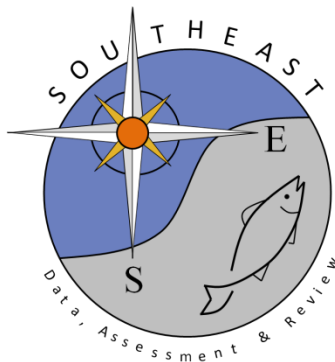


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Age and growth of the scalloped hammerhead shark, *Sphyrna lewini*, in the north-west Atlantic Ocean and Gulf of Mexico

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Abstract. The scalloped hammerhead, *Sphyrna lewini* (Griffith & Smith, 1834), is a globally exploited species of shark. In order to gain insight into the life history of this species in the USA waters, age and growth was examined from specimens ($n = 307$) captured from the north-west Atlantic Ocean and from the Gulf of Mexico. The von Bertalanffy growth model resulted in growth parameters of $L_{\infty} = 214.8$ cm fork length (FL), $k = 0.13$ year⁻¹, $t_0 = -1.62$ year for males and $L_{\infty} = 233.1$ cm FL, $k = 0.09$ year⁻¹, $t_0 = -2.22$ year for females. The oldest age estimates obtained for this population were 30.5 years for both males and females, which corresponded to FL of 234 cm and 241 cm respectively. Bowker's test of symmetry and Index of Average Per Cent Error suggests that our ageing method represents a non-biased and precise approach to the age assessment. Marginal increments were significantly different between months (Kruskal–Wallis $P = 0.017$) with a distinct trend of increasing monthly increment growth beginning in January. When compared to previously published studies, our growth estimates suggest slower growth than populations in the Pacific Ocean but faster growth than previously reported in the Gulf of Mexico.

Additional keywords: Sphyrnidae, vertebrae.

Introduction

The scalloped hammerhead shark, *Sphyrna lewini* (Griffith & Smith, 1834), is a cosmopolitan species, residing in coastal warm temperate and tropical seas (Bigelow and Schroeder 1948). In the western Atlantic Ocean, this shark is found from New Jersey (USA) south to Brazil, including the Gulf of Mexico and Caribbean. In the USA and other world markets, *S. lewini* is commonly caught in both coastal bottom long-line and pelagic long-line fisheries, where it suffers high hook mortality (A. Morgan and G. Burgess, unpublished Commercial Shark Fishery Observer Program data). The general slow growth and low fecundity of sharks results in low intrinsic rates of increase (Smith *et al.* 1998). Because of their low population resilience, most shark stocks can only withstand modest levels of fishing without depletion (Musick *et al.* 2000).

In an effort to manage shark stocks, the first Fishery Management Plan for Sharks (NMFS 1993) was developed in 1993 for shark populations in waters of the USA Atlantic and Gulf of Mexico. Because species-specific catch and life history information were limited, sharks were grouped and managed under three categories – Large Coastal, Small Coastal and Pelagic – based on known life history, habitat and market characteristics (NMFS 1993). The Large Coastal Shark Complex consists of a broad range of species, including *S. lewini*, that are generally described as large, slow-growing, and long-lived.

Recent stock assessments of the Large Coastal Shark Complex indicate that its status has improved since 1998, but that it is likely to be overfished and overfishing is still occurring (Cortés *et al.* 2002). Although recent assessments suggest that stocks of some species such as the blacktip shark (*Carcharhinus limbatus*) in the Gulf of Mexico may be improving, other species in this complex, such as the sandbar shark (*C. plumbeus*), are still overfished (Cortés *et al.* 2002; NMFS 2006). Variation in shark population trends among the many species in the Large Coastal Complex hinders management decisions. To address this, species-specific stock assessments are essential.

Biomass dynamic models have traditionally been used to assess shark stocks because of their relatively low data requirements and ease of implementation (Cortés 2002; Cortés *et al.* 2002). As relevant biological data become available, more sophisticated models can be used to assess shark stocks. Age-structured models require catch information by age, mortality rates, and a reliable age–length relationship (growth curve). As a result, accurate knowledge of growth parameters is paramount for reliable modelling of shark stocks and, ultimately, proper management of these populations.

The life history of the scalloped hammerhead shark in the northern Gulf of Mexico was previously examined by Branstetter (1987). However, that study contained a low sample size ($n = 25$) and had few or no data for many ages. Therefore, the growth

models presented by Branstetter (1987) were not useful in the development of an age-structured model. The purpose of the present study was to re-examine age and growth of scalloped hammerhead populations in the Gulf of Mexico and north-west Atlantic Ocean.

Materials and methods

Animal collection

Vertebral samples were obtained from sharks captured through fishery-independent surveys (Grace and Henwood 1998; Carlson and Brusher 1999; W. Driggers, personal communication; F. F. Snelson Jr., personal communication) and from observer programs in two directed shark fisheries (Trent *et al.* 1997; Burgess and Morgan 2002). Depending on the data source, precaudal (PC), fork (FL), total (TL), and/or stretched total (STL) length (cm), sex and maturity state were determined for each shark. When possible, weight was measured to the nearest kg (± 0.1).

Age and growth

Depending on the source, vertebrae for age determination were collected 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 this study because growth increment counts were shown not to differ between them (A. Piercy, unpubl. data). Vertebrae were placed on ice after collection and frozen upon return to the laboratory. Thawed vertebrae were manually cleaned of excess tissue, and soaked in varying concentrations of sodium hypochlorite solution for 5 to 30 min to remove 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 (Crystal bond 509 or thermoplastic cement, Electron Microscopy Sciences, Hatfield, Pennsylvania, USA) and sectioned using a Buehler 82 Isomet low-speed saw. Each section was mounted on a glass microscope slide with clear resin (Cytoseal 60, Fisher Scientific, Pittsburg, Pennsylvania, 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 apparent on crystal violet-stained sagittal sections with a thickness of 0.6 mm.

Opaque bands representing summer growth and translucent bands representing winter growth were identified following the description and terminology of Cailliet and Goldman (2004) (Fig. 1). As no validation is available for this species, verification of the annual period of band formation was performed using the relative marginal increment analysis (Conrath *et al.* 2002; Sulikowski *et al.* 2003, 2005):

$$\text{MIR} = R_n/R_{n-1},$$

where MIR = marginal increment ratio; R_n = distance to the outer edge of the last complete band; and R_{n-1} = distance between the penultimate and last band. Mean MIR was plotted

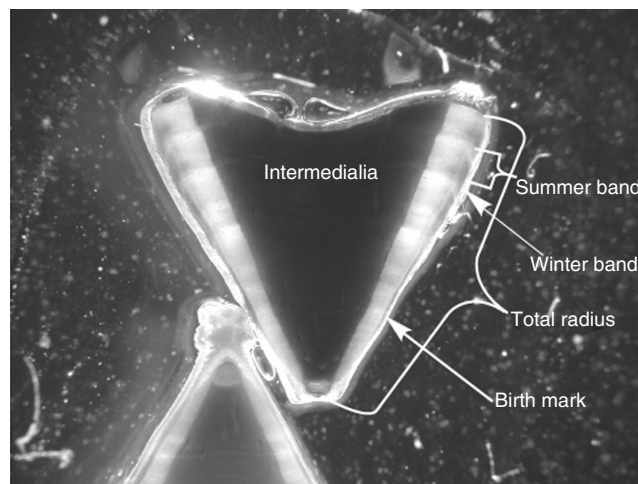


Fig. 1. *Sphyrna lewini*. Sagittal vertebral section from a 4-year-old scalloped hammerhead, illustrating the banding pattern and winter marks (annuli) used to assign age.

against month to determine trends in band formation. A Kruskal–Wallis one-way test by ranks was used to test for differences in MIR by month (Simpfendorfer 2000; Sulikowski *et al.* 2003, 2005).

Two readers (A. Piercy and J. Carlson) randomly read vertebrae independently, without knowledge of sex or length of specimens. Vertebral age estimates for which the readers disagreed were re-read simultaneously using a Meiji Techno R2 Dissecting Microscope equipped with a Hitachi KP-D50 Digital Camera and software. If no agreement was reached, samples were discarded. Several methods were used to evaluate precision and bias among age determinations following recommendations of Cailliet and Goldman (2004). Per cent agreement ($\text{PA} = [\text{number agreed}/\text{number read}] \times 100$) and per cent agreement ± 1 year were calculated for 10-cm length intervals (e.g. 76 to 85 cm FL) to evaluate precision (Goldman 2002). The index of average per cent error (IAPE; Beamish and Fournier 1981) was calculated to compare the average deviation of readings from means of all readings for each vertebral section:

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

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

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

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

Table 1. Percentage agreement and percentage agreement (± 1 band) from the initial set of readings for *Sphyrna lewini* FL, Fork length

FL interval	Sexes combined			Males			Females		
	Total read	Percentage agreement	Percentage agreement ± 1 band	Total read	Percentage agreement	Percentage agreement ± 1 band	Total read	Percentage agreement	Percentage agreement ± 1 band
30–39	27	96.3	100.0	12	100.0	100.0	15	93.3	100.0
40–49	23	87.0	100.0	8	87.5	100.0	15	86.7	100.0
50–59	8	62.5	87.5	7	57.1	85.7	1	100.0	100.0
60–69	18	38.9	83.3	9	22.2	77.8	9	66.7	88.9
70–79	7	42.9	71.4	4	25.0	50.0	3	66.7	66.7
80–89	5	80.0	80.0	2	50.0	50.0	3	100.0	100.0
90–99	7	42.9	85.7	3	0.0	100.0	4	75.0	75.0
100–109	15	73.3	93.3	7	57.1	100.0	8	87.5	87.5
110–119	10	50.0	80.0	4	75.0	75.0	6	33.3	83.3
120–129	21	95.2	100.0	10	90.0	100.0	11	100.0	100.0
130–139	12	91.7	91.7	4	100.0	100.0	8	87.5	87.5
140–149	19	68.4	94.7	10	60.0	90.0	9	77.8	100.0
150–159	14	71.4	85.7	6	66.7	83.3	8	87.5	87.5
160–169	11	45.4	90.9	7	42.9	85.7	4	50.0	75.0
170–179	16	56.3	87.5	11	45.4	72.7	5	80.0	100.0
180–189	24	54.2	70.8	22	50.0	68.2	2	100.0	100.0
190–199	29	69.0	79.3	29	69.0	79.3	–	–	–
200–209	17	70.6	76.5	17	70.6	76.5	–	–	–
210–219	9	55.5	55.5	7	57.1	57.1	2	50.0	50.0
220–229	9	66.7	77.7	8	55.5	75.0	1	100.0	100.0
230–239	4	75.0	75.0	2	50.0	50.0	2	100.0	100.0
240–249	1	100.0	100.0	–	–	–	1	100.0	100.0

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

An alternate 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), is described as:

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

where $b = (L_\infty - L_0)/L_\infty$ and L_0 = length at birth. Estimated median length at birth for scalloped hammerhead shark is 38 cm FL (J. Carlson, unpublished data).

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

$$L_t = L_0(e^{G(1-e^{-kt})})$$

where $G = \ln(L_0/L_\infty)$.

All growth model parameters were estimated using Marquardt least-squares non-linear regression using SAS statistical software PROC NONLIN (SAS Institute, Cary, NC, USA). Models were assessed based on a combined examination of residual mean square error (MSE), coefficient-of-determination (r^2), level of significance ($P < 0.05$) and standard residual analysis.

In developing theoretical growth models, we assigned an arbitrary birth date of 1 June – the approximate mid-point of the time-period when neonates were present in field collections (J. Carlson, unpublished data) – and assumed that (1) the

birth mark is the band associated with a pronounced change in angle in the intermedialia, (2) the translucent bands that represent winter growth form approximately six months later (i.e. 0.5 years), and (3) subsequent translucent bands representing winter growth form at yearly intervals thereafter. Thus, ages (year) were calculated following the algorithm of Carlson *et al.* (1999): age = birth mark + number of translucent winter bands – 1.5. If only the birth mark was present, age was determined to be 0+ years. All age estimates from growth-band counts were based on the hypothesis of annual growth-band deposition (Branstetter 1987). Chi-squared tests of likelihood ratios (Kimura 1980; Cerrato 1990) were used to determine possible growth differences between sexes. Theoretical longevity was estimated as the age at which 95% of L_∞ is reached ($5 \times [\ln 2/k]$) (Fabens 1965; Cailliet *et al.* 1992).

Results

Previous studies on scalloped hammerhead sharks (*Sphyrna lewini*) have reported size as total length (TL), i.e. a straight line from the tip of the snout to the tip of the tail in a natural position. For comparison with these studies, we derived several morphometric relationships with other size metrics. Linear regression formulae were determined as: TL = 1.296FL + 0.516, $n = 1488$, $r^2 = 0.99$, $P < 0.0001$; PCL = 0.918FL – 0.365, $n = 709$, $r^2 = 0.99$, $P < 0.0001$.

Of the original 311 samples, only 4 (1.2%) were considered unreadable and were discarded. The first set of band counts resulted in an index of average per cent error (IAPE) of 3.2%. When grouped into 10-cm length intervals, agreement for combined sexes was reached for an average of 69% and 89% ± 1

band for sharks <150 cm FL (Table 1). Above 150 cm FL, agreement was reached for 56% and 70% ± 1 band of samples initially read. Bowker's test of symmetry (Hoenig *et al.* 1995) indicated no systematic disagreement between readers ($\chi^2 = 38$, d.f. = 46, $P = 0.75$).

A total of 65 sharks were usable for relative marginal increment analysis, spanning eight months. Sample size was low in March ($n = 1$), and no suitable samples were collected in October, November, and December. Despite the low sample size, marginal increments were significantly different among months (Kruskal–Wallis $\chi^2 = 17.02$, $P = 0.017$), with a trend of increasing monthly increment growth that peaked in May and began to decline in June (Fig. 2). These results suggest that a single translucent band is formed annually on vertebrae during the winter months. The majority of relative marginal increment ratios were only conclusive for juvenile fish (sharks ≤15 years old). Marginal increments of many older sharks were not suitable for MIR analysis, because monthly changes in margin widths were difficult to accurately measure owing to insufficient spacing of later bands.

Under the statistical criteria defined by Carlson and Baremore (2005), all growth models fitted the data well. All models were highly significant ($P < 0.001$) and exhibited high coefficients of determination ($r^2 \geq 0.86$). Residual mean square error (MSE) was generally lowest for the von Bertalanffy model and the von Bertalanffy model with a size-at-birth intercept. Plots of residuals against predicted sizes indicated no pattern in residuals for any model. The standard deviation of the residuals was also lowest for the von Bertalanffy model and the von

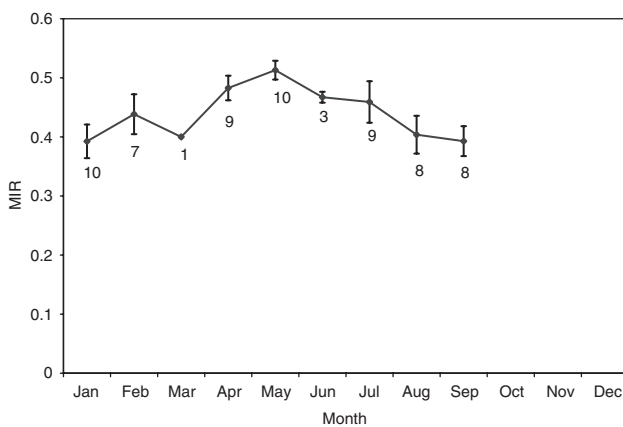


Fig. 2. *Sphyrna lewini*. Mean marginal increment analysis by month for combined sexes of scalloped hammerhead sharks ranging in size from 74 to 236 cm FL. Vertical bars are ±s.e.m. Numbers below the line represent the monthly sample size.

Table 2. *Sphyrna lewini*. Estimates of growth and goodness-of-fit from the von Bertalanffy growth model for male, female, and sexes combined. Values in parentheses are standard error. FL, fork length; MSE, mean square error

Sex	Asymptotic size (cm FL)	Growth coefficient k (year ⁻¹)	t_0 (year)	F	P	r^2	MSE	s.d. of residuals
Male	214.8 (± 4.19)	0.13 (± 0.01)	-1.62 (± 0.20)	913.01	<0.001	0.86	337.0	18.26
Female	233.1 (± 11.52)	0.09 (± 0.01)	-2.22 (± 0.24)	608.05	<0.001	0.92	252.0	15.73
Combined	219.8 (± 4.08)	0.12 (± 0.01)	-1.84 (± 0.15)	1684.53	<0.001	0.89	311.4	17.58

Bertalanffy model with a size-at-birth intercept. Values of k and L_∞ from all equations varied slightly, but fits to the observed data were better for the von Bertalanffy equation. Because of the similarity among models and the general ubiquitous use of the von Bertalanffy equation, we present and compare further age and growth results using only the von Bertalanffy model (Table 2).

Observed von Bertalanffy parameters and growth rates differed between males and females (Kruskal–Wallis $\chi^2 = 9.54$, $P = 0.02$). Growth of both sexes was rapid until age 12, after which the growth rate of males slowed down considerably; reduction in the growth rate of females was not as accentuated (Fig. 3). Females had a lower growth coefficient ($k = 0.09$ year⁻¹) and higher asymptotic size (233.1 cm FL) than males ($k = 0.13$ year⁻¹ and 214.8 cm FL respectively). Theoretical longevity estimates were 38.5 years for females and 26.6 years for males. Observed size-at-age was relatively similar between the sexes with no clear trend (Table 3). The oldest aged sharks were 30.5 years for both sexes, with lengths of 241 cm (females) and 234 cm (males) FL.

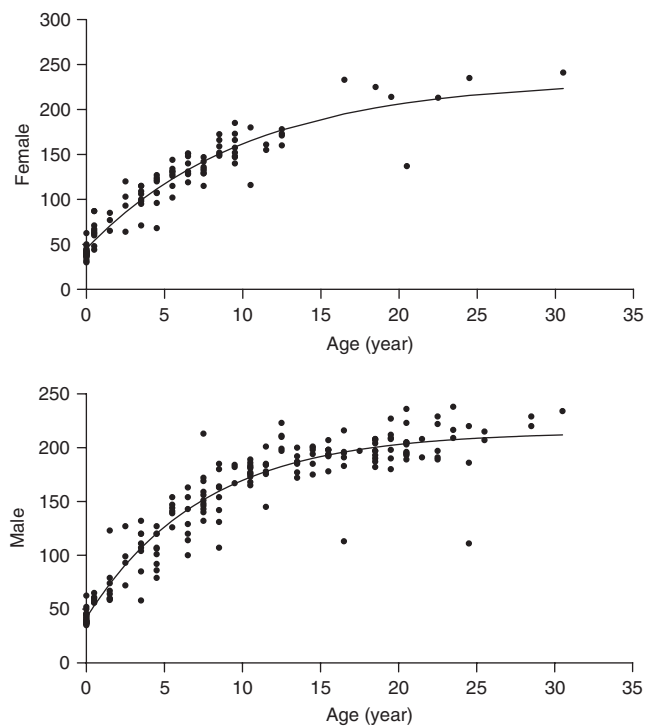


Fig. 3. *Sphyrna lewini*. The von Bertalanffy growth model for scalloped hammerhead sharks collected off the coasts of the Gulf of Mexico and south-east USA.

Discussion

No systematic bias in band counts was detected using Bowker's chi-squared tests of symmetry as described by Hoenig *et al.* (1995). Although not directly comparable between studies (Cailliet and Goldman 2004), the index of average per cent error (IAPE) of ageing was relatively low (3.2%). IAPE values as low as 3% (oceanic whitetip shark, *Carcharhinus longimanus*) (Lessa *et al.* 1999) and as high as 13% (blacktip shark, *Carcharhinus limbatus*) (Wintner and Cliff 1995) have been reported. These results suggest that our ageing method produced a consistent age estimate for *Sphyrna lewini* (Hoenig *et al.* 1995; Campana 2001; Cailliet and Goldman 2004).

The trend in marginal increment analysis suggests that band formation occurs annually, with a thin translucent band forming during the boreal winter. This pattern of band formation is commonly reported in age and growth studies of large coastal sharks in the north-west Atlantic Ocean (e.g. Natanson *et al.* 1995; Carlson *et al.* 1999, 2003; Carlson and Baremore 2005). Branstetter (1987) also reported annual band formation for the scalloped hammerhead; however, a low sample size precluded any marginal increment ratio (MIR) analysis. Our MIR results differ from other studies of the growth of *Sphyrna lewini* in the Pacific Ocean. Chen *et al.* (1990) and Tolentino and Mendoza (2001) reported semi-annual growth band formation, with marginal increments lowest in June and December. However, the sample sizes of Tolentino and Mendoza (2001) were low for most months, and varied widely. Chen *et al.* (1990) did not report monthly sample sizes, but variability in MIR appeared high in most months. Both studies supported the two growth bands per year hypothesis through citation of previous studies

of other shark species, including that of Pratt and Casey (1983). Pratt and Casey (1983) reported age and growth estimates of *Isurus oxyrinchus* in the north-west Atlantic Ocean based on a two growth bands per year hypothesis. However, a preliminary study of *I. oxyrinchus* using bomb radiocarbon methods suggests that growth-band deposition is annual (Campana *et al.* 2002).

Although our marginal increment data indicate annual formation in juvenile scalloped hammerheads, validation of band formation in adults is still needed, because validation in immature sharks may not be applicable to mature sharks (Campana 2001). Nevertheless, we assumed that annual ring deposition continued throughout their lifetime growth (Conrath *et al.* 2002; Sulikowski *et al.* 2005). Other methods of age validation such as bomb radiocarbon techniques (Campana *et al.* 2002), oxytetracycline marking (e.g. Simpfendorfer *et al.* 2002; Skomal and Natanson 2003; Driggers *et al.* 2004) and calcein marking (Gelsleichter *et al.* 1997) would provide direct validation of growth rings in mature sharks and should be pursued in order to resolve this issue.

Scalloped hammerhead sharks in the Gulf of Mexico and western Atlantic appear to grow more slowly and have smaller asymptotic sizes than previously reported for this species in the Pacific Ocean (Table 4). However, these differences may be due to interpretation of band formation rather than geographic differences. Tolentino and Mendoza (2001) reported a growth coefficient of male sharks that was similar to that obtained in the present study, despite a hypothesis of two growth bands per year (Table 4). If growth data presented by Chen *et al.* (1990) were transformed to reflect a one growth band per year hypothesis, then the growth parameters of the Gulf of Mexico and north-west

Table 3. Mean size-at-age (cm FL) for male and female *Sphyrna lewini*
s.d., standard deviation

		Age (year)															
		0.0	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5
Male																	
Size		41.9	59.3	73.1	97.8	104.6	92.2	141.8	131.9	157.2	153.2	177.7	177.8	179.0	208.0	185.6	192.2
s.d.		6.3	3.4	21.4	22.7	23.4	33.8	9.4	22.6	22	25.9	9.3	7.4	17	10.5	9.2	10.2
n		23	6	8	4	8	9	6	7	11	8	3	11	7	5	7	6
		15.5	16.5	17.5	18.5	19.5	20.5	21.5	22.5	23.5	24.5	25.5	26.5	27.5	28.5	29.5	30.5
Size		194.6	182.3	197.0	197.3	203.4	203.9	199.5	205.6	221.3	172.3	211.0	–	–	224.5	–	234.0
s.d.		7.7	35.7	–	9.3	15.5	14.1	12.0	18.6	15.0	55.8	5.7	–	–	6.4	–	–
n		9	6	1	10	7	11	2	5	3	3	2	–	–	2	–	1
		0.0	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5
Female																	
Size		40.5	65.4	75.7	95	101.1	109.0	126.4	137.1	133.0	158.0	158.6	148.0	158.0	170.5	–	–
s.d.		6.0	14.0	10.1	23.5	14.3	19.6	12.7	12.1	9.6	9.7	15.1	45.2	4.2	7.6	–	–
n		30	10	3	4	8	8	8	8	8	6	8	2	2	4	–	–
		15.5	16.5	17.5	18.5	19.5	20.5	21.5	22.5	23.5	24.5	25.5	26.5	27.5	28.5	29.5	30.5
Size		–	233.0	–	225.0	214.0	137.0	–	213.0	–	235.0	–	–	–	–	–	241.0
s.d.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
n		–	1	–	1	1	1	–	1	–	1	–	–	–	–	–	1

Table 4. Comparison of von Bertalanffy growth parameters in four *Sphyrna lewini* growth studies
Numbers in italics are converted fork lengths from published total lengths. FL, fork length

Sex	<i>n</i>	Asymptotic size (cm FL)	Growth coefficient (year ⁻¹)	<i>t</i> ₀ (year)	Study
Male	191	214.8	0.13	-1.62	Present study
Female	116	233.1	0.09	-2.22	
Male	50	<i>259.2</i>	0.131	-1.09	Tolentino and Mendoza 2001
Female	51	<i>272.2</i>	0.156	-0.63	
Male	49	<i>247.0</i>	0.222	-0.746	Chen <i>et al.</i> 1990
Female	276	<i>246.3</i>	0.249	-0.413	
Combined	25	<i>253.5</i>	0.073	-2.2	Branstetter 1987

Atlantic Ocean and western Pacific Ocean populations would agree more closely. However, this issue will only be resolved when the periodicity of growth-band deposition is validated for both the Pacific and Atlantic populations.

Growth coefficients (*k*) presented in this study are higher than the combined sexes growth coefficient reported by Branstetter (1987). It is unclear whether these differences are related to sample size, methodology or changes resulting from density-dependence. Sharks have been heavily harvested in the Gulf of Mexico and north-west Atlantic Ocean since the 1980s (NMFS 2003), facilitating the potential for a density-dependent compensatory response. Compensatory growth and reproductive responses were documented in several species of sharks (Sminkey and Musick 1995; Carlson and Baremore 2005). However, a lack of larger sharks and the overall low sample size of Branstetter's (1987) study hinders the documentation of any change in growth parameters.

This study adds to knowledge of the vital life-history parameters of scalloped hammerhead sharks in the Gulf of Mexico and north-west Atlantic Ocean. Our results support the hypothesis that this species, like other elasmobranchs, requires conservative management due to its slow growth and subsequent susceptibility to over-exploitation (Musick 2004). However, further research on the reproduction of this species (specifically, updated size-at-maturity and fecundity estimates) is required. These combined data may allow for species-specific management of *S. lewini* populations.

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