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Length at life stages of the white shark *Carcharodon carcharias* in the western North Atlantic

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ABSTRACT: Length at life stages of the white shark *Carcharodon carcharias* is not well known for most of the 9 populations of this species, including in the western North Atlantic (WNA). We analyzed length and maturity data by sex for 87 white sharks with sizes ranging 138–501 cm total length (TL), captured, studied, and released by OCEARCH during 2012–2022, off the US and Canadian Atlantic coasts. A binary logistic regression was used to estimate the length-at-maturity (L_{50}) for the WNA white shark with a Bayesian statistical framework using a Markov chain Monte Carlo method for numerical integration. Different trials using noninformative and informative priors were tested. The posterior probability distribution for L_{50}, steepness of the model (ϕ), and 95% credible intervals (CI) of the logistic model for females were L_{50} = 411.3 cm TL (CI: 390.8–432.6 cm TL) and ϕ = 10.5 (CI: 5.7–17.8) and for males were L_{50} = 334.9 cm TL (CI: 321.2–348.2 cm TL) and ϕ = 7.5 (CI: 4.2–12.4). These L_{50} values are somewhat smaller than previously reported sizes-at-maturity for both sexes of this species. An ordinal logistic regression allowed us to determine the probability of being in the various life stages (young-of-the-year, juvenile, and adult) at a particular size. Estimating the length at any life-history stage of white sharks along with age estimates is useful for determining the reproductive value of the population and ultimately for estimating the relative contribution (elasticity) of vital rates to population growth.

KEY WORDS: Size-at-maturity · Bayesian approach · Apex predator · Markov chain Monte Carlo

1. INTRODUCTION

Large, highly migratory species of marine animals are often difficult to study in the wild. Marine species that have been designated as protected, prohibited, threatened, or endangered may be even more difficult to study, due to restrictions on obtaining specimens for research, making data collection challenging and often opportunistic. Among such species is the white shark *Carcharodon carcharias*, which is afforded protection in a number of areas around the world and is classified in the IUCN Red List as Vulnerable with a Decreasing Population Trend (Rigby et al. 2022). Despite the charismatic nature of this top predator and the considerable effort that has been made to learn about the white shark, most studies of this species have focused on ecological and behavioral aspects, such as horizontal and vertical migration using satellite technology (Bonfil et al. 2005, Domeier 2012, Franks et al. 2021). A comprehensive understanding of some of the basic aspects of white shark biology, such as age, growth, and maturity over its multiple populations, is still incomplete.

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The incidental capture of white sharks to provide specimens for research depends on the nature of regional fisheries. In some countries where coastal artisanal fisheries are intense, the chances of encountering a white shark may be higher (Galván-Magaña et al. 2010, Márquez-Farías & Lara-Mendoza 2017). In oceanic regions where longline fleets operate, the catch rates of white sharks are relatively unknown. Regardless of the fishery with which white sharks might interact, however, captured specimens are rarely available for scientific study, precluding advances in understanding their life history (Adams et al. 1994). In some isolated regions, such as Kwazulu-Natal, South Africa (Cliff et al. 1989), and Queensland and New South Wales, Australia (Reid & Krogh 1992), a source of white shark specimens for science is beach nets set to reduce the risk of shark attack, but such sources are rare over the species' worldwide range.

The global distribution of white sharks comprises 9 distinct populations (Rigby et al. 2022), including the relatively understudied component in the western North Atlantic (WNA). This population is thought to be currently undergoing rebuilding after decades of depletion that occurred between the 1960s and 1990s (Curtis et al. 2014). Reports on size-at-maturity of the white shark come from multiple populations and are consistent in that males mature at a smaller size than females. Pratt (1996) stated that males mature at 380 cm total length (TL), corresponding to 352 cm fork length (FL), in the WNA. Francis (1996) summarized the available information on white sharks from multiple populations and concluded that most females mature within the size range 450–500 cm TL. A more recent report on WNA white sharks (Skomal et al. 2017) used similar length ranges for life stages, but these ranges were obtained from a study of the eastern Australia population (Bruce & Bradford 2012) due to a lack of information for the WNA population. More recently, Franks et al. (2021) provided information on size by life stage in the WNA by classifying male and female white sharks into juvenile, subadult, maturing (for females only), and mature life stages. Their classification was based on TL, clasper development (in males), length/girth ratios (in females), estradiol levels measured in blood collected from female sharks, and other characteristics. Efforts to determine maturity through hormonal analysis of small muscle samples from white sharks seem promising but so far have been inconclusive (Verkamp et al. 2021).

The use of a large research vessel to capture white sharks and attach satellite tags for tracking studies provides an opportunity to obtain additional pertinent biological information (Bonfil et al. 2005, Franks et al. 2021). Precise body measurements of live, large sharks in the water can be difficult if not impossible, whereas sharks that are accessible for researchers to examine out of the water under controlled conditions allow for precise measurement. The M/V 'OCEARCH', a privately owned vessel with a movable platform for research on large animals, provides such an opportunity to obtain body measurements and classify life stages, among other research protocols. The animals are then released to continue their normal behavior in the wild (Franks et al. 2021).

Using the OCEARCH database of WNA white shark sex, length, and life stage, the present study aimed to determine the proportion of mature individuals by size for both sexes. We used a Bayesian approach to estimate the parameters of the logistic function and thus describe the proportion of mature individuals by length (maturity ogive). The resulting estimated parameters are presented as a posterior probability distribution (marginal posteriors). We also estimated the probability of individuals being in a particular life stage given their size by applying an ordinal logistic regression. Our goal was to advance our knowledge of the life history of the WNA white shark so that quantitative population analyses can provide more accurate predictions of stock recovery, the effects of fishing, and other critical parameters for conservation of this highly migratory apex predator.

2. MATERIALS AND METHODS

2.1. Surveys and biometrics

From 2012–2022, 17 OCEARCH research cruises targeting white sharks were conducted along the Atlantic coast of the USA and Canada (Fig. 1). These efforts provided access to 87 white sharks of both sexes of all life stages, from young-of-the-year (YOY) to mature adults. Sharks were captured by several hook-and-line methods and were led to the M/V 'OCEARCH' research platform, where they were provided cool seawater ventilation. At the same time, researchers took measurements and samples, conducted health examinations, and applied tracking tags, after which the sharks were released back into the wild (Franks et al. 2021). The TL of the sharks was measured as the straight-line distance along the body's midline between the tip of the rostrum and the perpendicular line corresponding with the rearmost

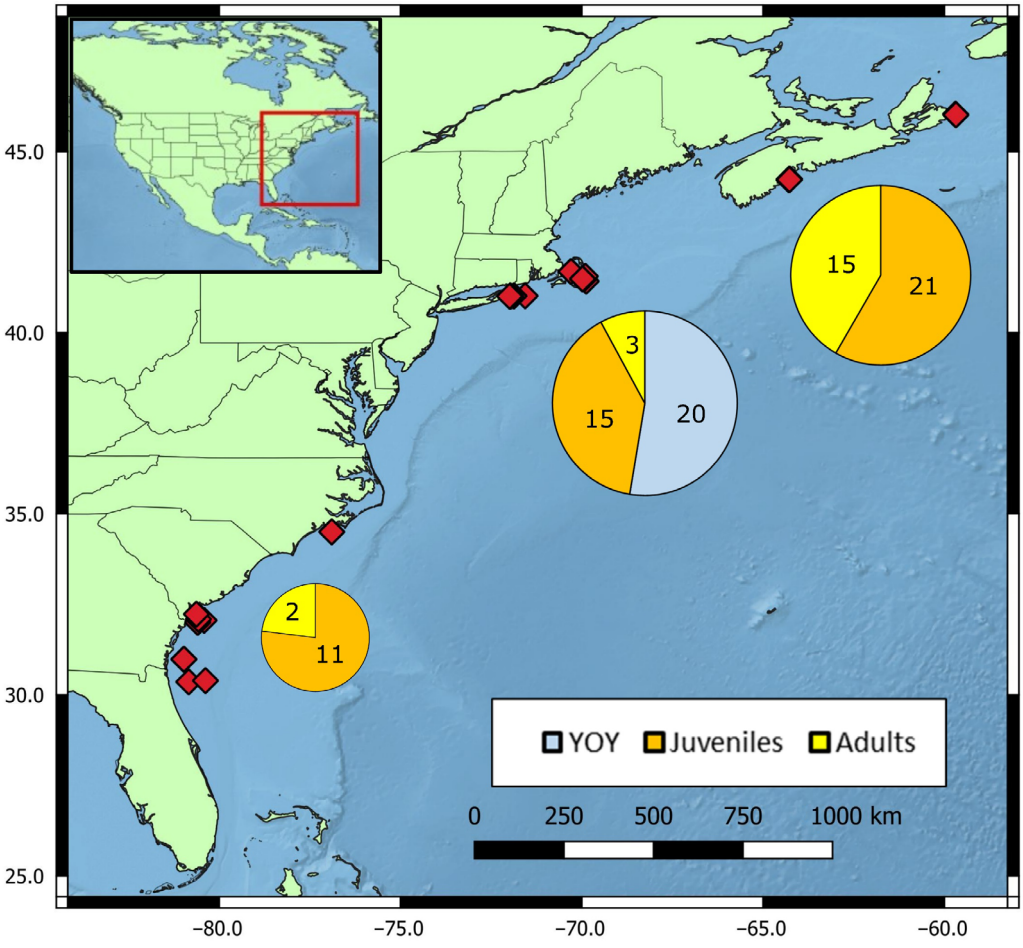

Fig. 1. Locations of the capture and sampling of 87 white sharks *Carcharodon carcharias* in the present study (red diamonds). Pie charts indicate the number of sampled individuals by maturity stage in each of 3 geographic areas (top to bottom: Nova Scotia, northeast USA, southeast USA). YOY: young-of-the-year

tip of the upper caudal fin (Fig. 2). In 3 instances (males), TL was not measured but was obtained by converting from measured FL with a formula derived from our data collected from males in the present study (TL = 8.2371 + 1.037FL; r^2 = 0.996; n = 40). The entire process on the platform took 15–20 min, and all procedures were approved by the Institutional Animal Care and Use Committees of Jacksonville University and Georgia Aquarium.

2.2. Life stages by length and sex

We modified the criteria of Franks et al. (2021), and included new data on YOY individuals, to classify each of the 87 sharks into a life stage from YOY to adult. We pooled all post-YOY juveniles into a single category (i.e. combining juveniles, subadults, and maturing animals), thereby sorting sharks into the 3 categories of YOY, juveniles, and adults for both sexes. We also included additional data on post-YOY sharks, since the Franks et al. (2021) study was completed. This updated classification of life stages and inclusion of new data eliminated missing values in some length intervals and provided more contrast for statistical inferences.

Length–frequency distributions were constructed to examine the size structure of the sample. A chi-square test was used to compare the observed sex ratio of the entire sample and by maturity stage against the expected value of 1:1. White sharks for each sex were classified as 0 or 1 for immature or mature individuals, respectively. The maturity ogives were described by fitting the following logistic function (Márquez-Farías 2007):

$$\mathrm{Pm} = \frac{1}{1 + \exp\left[-\frac{(\mathrm{TL} - L_{50})}{\phi}\right]} \quad (1)$$

Fig. 2. Measuring a white shark *Carcharodon carcharias* on the hydraulic platform of the OCEARCH research vessel. A hose in the mouth provides seawater for ventilation, and a wet towel covers the eyes and gill slits for protection, while cool seawater is poured on the body to help maintain body temperature

where Pm is the proportion of maturity given the length (TL), L_{50} is the median length when half of the individuals reached maturity, and ϕ is the steepness of the model, which should be forced to be positive. We chose Eq. (1) for the convenience of building priors with biologically meaningful parameters such as L_{50}. We applied both a frequentist and a Bayesian approach to compare the 2 methods and estimate the parameters of the logistic function.

Before applying the frequentist approach, we tested the significance of the difference in maturity stages (0 and 1) between sexes and TL with a generalized linear model. If differences were significant, we applied a binary logistic regression between TL and coded maturity data (0 and 1) to estimate the parameters (L_{50},ϕ) and their 95% confidence intervals for each sex. We then implemented a Bayesian binary logistic regression to estimate the parameters of the logistic functions to describe the length-at-maturity (Eq. 1). The Bayesian approach requires a prior probability distribution that summarizes the knowledge of the model parameters. Thus, we explored a base scenario using noninformative priors as the uniform distribution (UD) for the parameters (L_{50},ϕ) for both sexes combined: L_{50} = UD(200,600) and steepness ϕ = UD(0,100). Next, we adopted a scenario with informative priors for both parameters for separate sexes, using averages of size-at-maturity values previously reported in the literature (Francis 1996, Pratt 1996, Castro 2011). In females, we set a normal distribution (ND) for L_{50} = ND(440.75, 47.00) [where the second term, SD, is expressed as $\tau = 1/\sigma^2 = 0.0004526$] and a log-normal distribution (LND) for ϕ = LND(2.5,10). For males, L_{50} = ND (329.00, 17.18) [τ= 0.0033881] and an LND for ϕ = LND(2.0,10) were used. An LND for ϕ was chosen to ensure non-negative values and concentrate most of the density in the lower limit. The SD for LND was calculated as $\sigma = \sqrt{\ln(1 + [SD/\bar{x}]^2)}$ and $\tau = 1/\sigma^2$ (Cortés 2002a, McAllister et al. 2001).

The Bayesian framework adopted requires the integration of the prior probability distribution Pr(θ) of model parameters and the likelihood of the data Pr(d|θ) given those parameters. These 2 elements are necessary to compute the posterior distribution for the parameters Pr(θ|d) using the Bayes formula (Gelman et al. 2013):

$$\Pr(\theta \mid d) = \frac{\Pr(d \mid \theta)\ \Pr(\theta)}{\int \Pr(d \mid \theta)\ \Pr(\theta)\ \partial\theta} \quad (2)$$

Thus, substituting the actual parameters of the logistic function into the Bayes formula and simplifying terms, we obtain:

$$\Pr(L_{50}, \phi \mid d) = \frac{\Pr(d \mid L_{50}, \phi)\ \Pr(L_{50}, \phi)}{\int \Pr(d \mid L_{50}, \phi)\ \Pr(L_{50}, \phi)\ \partial\theta} \quad (3)$$

where Pr(L_{50},ϕ) is the prior defined in the above-described scenarios, Pr(d|L_{50},ϕ) is the likelihood of the data given the parameters, and Pr(L_{50},ϕ|d) is the posterior probability distribution for the parameters of the logistic model given the data.

We used the Markov chain Monte Carlo (MCMC) numerical algorithm to obtain the joint posterior probability distribution of the parameters by drawing random samples from the parameters using MultiBUGS (Goudie et al. 2020). We used 3 chains with the MCMC algorithm of initial values, with overdispersed initial values for L_{50},ϕ to assess the convergence of the parameter's value. We performed 100 000 iterations, with a burn-in of 1000 and a thinning rate of 1. Convergence of the MCMC algorithm was visually examined with the trace of the 3 chains, lag autocorrelation of parameters, the Brooks-Gelman-Rubin (BGR) diagnostics (Gelman & Rubin 1992), the dispersion of particles between param-

eters, and the shape of their marginal profiles. Summary statistics with the posterior mean, the 95% credible intervals (95% CI), and quantities related to the fitting process, such as deviance information criterion (DIC) and Watanabe-Akaike information criterion (WAIC), were derived (Gelman et al. 2014). Plots of the posterior probability distribution for the parameters and the resulting maturity ogives were generated.

2.3. Probability of life stages by length

Life history development through life stages is a gradual process that can be ordered in consecutive categories. Using our classification of life stages into YOY, juvenile, and adult white sharks, we used an ordinal logistic regression (OLR) to estimate the probability of an individual of a given size being in a particular life stage. Briefly, following Agresti (2002), in the parameterization for the cumulative logit model, j represents the life stage categories (1 = YOY, 2 = juveniles, and 3 = adults) as an ordinal response variable and x represents the explanatory variable (TL) (i.e. logit $(P(Y \leqslant j) = \alpha_j + \beta x$, where $j = 1, 2, ..., c-1)$. The intercept α_j varies for each cumulative logit. The parameter β describes the effect of the explanatory variable x on the log odds of response category j. Categories 1 to j combine to form 1 category and categories $j + 1$ to c form the other: $P(Y \leqslant 1) \leqslant P(Y \leqslant 2) \leqslant 2 ... \leqslant P(Y \leqslant c) = 1$. The cumulative logit functions are:

$$\text{logit}\,[P(Y \leqslant j)] = \log\left[\frac{P(Y \leqslant j)}{1 - P(Y \leqslant j)}\right] \quad (4)$$

Because there was no source of information to formulate prior distributions for the estimation of the OLR coefficients, the MCMC was applied with 100 000 iterations using reference priors. The result of the OLR was displayed in plots depicting the probability of belonging to a particular life stage given the size. The 95% CI of the models and the coefficients also were displayed.

3. RESULTS

3.1. Length structure

The 87 white sharks we examined had a nearly equal sex ratio (female:male = 1.02:1, $\chi^2 = 0.011$, p = 0.915). The length–frequency distribution of female white sharks was bimodal, with peaks at length classes 140–160 cm TL and 300–320 cm TL (Fig. 3A). The mean lengths of life stages of females were: YOY 155.8 cm TL (range = 142.0–165.0, SD = 7.4, n = 9); juveniles 315.2 cm TL (range = 200.0–388.0, SD = 53.5, n = 28); and adults 452.6 cm TL (range = 425.0–501.0, SD = 29.7, n = 7) (Fig. 3B). The length–frequency distribution of males showed peaks at length classes 140–160 cm TL, 260–280 cm TL and 380–400 cm TL (Fig. 3A). The mean lengths of life stages of males were: YOY 154.8 cm TL (range = 138.0–166.0, SD = 9.1, n = 11); juveniles 273.7 cm TL (range = 182.0–341.0, SD = 39.2, n = 19); and adults 373.7 cm TL (range = 332.0–396.0, SD = 20.1, n = 13) (Fig. 3B). Table 1 shows length–frequency distributions tabulated for each sex and by life stage. The length ranges of maturity condition coded as binary for each sex are presented in Fig. 4.

3.2. Diagnostics

For the binary logistic regression fit, the estimated parameters using noninformative priors were discarded for females, because the correlation between L_{50} and ϕ was truncated at zero values, producing an incomplete marginal profile ϕ. In males, the correlation between L_{50} and ϕ was not truncated, but the WAIC value was higher than that from the sce-

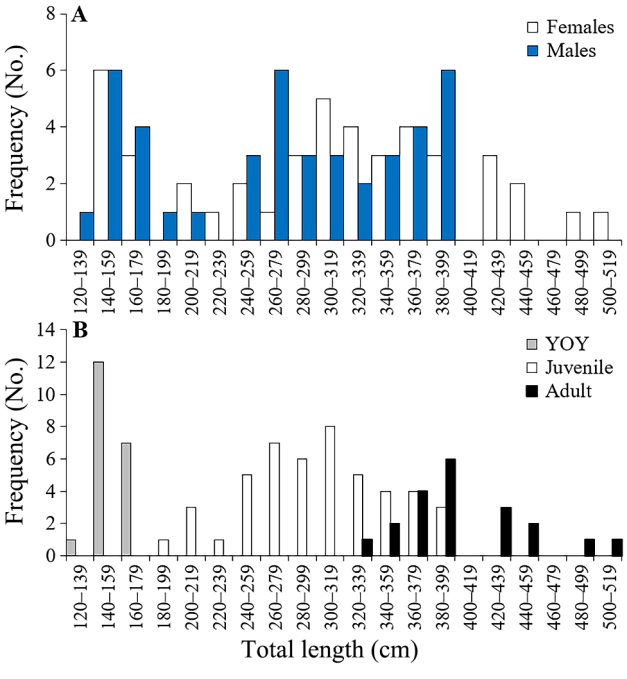

Fig. 3. Length–frequency distribution for (A) sex and (B) life stage of white sharks *Carcharodon carcharias* examined aboard the OCEARCH research vessel in the western North Atlantic from 2012–2022. YOY: young-of-the-year

Table 1. Length–frequency distribution by sex and life stage of the white shark *Carcharodon carcharias* examined onboard the OCEARCH research vessel in the western North Atlantic from 2012–2022. TL: total length; YOY: young-of-the-year

TL (cm)	Female				Male				Female & Male			
	YOY	Juvenile	Adult	n	YOY	Juvenile	Adult	n	YOY	Juvenile	Adult	Total
100–149	1			1	4			4	5			5
150–199	8			8	7	1		8	15	1		16
200–249		4		4		3		3		7		7
250–299		5		5		10		10		15		15
300–349		12		12		5	2	7		17	2	19
350–399		7		7			11	11		7	11	18
400–449			5	5							5	5
450–499			1	1							1	1
500–549			1	1							1	1
Total	9	28	7	44	11	19	13	43	20	47	20	87

nario using informative priors. In contrast, when we used informative prior probabilities for the parameters, the relationship between L_{50} and ϕ was more centered. Convergence of the 3 chains and the BGR diagnostics supported a good performance of the MCMC algorithm (Fig. 5). The marginal posterior probability distribution of the parameters was smooth, with a well-defined shape for every parameter (Fig. 6).

3.3. Maturity by length

The interaction term between TL and sex was not statistically significant ($\chi^2 = 30.21$, df = 1, p = 0.582). It was therefore removed from the model, obtaining a simplified version where the direct effects of TL and sex were highly significant ($\chi^2 = 30.79$, df = 1, $p < 0.0001$). Thus, maturity ogives were determined by sex. The frequentist estimation with the binary logistic regression between TL and maturity for each sex was unreliable, given the insufficient overlap between immature and mature individuals (Table 1). Such effects are evident not only in the coefficients but also in the estimation of maturity ogives with incorrect confidence intervals (Table 2; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n053p199_supp.pdf).

This faulty estimation prompted us to proceed with more robust statistical procedures. With the Bayesian approach, comparing the marginal posteriors for the parameters in the 2 scenarios (using informative and noninformative priors) revealed the advantages of informed priors despite the low level of overlap in the data between immature and mature sizes (Fig. S2).

Visual inspection of the performance of the trace plots for the estimation with informative priors indicated a stable pattern of L_{50} (Fig. 5A,E) and ϕ (Fig. 5B,F). The BGR ratio tended toward 1.0 and stabilized with increasing number of simulations (Fig. 5C,G). The scatter plot between the parameters (L_{50} and ϕ) was centered producing a smooth shape of the marginal posteriors (Fig. 5D,H). The overall diagnostics showed a lack of evidence against convergence of the 3 chains revealing a good performance of the MCMC algorithm.

The posterior probability distribution for the parameters that produced the best fit was from the scenario with informative priors (Fig. 6, Table 3). The posterior mean of L_{50} for females was 411.3 cm TL, and the steepness of the maturity ogives was $\phi = 10.5$ for the informative prior (noninformative prior L_{50} = 408.6 cm TL and $\phi = 6.5$). In contrast, for males, using the informative prior, the posterior mean of L_{50} was

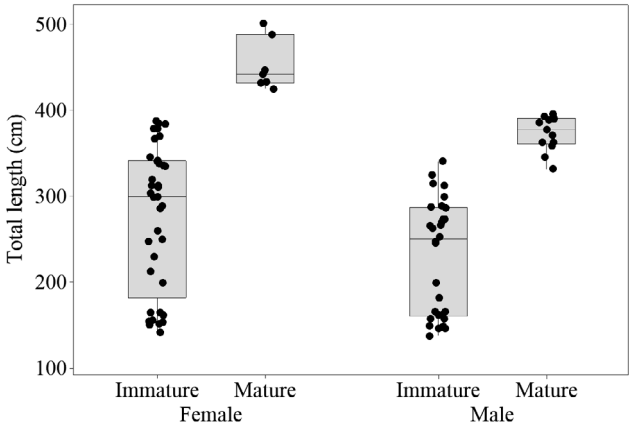

Fig. 4. Box plots of length range by sex and life stage for white sharks *Carcharodon carcharias* examined aboard the OCEARCH research vessel in the western North Atlantic from 2012–2022. The boxes represent interquartile ranges, the horizontal lines are the medians and the dots are the observed sizes in each life stage

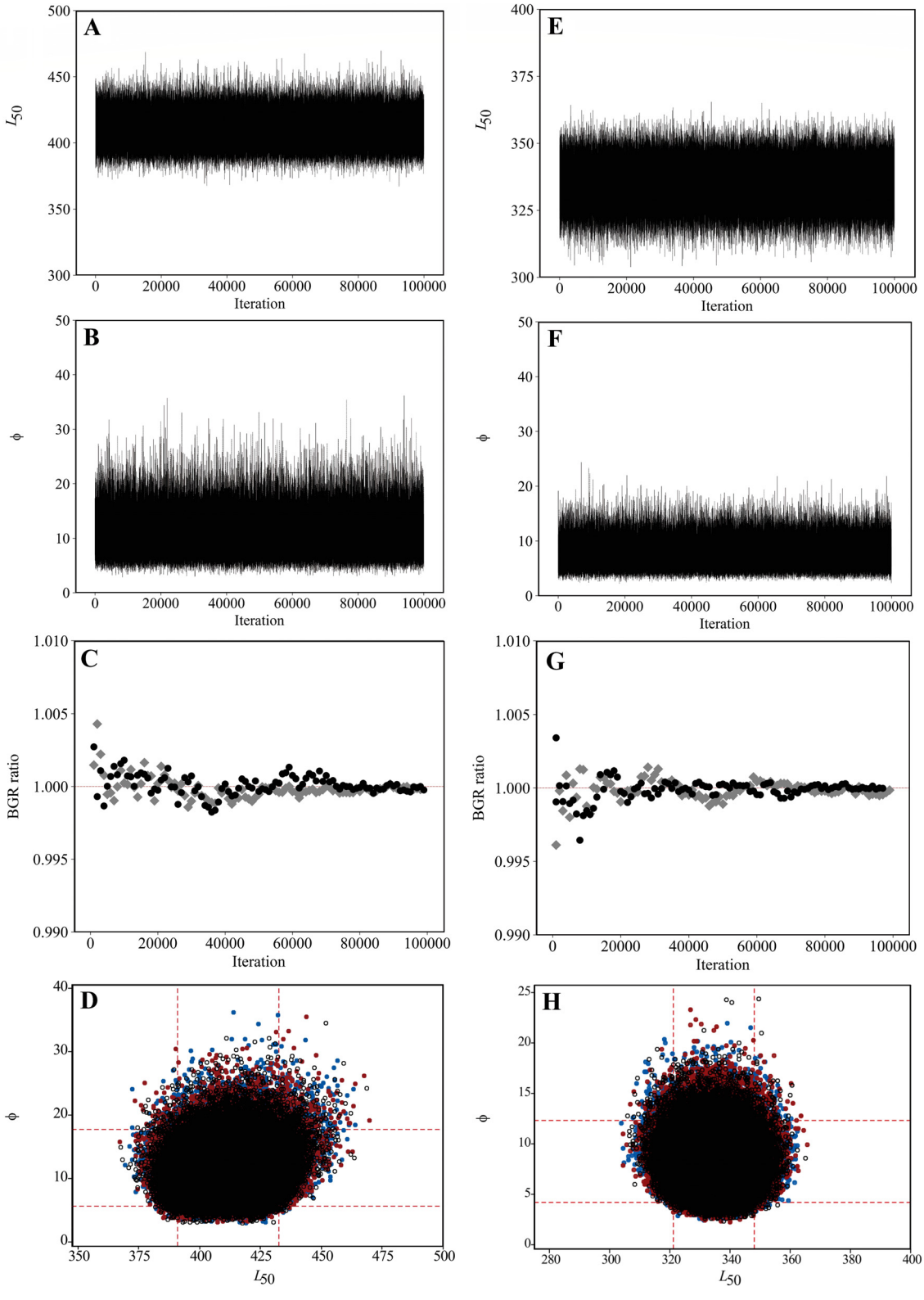

Fig. 5. Result of 100 000 iterations of the MCMC algorithm for each sex using informative priors for the parameters length-at-maturity (L_{50}) and model steepness (ϕ). For females, trace plots are for (A) L_{50}, (B) ϕ, (C) Brooks-Gelman-Rubin (BGR) ratio to examine the chain's convergence trend of L_{50} (gray) and ϕ (black), and (D) the bivariate scatter plot of the chains between L_{50} and ϕ. For males, trace plots are for (E) L_{50}, (F) ϕ, (G) BGR ratio, and (H) the bivariate scatter plot between L_{50} and ϕ. Dashed lines in the bivariate scatter plots of (D) and (H) are boundaries of credible intervals for L_{50} and ϕ (see Table 3) and the colors represent the 3 chains. In the BGR ratio (C) and (G) the chains tend to 1.000 (dashed line) to achieve convergence and stabilize

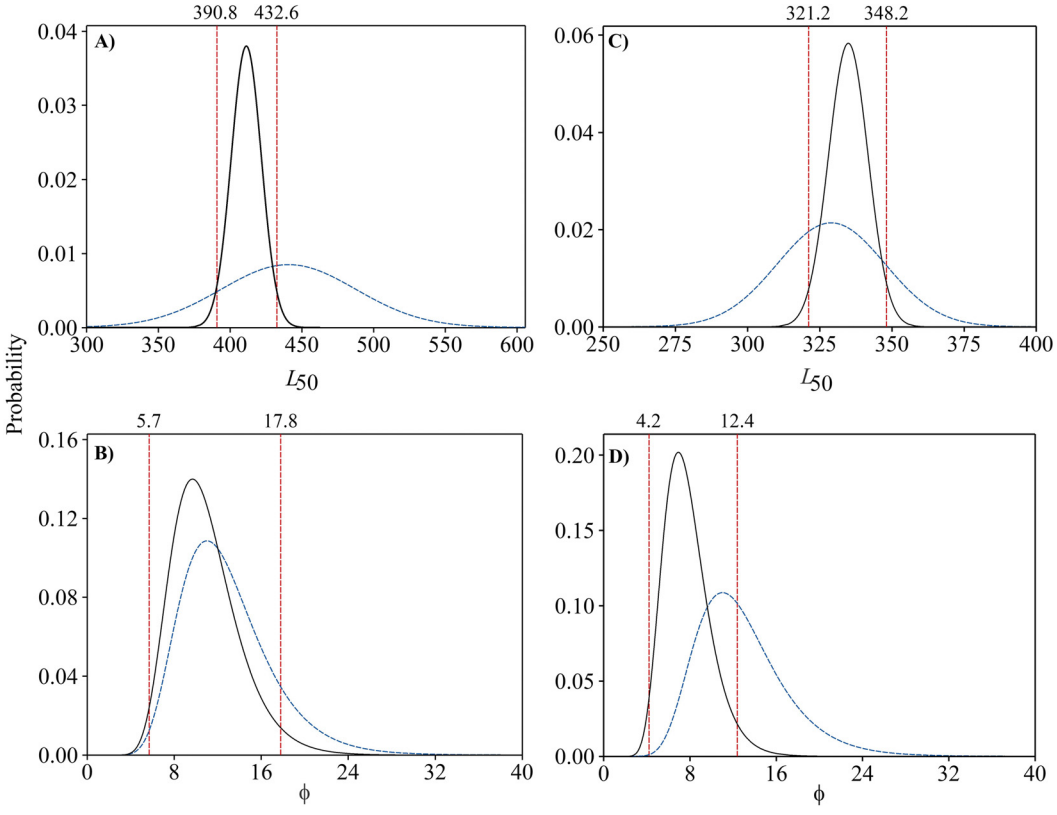

Fig. 6. Marginal posterior probability distribution of L_{50} and ϕ for (A,B) females and (C,D) males of the white shark *Carcharodon carcharias* in the western North Atlantic, resulting from the MCMC simulation using informative priors for these parameters. Solid lines are the posterior probability distributions. Dashed lines are the prior probability distributions (informative). Vertical dotted lines are the 95% credible intervals for each parameter with the corresponding values at the top (see Table 3)

334.9 cm TL, and the steepness of the maturity ogives was ϕ = 7.5 (noninformative prior L_{50} = 335.7 cm TL and ϕ = 10.4). The DIC and WAIC both indicated a better fit (lower value) for the noninformative prior scenario for females, but for males the informative prior scenario was better (Table 3). However, the value for females was questionable due to the overdispersion of the scatter plot between L_{50} and ϕ. The posteriors for L_{50} for both scenarios were very similar (for females and for males), but the posteriors for the ϕ parameter were different between scenarios, especially for females (see Fig. S2).

The ϕ value reflected a steeper slope of the maturity ogive in females (ϕ = 10.5) than males (ϕ = 7.5). The CIs of the maturity ogives representing the proportion of female and male individuals maturing by size were wider in females. The amplitude of the CIs of maturity ogives at L_{50} was wider in females (41.8 cm) than males (27.0 cm) due to the nature of samples available for each sex (Fig. 7).

Table 2. Results of the frequentist estimation from the binary logistic regression for white sharks *Carcharodon carcharias* sampled onboard the OCEARCH research vessel in the western North Atlantic from 2012–2022. The frequentist scenario produced an unreliable estimation of the parameters (L_{50},ϕ) and confidence intervals (CI). LL: lower limit; UL: upper limit; ND: not defined

Sex	Parameter	Median (SE)	– 95% CI – LL	UL	p
Female	L_{50}	406.4 (2980.00)	ND	ND	0.995
	ϕ	1.1 (178.80)	ND	ND	
Male	L_{50}	336.1 (6.85)	322.7	349.6	0.090
	ϕ	6.1 (3.63)	1.9	19.6	

3.4. Probability of life stages by length

The OLR analysis determined the probability of white sharks belonging to each life stage as a function of their length. The juvenile (intermediate) stage was shown to be the broadest in both sexes due to the amplitude of the lengths. The CI in the dome area was very narrow because the lengths did not overlap other stages (YOY and adult). Although the calculation is

Table 3. Results of Bayesian estimation from the binary logistic regression for white sharks *Carcharodon carcharias* sampled onboard the OCEARCH research vessel in the western North Atlantic from 2012–2022. Deviance information criterion (DIC) and Watanabe-Akaike information criterion (WAIC) are presented as measures of model fit. The Bayesian estimation presents the posterior mean values of L_{50} and ϕ, their SDs (in parentheses) and 95% credible intervals (CI) for each sex. Results are for the non-informative and informative prior scenarios using 3 chains with 100 000 MCMC iterations

Scenario	Sex	Parameter	Posterior mean	95% CI 2.5	95% CI 97.5	DIC	WAIC
Noninformative	Female	L_{50}	408.6 (11.40)	389.1	429.9	2.798	1.919
		ϕ	6.5 (6.27)	0.2	22.6		
Informative	Female	L_{50}	411.3 (10.81)	390.8	432.6	3.775	3.125
		ϕ	10.5 (3.03)	5.7	17.8		
Noninformative	Male	L_{50}	335.7 (8.61)	318.3	352.6	9.415	9.323
		ϕ	10.4 (5.63)	3.2	24.3		
Informative	Male	L_{50}	334.9 (6.84)	321.2	348.2	7.590	7.702
		ϕ	7.5 (2.10)	4.2	12.4		

fundamentally different, the shape of the adult life stage resembled the maturity ogive estimated with the binary logistic regression. Interestingly, in both sexes, the probabilities of the juvenile and adult stages crossed at similar lengths to the L_{50} estimated with a binary logistic regression (Fig. 8). Posteriors of the coefficients and 95% CIs from OLR for females were α_1 = 27.5 (CI: 14.7–45.0), α_2 = 58.5 (CI: 31.7–94.6), β = 0.2 (CI: 0.1–0.2) and for males, α_1 = 29.2 (CI: 15.5–46.6), α_2 = 53.6 (CI: 26.9–86.6), β = 0.2 (CI: 0.1–0.3).

4. DISCUSSION

4.1. White shark size and age-at-maturity

Determining the maturity of marine organisms is essential for studies of their population dynamics. Its usefulness can range from comparing the L_{50}-to-maximum length ratio to knowing the fraction of the mature population for age-structured models. In species of conservation interest whose capture is difficult or impossible, life history analyses from observations of free-swimming animals are problematic (Castro 2012, Skomal et al. 2017). Such uncertainty in estimating the size of free-swimming individuals inevitably affects the judgments of life stages, potentially impacting management decisions based on population parameters. Given these challenges, the OCEARCH methodology employed here provides a unique and valuable means of obtaining accurate information on the white shark's size, stage of maturity, and other biometric parameters (e.g. hormone and contaminant levels in blood and tissues, shark DNA, prey DNA in shark feces, microbiome samples). The methodology also provides the means to implant internal acoustic tags and attach external satellite-linked tags with greater reliability and duration, enhancing our knowledge of these animals' migratory behavior.

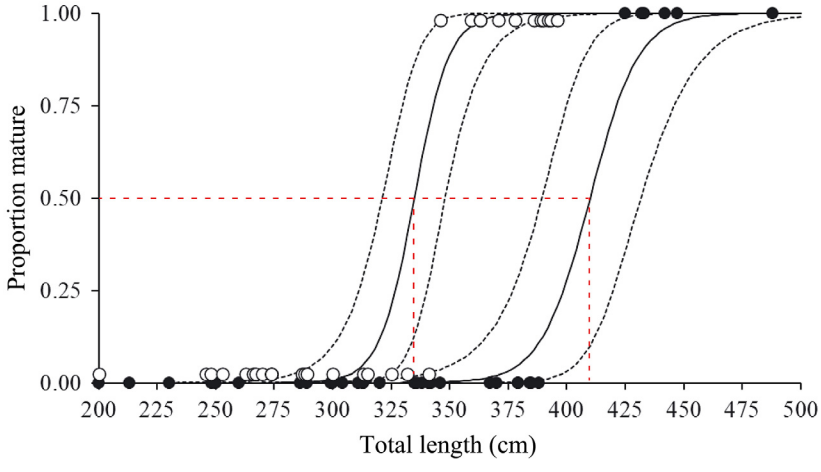

Fig. 7. Proportion of maturity at length for female (right) and male (left) white sharks *Carcharodon carcharias* examined on the OCEARCH research vessel in the western North Atlantic from 2012–2022. Circles represent observed data for females (●) and males (○). Solid curves are the fitted logistic models with informative priors; adjacent dashed curves represent the 95% credible intervals resulting from the Markov chain Monte Carlo (MCMC) simulation. Vertical dashed lines show the L_{50} for each sex (females 411.3 cm total length [TL], males 334.9 cm TL) that correspond to the lengths at which half of the individuals reach maturity (horizontal dashed line)

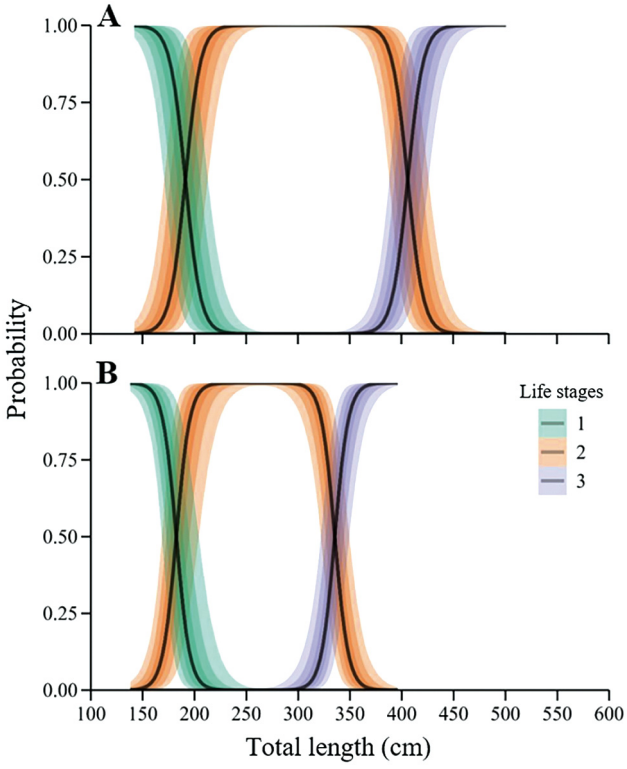

Fig. 8. Results of the ordinal logistic regression predicting the probability of each of the 3 life stages (1 = young-of-the-year, 2 = juveniles, 3 = adults) given the total length of (A) female and (B) male white sharks *Carcharodon carcharias*. Solid curves are the predicted means of the probability; shaded areas are the 95% credible intervals

The OCEARCH research cruises had broad spatial coverage along the Atlantic coast of Canada and the USA, from Nova Scotia to Florida. Satellite and acoustic tracking of OCEARCH-tagged white sharks has revealed latitudinal movements along this coastline, showing some preference areas for juveniles and adults (Franks et al. 2021). The satellite tracking data also show some extensive offshore movements, as far eastward as the Mid-Atlantic Ridge, especially in mature females (Franks et al. 2021). Large-scale movements could potentially influence the life history traits being studied, because data from individuals of mixed stocks would bias inferences on white sharks of the studied area (Natanson & Skomal 2015). In some cases, individual white sharks may carry out transoceanic migrations (Bonfil et al. 2005) and even unidirectional, long-distance movements (Bonfil & O'Brien 2015), showing major excursions from outside their ecological niche to farther than previously thought (Boustany et al. 2002). However, there is no evidence to date of any exchange between the WNA white shark and others, such as the Mediterranean white shark, and genetic studies suggest this population is differentiated from the Mediterranean, South African, and all other populations of white sharks (O'Leary et al. 2015). Therefore, we are confident that the results reported here are specific to the life history traits of the WNA population, with any differences with previous reports from other regions primarily attributable to population-level variation.

Size-at-maturity of the white shark reported in the literature is derived from a historical collection of data from many regions. Size-at-maturity in female white sharks is challenging to determine, given the paucity of relevant data (Castro 2011), and likely varies among populations. For females in our study, we report L_{50} = 411.3 cm TL, less than the 450 cm TL female size-at-maturity most often cited (Francis 1996). This same author noted that some females may mature at <450 cm TL, while highlighting examples of reportedly pregnant specimens ranging 420–427 cm TL (Norman & Fraser 1937 as cited by Francis 1996 and Bruce 1992). In the present study we report L_{50} = 334.9 cm TL for males, which is slightly smaller than the conclusion of Castro (2011) that males mature at about 340 cm TL in the WNA. His conclusion was based, in part, on the description of a 339.5 cm TL Florida specimen with calcified claspers and large volumes of sperm in the seminal vesicles (E. Clark unpubl. data). This is consistent with other observations of 6 male WNA specimens ranging 270–317 cm TL that were found to be transitioning to maturity (Pratt 1996). Females and males reach maturity at 82 and 85% of the maximum length recorded in our study.

Using the model reported by Natanson & Skomal (2015) for WNA white sharks, the L_{50} values estimated for females as 411.3 cm TL and 334.9 cm TL for males in the present study correspond to ages of 28.2 yr (CI: 26.7–29.8 yr) and 23.2 yr (CI: 20.8–23.2 yr), respectively. The ages-at-maturity estimated with our data are somewhat less than those discussed by Natanson & Skomal (2015) as 33 and 26 yr for females and males, respectively. The estimated 95% CI for both sexes is small and represents only a few years (i.e. 3.1 yr for females and 2.4 yr for males).

The lack of sufficient overlap in our dataset between mature and immature individuals at length limited the frequentist fit. However, the Bayesian approach we used allowed us to fit the model to the data in a robust manner. The construction of informative priors was carried out utilizing published information for white sharks from several regions. The version of the model we used includes L_{50} as a directly estimated parameter, so the construction of priors was more convenient than if we had used a version that included logistic regression coefficients

(a,b) for which it would be difficult to construct priors. As more data from OCEARCH cruises become available, other sigmoidal models for describing the maturity ratio can be tested using the posterior probabilities reported in the present study as priors.

4.2. Importance of maturity proportion for demographic studies and stock assessment

The characterization of stages of maturity in sharks has evolved over time. In early studies of shark biology, maturity was determined by considering the size between the largest immature specimens and the smallest mature individuals. Although this estimate is a baseline, it does not represent the proportion of the population that has actually reached sexual maturity (Márquez-Farías 2020). Current statistical techniques (e.g. logistic regression, generalized linear models, Bayesian inference) make it possible to determine the L_{50} robustly by considering it as momentum (e.g. L_{50} is the length at half of the logistic function) from a continuum of the proportion of maturity given the length. Estimating L_{50} can be done using the frequency of observations of immature and mature individuals by length bin (i.e. summarized data) or based on direct estimates with binary data coded as 0,1 for immature and mature individuals, respectively (i.e. raw data). These types of procedures (probit or logit) have advantages and disadvantages. Still, one important benefit is the proportion of mature individuals produced by the maturity ogives is a requirement of age-structured population models. For instance, in demographic models, expressing the reproductive rate of a population as a function of its age structure is more realistic than interpreting sexual maturity as a single quantity (knife-edge) after a given age. Bowlby & Gibson (2020) performed a demographic analysis of the WNA white shark population using a fixed value of age-at-first-maturity, confirming the low productivity of this population. A demographic study that includes both maturity and maternity ogives (Walker 2005) will produce more accurate and realistic results for the demographic parameters of the white shark.

The rationale behind the first scenario explored here, to estimate the parameters of the logistic function, was to perform the estimation by giving more weight to the data using the uniform prior probability of the parameters (noninformative). However, the complete or quasi-complete separation (overlap) of observed coded maturity (0,1) data is a problem that affects parameter estimation, due to the lack of convergence to determine likelihood. Such a parameter estimation problem has been thoroughly investigated, and alternative methods have been proposed (Firth 1993). However, as with frequentist estimation, parameter estimations will always depend on the information provided by the data (likelihood). To overcome this limitation, we developed a Bayesian approach in the present study to enable a more satisfactory estimation of parameters by expressing them as posterior probabilities that result from combining prior probabilities and the likelihood of the data (McCarthy 2007, Gelman et al. 2013). Using this approach, we improved the accuracy of parameter estimation and their interpretation and provided the CI of each parameter.

Despite the similarity of the maturity stage ogives produced by ordinal and binary logistic regression, their interpretation is not entirely comparable because the fundamentals of each procedure differ. In a similar study, Cao et al. (2021) performed an ordinal logistic regression analysis with Pacific skipjack tuna *Katsuwonus pelamis*. They reported that the family of curves represents the probability of progressing in life stages as the individual grows. This is a promising approach for analyzing a population structured by life stages, and we believe it has potential that should continue to be explored. For example, in the case of white sharks, a meta-analysis with such an approach would allow us to explore differences in the regional life stage structure of the populations. It can also be helpful for delimiting boundaries of life stages, increasing precision, and discarding imprecise or extreme estimates such as those reported for white sharks worldwide (Castro 2011).

4.3. Recommendations for studying and conserving white shark populations

Valuable progress has been made in understanding the age and growth of the white shark in the WNA (Natanson & Skomal 2015), which is a necessary component for the effective management of this rebuilding population (Curtis et al. 2014). Still, we require basic life history information like that reported in the present study from all 9 populations around the world. Furthermore, combining the white shark's age/growth and other life history parameters in a demographic analysis can help us delineate its potential reproductive value and population growth rate to profile species productivity (Mollet & Cailliet 2002). Understanding the life stage structure is helpful for demographic analyses exploring

stock resilience and determining the relative contribution (elasticities) of life history parameters to the population growth through perturbation analyses (Caswell 2000, Tuljapurkar & Caswell 2012). The posterior probability of the parameters reported here and the result of the OLR are helpful baselines for modeling the life stage at size of white sharks in other areas. In addition, further quantitative population analyses of the white shark can use the parameters provided here to improve the estimation of demographic parameters or other quantities of conservation interest. The longevity estimate (in excess of 70 yr) for the white shark (Hamady et al. 2014, Natanson & Skomal 2015, Bowlby & Gibson 2020, Bowlby et al. 2022) indicates its growth rate is slower than previously thought, which affects the estimates of age-at-maturity (a_{50}) and natural mortality (M) and might alter our understanding of the biological productivity of this species. Further research on this important topic is required (Cortés 2002b; Mollet & Cailliet 2002).

Conservation actions for this iconic species at regional and international levels must be adjusted accordingly. An effective conservation initiative for highly migratory sharks relies on accurate life history data of the species and requires international coordination. For white sharks, threats from fishing pressure, essential habitats or migratory routes that need protection, or other needs for their effective conservation must be identified. Data sharing among countries to participate in species conservation should guarantee the comparability of the results using standard methods and statistical procedures. In the present study, we demonstrate a robust methodology for generating the probability of length at life stages for the white shark, which is vital for accurate, quantitative population analysis.

In conclusion, our Bayesian approach shows size-at-maturity for the WNA population of white sharks to have L_{50}s of 411.3 cm TL for females and 334.9 cm TL for males. We recommend these 2 criteria be used to classify adult vs. juvenile stages of WNA white sharks for which direct empirical evidence of sexual maturity is unavailable.

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