dogfish (*Mustelus canis*) in the northwest Atlantic Ocean. *Fishery Bulletin* **100**, 674–682.

Cortés, E. (2000). Life history patterns and correlations in sharks. *Reviews in Fisheries Science* **8**, 299–344.

Dudley, S., and Simpfendorfer, C. (2006). Population status of 14 shark species caught in the protective gillnets off KwaZulu-Natal beaches, South Africa, 1978–2003. *Marine and Freshwater Research* **57**, 225–240. doi:10.1071/MF05156

Fabens, A. J. (1965). Properties and fitting of the von Bertalanffy growth curve. *Growth* **29**, 265–289.

Ferretti, F., Myers, R. A., Serena, F., and Lotze, H. K. (2008). Loss of large predatory sharks from the Mediterranean Sea. *Conservation Biology* **22**, 952–964. doi:10.1111/J.1523-1739.2008.00938.X

Francis, M. P., Campana, S. E., and Jones, C. M. (2007). Age underestimation in New Zealand porbeagle sharks (*Lamna nasus*): is there an upper limit to ages that can be determined from shark vertebrae? *Marine and Freshwater Research* **58**, 10–23. doi:10.1071/MF06069

Garza Gisholt, E. (2004). Edad y crecimiento de *Sphyrna zygaena* (Linnaeus 1758) en las costas de Baja California Sur, México. Thesis, Universidad Autónoma de Baja California Sur, Área Interdisciplinaria de Ciencias del Mar, La Paz, Mexico.

Goldman, K. J. (2002). Aspects of age, growth, demographies, and thermal biology of two lamniform shark species. Ph.D. Thesis, College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, VA.

Goosen, A. J., and Smale, M. J. (1997). A preliminary study of the age and growth of the smoothhound shark *Mustelus mustelus* (Triakidae). *South African Journal of Marine Science* **18**, 85–91.

Grace, M., and Henwood, T. (1998). Assessment of the distribution and abundance of coastal sharks in the US Gulf of Mexico and eastern seaboard, 1995 and 1996. *Marine Fisheries Review* **59**, 23–32.

Hale, L. F., Gulak, S., and Carlson, J. K. (2009). Characterization of the shark bottom longline fishery, 2008. NOAA Technical Memorandum NMFS-SEFSC-586.

Hoenig, J. M., Morgan, M. J., and Brown, C. A. (1995). Analysing differences between two age determination methods by tests of symmetry. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 364–368. doi:10.1139/F95-038

Hueter, R. E., and Tyminski, J. P. (2007). Species-specific distribution and habitat characteristics of shark nurseries in Gulf of Mexico waters off peninsular Florida and Texas. *American Fisheries Society Symposium* **50**, 193–223.

Jiao, Y., Hayes, C., and Cortés, E. (2009). Hierarchical Bayesian approach for population dynamics modelling of fish complexes without species-specific data. *ICES Journal of Marine Science* **66**, 367–377. doi:10.1093/ICESJMS/FSN162

Johnson, A. G. (1979). A simple method for staining the centra of teleost vertebrae. *Northeast Gulf Science* **3**, 113–115.

Kimura, D. K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin* **77**, 765–776.

Mollet, H. F., Ezcurra, J. M., and O'Sullivan, J. B. (2002). Captive biology of the pelagic stingray, *Dasyatis violacea* (Bonaparte, 1832). *Marine and Freshwater Research* **53**, 531–541. doi:10.1071/MF01074

Morgan, A., Cooper, P., Curtis, T., and Burgess, G. (2009). Overview of the US east coast bottom longline shark fishery, 1994–2003. *Marine Fisheries Review* **71**, 23–38.

Natanson, L. J., Casey, J. G., and Kohler, N. E. (1995). Age and growth estimates of the dusky shark, *Carcharhinus obscurus*, in the western North Atlantic Ocean. *Fishery Bulletin* **93**, 116–126.

NSRC (National Shark Research Consortium) (2007). Highly migratory shark fisheries research by the National Shark Research Consortium 2002–2007. Mote Marine Laboratory Technical Report No. 1241. Mote Marine Laboratory, Sarasota, FL.

Passerotti, M. S., Carlson, J. C., Piercy, A. N., and Campana, S. E. (2010). Age validation of great hammerhead shark (*Sphyrna mokarran*), determined by bomb radiocarbon analysis. *Fishery Bulletin* **108**, 346–351.

Piercy, A., Carlson, J., Sulikowski, J., and Burgess, G. (2007). Age and growth of the scalloped hammerhead shark, *Sphyrna lewini*, in the northwest Atlantic Ocean and Gulf of Mexico. *Marine and Freshwater Research* **58**, 34–40. doi:10.1071/MF05195

Pratt, H. L., Jr, and Casey, J. G. (1983). Age and growth of the shortfin mako, *Isurus oxyrinchus*, using four methods. *Canadian Journal of Fisheries and Aquatic Sciences* **40**, 1944–1957. doi:10.1139/F83-224

Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fishery Research Board of Canada* **191**, 1–382.

Sadowsky, V. (1971). First record of the occurrence of an adult hammerhead shark (*Sphyrna mokarran*) in southern Brazilian waters. *Contribuicoes Avulsas do Instituto Oceanografico* **24**, 1–3. [Oceanografia Biologica].

Schwartz, F. J. (1983). Shark ageing methods and age estimation of scalloped hammerhead, *Sphyrna lewini*, and dusky, *Carcharhinus obscurus*, sharks based on vertebral ring counts. *NOAA Technical Report NMFS* **8**, 167–174.

Skomal, G., and Natanson, L. (2003). Age and growth of the blue shark (*Prionace glauca*) in the North Atlantic Ocean. *Fishery Bulletin* **101**, 627–639.

Sminkey, T., and Musick, J. (1995). Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. *Copeia* **1995**, 871–883. doi:10.2307/1447035

Springer, S. (1963). Field observations on large sharks of the Florida–Caribbean region. In 'Sharks and Survival'. (Ed. P. W. Gilbert.) pp. 95–113. (Heath & Co.: Boston, MA.)

Stevens, J. D., and Lyle, J. M. (1989). Biology of three hammerhead sharks (*Eusphyra blochii*, *Sphyrna mokarran* and *S. lewini*) from Northern Australia. *Marine and Freshwater Research* **40**, 129–146. doi:10.1071/MF9890129

Strong, W. R., Snelson, F. F., and Gruber, S. H. (1990). Hammerhead shark predation on stingrays: an observation of prey handling by *Sphyrna mokarran. Copeia* **1990**, 836–840. doi:10.2307/1446449

Tolentino, V. A., and Mendoza, C. R. (2001). Age and growth for the scalloped hammerhead shark, *Sphyrna lewini* (Griffith and Smith, 1834) along the central Pacific coast of Mexico. *Ciencias Marinas* **27**, 501–520.

Trent, L., Parshley, D. E., and Carlson, J. K. (1997). Catch and bycatch in the shark drift gillnet fishery off Georgia and Florida. *Marine Fisheries Review* **59**, 19–28.

Van Dykhuizen, G., and Mollet, H. F. (1992). Growth, age estimation, and feeding of captive sevengill sharks, *Notorynchus cepedianus*, at the Monterey Bay Aquarium. *Australian Journal of Marine and Freshwater Research* **43**, 297–318. doi:10.1071/MF9920297

von Bertalanffy, L. (1938). A quantitative theory of organic growth (inquiries on growth laws. II). *Human Biology* **10**, 181–213.

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