



**Abstract**—Prompted by recent concern about the stock status of the shortfin mako (*Isurus oxyrinchus*) in the North Atlantic Ocean, we examined reproductive data from 731 individuals (351 females and 380 males) collected by 3 scientific organizations to improve estimates of size and age at maturity. Males ranged in size from 70 to 283 cm fork length (FL) and females from 71 to 338 cm FL. Females matured between 263 and 291 cm FL, with an estimated median length at maturity ( $L_{50}$ ) of 280 cm FL and a median weight at maturity ( $WT_{50}$ ) of 275 kg. Males matured between 173 and 187 cm FL, with an  $L_{50}$  of 182 cm FL and  $WT_{50}$  of 64 kg. Catch records from 4 international programs were also examined to investigate spatiotemporal variation in the distribution of life history stages based on updated size-at-maturity estimates and to identify potential partitioning and nursery grounds. These records identified the Gulf of Mexico and the eastern North Atlantic Ocean off Portugal as birthing and nursery areas, with the most important nursery area occurring in the western North Atlantic Ocean.

## Updated reproductive parameters for the shortfin mako (*Isurus oxyrinchus*) in the North Atlantic Ocean with inferences of distribution by sex and reproductive stage

Lisa J. Natanson (contact author)<sup>1</sup>

Megan Winton<sup>2</sup>

Heather Bowlby<sup>3</sup>

Warren Joyce<sup>3</sup>

Bethany Deacy<sup>4</sup>

Rui Coelho<sup>5</sup>

Daniela Rosa<sup>5</sup>

Email address for contact author: [lisa.natanson@noaa.gov](mailto:lisa.natanson@noaa.gov)

<sup>1</sup> Northeast Fisheries Science Center  
National Marine Fisheries Service, NOAA  
28 Tarzwell Drive  
Narragansett, Rhode Island 02882

<sup>2</sup> Atlantic White Shark Conservancy  
235 Orleans Road  
Chatham, Massachusetts 02650

<sup>3</sup> Bedford Institute of Oceanography  
Fisheries and Oceans Canada  
1 Challenger Drive  
P.O. Box 1006  
Dartmouth, Nova Scotia B2Y 4A2, Canada

<sup>4</sup> Riverside Technologies Inc.  
for Southeast Fisheries Science Center  
National Marine Fisheries Service, NOAA  
3500 Delwood Beach Road  
Panama City, Florida 32408

<sup>5</sup> Portuguese Institute for the Ocean and  
Atmosphere  
Avenida 5 de Outubro s/n  
8700-305 Olhão, Portugal

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The shortfin mako (*Isurus oxyrinchus*) is a large, highly migratory, coastal-pelagic shark species in the family Lamnidae that occurs in temperate and subtropical seas worldwide (Bigelow and Schroeder, 1948). In the North Atlantic Ocean, this species is considered to consist of one stock that migrates throughout the North Atlantic Basin (ICCAT<sup>1</sup>). Shortfin makos are commonly caught in both commercial and recreational fisheries throughout their range; although often not

the target species, they are frequently retained for their meat, fins, and jaws (Casey and Kohler, 1992; Babcock and Nakano, 2008). Although the species has long been considered vulnerable to overexploitation because of its late age at maturity, low reproductive potential, and commercial value (Dulvy et al., 2008; Cortés et al., 2010), catch levels were considered sustainable (ICCAT<sup>2</sup>). However, the results of an electronic tagging study conducted in 2013–2015

<sup>1</sup> ICCAT (International Commission for the Conservation of Atlantic Tunas). 2017. Report of the 2017 ICCAT shortfin mako assessment meeting (Madrid, Spain 12–16 June 2017), 42 p. ICCAT, Madrid, Spain. [Available from [website](#).]

<sup>2</sup> ICCAT (International Commission for the Conservation of Atlantic Tunas). 2013. 2012 shortfin mako stock assessment and ecological risk assessment meeting (Olhão, Portugal—June 11 to 18, 2012). Collect. Vol. Sci. Pap. ICCAT 69:1427–1570. [Available from [website](#).]

indicate that fishing mortality rates in the North Atlantic Ocean may be 10 times higher than previously estimated, prompting an increase in concern about the status of the species (Byrne et al., 2017; ICCAT<sup>1,3</sup>) and its listing as endangered on the IUCN Red List of Threatened Species in 2019 (Rigby et al., 2019).

The recent change in the estimated status of the stock has been attributed to improvements in available data as well as in the assessment model used (ICCAT<sup>1,4</sup>). Shortfin mako assessments have traditionally been based on surplus production models, which pool recruitment, growth, and mortality into a single production function (Haddon, 2011). Such models have often been applied to assess the status of elasmobranchs lacking empirical estimates of vital rates and life history characteristics (Cortés, 2004), but they do not adequately depict the biology of the species. Because these models have not been adequate, the International Commission for the Conservation of Atlantic Tunas (ICCAT) has moved toward age-structured integrated approaches that incorporate estimates of important biological characteristics for the assessment of the North Atlantic Ocean stock of shortfin makos (ICCAT<sup>1</sup>). Although the new assessment approaches will likely provide a better representation of the stock's dynamics, they require empirical estimates of biological parameters, as well as uncertainty associated with those estimates (Patterson et al., 2001; ICCAT<sup>4</sup>).

Reproductive potential is a critical component to age-structured stock assessments and necessitates precise estimates of size and age at maturity, particularly for sexually dimorphic species (Quinn, 2003). However, maturity data are often lacking or unreliable for highly migratory pelagic sharks (Cortés, 1998, 2002); available estimates are often derived from sparse, opportunistic data sets (e.g., Francis and Duffy, 2005) or from samples originating in multiple ocean basins (Mollet et al., 2000). The most recent study on the reproductive biology of female shortfin makos was published in 2000 (Mollet et al., 2000), and there has never been a comprehensive study on male reproduction (although maturity estimates based on limited data are available; see Natanson et al., 2006, and Maia et al., 2007). The lack of data is largely due to difficulties in obtaining specimens representing all stages of maturity. In particular, mature females are rarely captured, either because they escape or break fishing gear (Pratt and Casey, 1983; Maia et al., 2007) or they are not in the commercial fishing grounds. Consequently, large mature females are seldom encountered by scientists, and estimates of maturity have often been based on a combination of reproductive data compiled from specimens collected in different areas.

Because life history variability arises through genetic isolation (Francis et al., 2007) as well as through differences in historical fishing pressure or environmental conditions (Tanaka et al., 1990; Bradley et al., 2017), combining data from multiple regions could be misleading and ultimately result in inappropriate management. Mollet et al. (2000) found significant differences in size at maturity between populations in the Northern and Southern Hemispheres, with females from the western North Atlantic Ocean being larger (2.98 m total length [TL], compared with 2.73 m TL for females in the southern population). Although these data and conclusions are limited because of sample availability at the time, the value for females from the western North Atlantic Ocean (298.6 cm TL, which corresponds to 275.6 cm fork length [FL]) is currently used in stock assessments (ICCAT<sup>1</sup>). From limited sampling, it is difficult to determine how representative each estimate is of the entire population. A better understanding of reproductive potential would further increase the reliability of projections used for management advice.

In addition to their application in stock assessments, improved estimates of life history parameters can enhance understanding of the demographic characteristics of populations. For example, combining size and maturity information with spatial data could improve understanding of the demographic structure and seasonal movement patterns of the various life stages of shortfin makos (Barreto et al., 2016). For the population in the North Atlantic Ocean, ICCAT has requested the development of spatial management measures that promote conservation, with an initial focus on identifying birthing areas to improve management advice (ICCAT<sup>5</sup>). For several species, the distribution of mature females has been used to infer breeding or parturition areas (Casey and Pratt, 1985; Coelho et al., 2018). The extent of overlap in the distributions of males and females may also provide insight into sex-specific selectivity or vulnerability to fisheries in specific locations or at specific times (Mucientes et al., 2009).

In this study, we updated the reproductive parameters of both male and female shortfin makos from the western North Atlantic Ocean, and we present here comprehensive estimates of median length at maturity ( $L_{50}$ ) and median weight at maturity ( $WT_{50}$ ) for males and females. We used the updated reproductive parameters to classify data collected in the broader North Atlantic Basin by life stage and examined potential variation in spatial and seasonal distributions by sex. We also examined locations and stages of mature females and neonates to identify possible parturition grounds and consider the distribution of young-of-the-year (YOY) shortfin makos to identify potential nursery areas.

<sup>3</sup> ICCAT (International Commission for the Conservation of Atlantic Tunas). 2017. Report of the Standing Committee on Research and Statistics (SCRS) (Madrid, Spain, 2 to 6 October 2017), 301 p. ICCAT, Madrid, Spain. [Available from [website](#).]

<sup>4</sup> ICCAT (International Commission for the Conservation of Atlantic Tunas). 2019. Report of the 2019 ICCAT shortfin mako shark stock assessment meeting (Madrid, Spain 20–24 May 2019), 27 p. ICCAT, Madrid, Spain. [Available from [website](#).]

<sup>5</sup> ICCAT (International Commission for the Conservation of Atlantic Tunas). 2017. Recommendation by ICCAT on the conservation of North Atlantic stock of shortfin mako caught in association with ICCAT fisheries. ICCAT Rec. 17-08, 3 p. [Available from [website](#).]

## Materials and methods

Specimens of shortfin makos were collected from research cruises, recreational fishing tournaments, commercial fishing trips, and strandings along the north-eastern coast of North America between Newfoundland, Canada, and the west coast of Florida, including the Gulf of Mexico, between 1971 and 2018. A subset of the female maturity data that were analyzed in this study ( $n=61$ , 17%) was previously used to estimate median  $L_{50}$  by Mollet et al. (2000). Biologists from the Apex Predators Program and the Panama City Laboratory of the National Marine Fisheries Service (NMFS) and the Maritimes Region of Fisheries and Oceans Canada assessed maturity for 730 shortfin makos ( $n=675$ ,  $n=20$ , and  $n=35$ , respectively; [Suppl. Table 1](#)). Data collection was overseen by the senior author, and measurements were taken by experienced personnel by using a consistent sampling protocol. Full dissections (described later in the “Maturity indicators” section) were completed on the majority of specimens. However, because of time constraints at shark tournaments, it was not possible to perform a full workup of all specimens. In such instances, maturity for each sex was determined by visual examination only by using criteria based on detailed examinations as described later. Each shark was classified as mature or immature, and these data were used in calculating ogives for the analyses of median size at maturity (see the “Maturity indicators” and “Size at maturity” sections).

### Morphometrics

Fork lengths were either measured directly (i.e., from the tip of the snout to the fork in the tail, over the body [OTB]) or calculated from OTB TL (i.e., from the tip of the snout to a point on the horizontal axis intersecting a perpendicular line extending downward from the tip of the upper caudal lobe to form a right angle) by using conversions from Kohler et al. (1995). In some cases, measurements were converted to straight-line FL ( $FL_S$ ; these converted lengths are presented in parentheses) to facilitate comparison of lengths with those from other studies. Measurement of  $FL_S$  was taken from the tip of the nose to the fork in the tail by placing a tape measure under the shark so that the body curvature was not included in the measurement. Linear regression was used to derive a conversion from  $FL_S$  to  $FL_{OTB}$  by using data collected during this study ( $n=20$ ). There was low variability around the fitted relationship (coefficient of determination [ $r^2$ ]=0.996; [Suppl. Fig. 1](#)):

$$FL_S = 0.1821 + 0.9792(FL_{OTB}) \quad (1)$$

The equation derived by Francis (2006) was used to convert between  $FL_S$  and straight-line TL ( $TL_S$ ). Throughout the text, converted values are indicated by an asterisk (\*). Whole weight (WT) was taken when possible and is presented in kilograms.

### Maturity indicators

Maturity indicators were developed from the organ measurement data collected during detailed dissections. We used the standardized terminology for dissection measurements from Hamlett (1999) and Hamlett and Koob (1999) and followed the protocols for measuring and weighing of reproductive organs detailed by Natanson and Gervelis (2013). Although most specimens were measured fresh, samples collected by commercial fishermen were frozen at sea and thawed prior to sampling in the laboratory. Measurements from the frozen tracts were used only if they fell within the range of the fresh measurements to minimize potential biases from extreme values. Maturity status was assigned to each shark in the field on the basis of visual inspection of reproductive organs as described later in the “Results” section. For specimens that were not classified at the time of dissection, maturity stage was later determined through comparison of organ measurements with maturity criteria derived from staged individuals (see the “Results” section). Morphometric measurements of the reproductive organs of both sexes were plotted against FL to show how growth of the reproductive system changed as an individual approached maturity. Reproductive organs grow rapidly when approaching maturity; therefore, the location of the inflection in these relationships relates to  $L_{50}$ .

Initial internal examination for female maturity noted presence or absence of embryos, ovulation, and presence or absence of nutritive capsules following Jensen et al. (2002). Prior mating activity was assessed on the basis of the presence or absence of a membrane over the urogenital sinus, which was determined by passing a probe through the posterior end of the uterus into the cloaca. For males, initial maturity was obtained by examining the external claspers manually for functionality by using 3 criteria: rotation, rigidity, and the ability of the rhipidion to splay (Clark and von Schmidt, 1965). Clasper length was measured from the posterior tip to the insertion of the pelvic fin (Pratt, 1996; outer clasper length as defined by Compagno, 2001). Siphon sacs were measured as per Natanson and Gervelis (2013).

All internal measurements (in millimeters) were taken at the widest portion of the organ from the right side of the shark. These measurements included the anterior oviduct width, oviducal gland width, uterus width and length, ovary width and length, and the largest yolke follicle for females and the siphon sac length and testis diameter and length for males. When possible, the ovary or testis was weighed to the nearest gram. Trophonemata were measured to the nearest millimeter when present. For sharks that did not undergo full dissection, the internal organs were visually assessed for maturity on the basis of the criteria from Natanson and Gervelis (2013); in particular, this assessment included a characterization of the epigonal tissue around the ovaries, follicle size and color, and the general appearance of the uterus and oviducal gland for females and a characterization of clasper condition and epigonal tissue around the testis for males. Individuals

that appeared to have given birth in the current year were defined as postpartum, although those that had given birth, with indications of recovery, were considered in a resting stage (Castro, 2009).

### Size at maturity

Median size at maturity was estimated for both sexes by using maturity ogives fit to binomial maturity data from both dissections and visual assessments. Data from all years were combined on the basis of the results of a preliminary analysis that indicated no evidence of variation in parameters between 2 time periods (1971–1987 and 2003–2018) (senior author, unpubl. data). The probability that a given individual  $i$  was mature was modeled as the outcome of a Bernoulli random variable, where  $y_i=0$  for immature and  $y_i=1$  for mature individuals, respectively:

$$y_i \sim \text{Bernoulli}(p_i), \quad (2)$$

where  $p_i$  = the probability shark  $i$  is mature.

We modeled  $p_i$  as a function of size (separately in terms of FL and weight) as follows:

$$\text{logit}(p_i) = \beta_0 + \beta_1 \text{Size}_i, \quad (3)$$

where  $\text{logit}(p_i)$  = the logit link function.

The function constrains  $p_i$  to values between 0 and 1;

$\beta_0$  = an intercept term, and

$\beta_1$  = the effect of size in terms of either FL or weight.

Models were fit to each sex separately through maximum likelihood methods by using functions available in R (vers. 3.5.1; R Core Team, 2018). The inflection point of the relationship (where  $P=0.5$ ) for either sex represents the median size at maturity (i.e.,  $L_{50}$  or  $WT_{50}$ ) and was calculated from the fitted model parameters as  $-\beta_0/\beta_1$ . By using the boot package (vers. 1.3-20) in R (Canty and Ripley, 2017), 95% confidence intervals around  $L_{50}$  and  $WT_{50}$  were bootstrapped from fits of a binomial generalized linear model to 1000 resamples of the maturity data (Harry et al., 2013). Given the well-established relationship between size and maturity and previously documented differences in size at maturity between male and female shortfin makos (Natanson et al., 2006), we did not conduct formal model selection in this study. For all models, normalized diagnostic plots of the residuals were examined visually to evaluate the appropriateness of model assumptions (Zuur et al., 2010).

### Demographic structure

To investigate the spatial distribution of the population by life stage, shortfin mako catch records were obtained from 4 long-term, fishery-dependent sampling programs: 1) NMFS Cooperative Shark Tagging Program, 1962–2017; 2) NMFS Pelagic Observer Program, 1992–2017; 3) Canadian At-Sea Observer Program from the Maritimes region,

1979–2018; and 4) Portuguese Institute for the Ocean and Atmosphere onboard pelagic longliners from the Portuguese fleet, 2008–2016 (Suppl. Table 2). Data from 18,119 shortfin makos were used in distribution analyses, with the majority of samples (87%) collected from west of longitude 45°W. These data include date, size, sex, and location (Suppl. Table 2).

Females ( $n=9310$ ) ranged in size from 23.0 to 325.0 cm  $FL_{OTB}$ . Only 22 of those females were classified as mature on the basis of an  $FL_{OTB} > 291.0$  cm (the length of the largest immature female observed; Tables 1 and 2). Males ( $n=8809$ ) ranged in size from 25.0 to 310.0 cm, and 1174 of those males were considered mature on the basis of an  $FL_{OTB} > 187.1$  cm (the length of the largest immature male observed; Tables 1 and 3). The 5 largest males in the data set were larger than the verified size limit for male shortfin makos. Attempts to confirm the accuracy of the sizes through the original archived data were inconclusive; therefore, caution should be exercised in taking these values as a new size range for male shortfin makos. Regardless, they would be classified as mature males and, for that reason, were included in our analyses. The majority of the catch data provide lengths in  $FL_S$ ; therefore, for these analyses, measurements provided as  $FL_{OTB}$  or  $TL_S$  were converted to  $FL_S$ , as described previously. In instances where  $TL_{OTB}$  or  $WT$  had been previously converted to  $FL_{OTB}$ , we assessed maturity on the basis of  $FL_{OTB}$  rather than apply a second conversion; this approach was deemed reasonable given our conservative rationale for maturity classification (see the next paragraph). All estimated  $FL_S$  were considered  $FL_S$  (Suppl. Table 2).

Shortfin mako catch records were assigned to sex-specific maturity stages, representing neonate, YOY, immature, or mature individuals as follows: shortfin makos  $\leq 68$  cm  $FL_{OTB}$  were considered neonates on the basis of the average size at birth (63.2 cm  $FL_{OTB}^*$ ) and the size of the largest full-term embryo observed (estimated at 68 cm  $FL_{OTB}^*$ ; Molllet et al., 2000). Sharks  $> 68$  cm  $FL_{OTB}$  and  $< 100$  cm  $FL_{OTB}$  were classified as YOY (Natanson et al., 2006). For the older age classes,  $L_{50}$  estimates for males and females could be used to separate immature from mature sharks; however, misclassifications would result for both categories and distribution patterns potentially could be obscured because of individuals that fall into the transitional size range. To minimize the extent of overlap between the immature and mature sizes, sharks smaller than the smallest observed mature shark were considered immature. All sharks greater than the largest observed immature specimen by sex were considered to be mature. This method eliminated the portion of the length distribution during which maturity stage is the most uncertain and, therefore, the majority of the potential for differences in maturity stage to obscure distribution patterns.

To visualize potential variation in the spatial distribution of the life stages of shortfin makos, catch locations were binned by sex, maturity stage, and season and aggregated over a 1°-by-1° grid by using functions available in the R package tidyverse (vers. 1.2.1; Wickham, 2017). The seasons were winter (January–March), spring



**Table 1**

Number of shortfin makos (*Isurus oxyrinchus*), by sex, captured per month in the western North Atlantic Ocean between 1971 and 2018 for maturity analyses and between 1962 and 2018 for investigation of demographic structure. Values for maturity analyses include both dissected and visually assigned specimens. I=immature; T=transitional (length range, where individuals are approaching maturity, bracketed by the smallest mature and largest immature female (263.0 and 291.0 cm FL, respectively); and M=mature.

Month of Capture	Maturity analyses			Demographic structure						
	Male	Female	Total	Male			Female			
				I	T	M	Total	I	T	M
January	7	2	474	322	67	85	383	376	5	2
February	0	2	394	243	69	82	317	311	4	2
March	7	0	250	150	25	75	164	161	1	2
April	7	3	507	301	107	99	273	271	1	1
May	13	5	485	311	72	102	381	377	1	3
June	166	126	893	744	75	74	1258	1255	3	0
July	70	115	1650	1445	104	101	2254	2250	2	2
August	85	88	1404	1169	102	133	1758	1753	3	2
September	15	6	814	638	77	99	909	897	6	6
October	8	2	814	607	95	112	710	709	1	0
November	1	2	742	527	91	124	552	551	0	1
December	0	0	382	252	42	88	351	346	4	1

(April–June), summer (July–September), and fall (October–December) (Campana et al.<sup>6</sup>). The distribution of neonate and YOY catch records were examined for patterns related to pupping and nursery grounds.

## Results

We examined 731 (351 female and 380 male) shortfin makos for maturity and completed full dissections of 197 females and 241 males. Females and males ranged in size from 70.6 to 338.5 cm FL<sub>OTB</sub> and from 70.0 to 283.0 cm FL<sub>OTB</sub>, respectively (Fig. 1). Several male shortfin makos in this sample are larger than previously measured males (260 cm FL<sub>OTB</sub>; Natanson et al., 2006); however, these measurements are verified and can be considered to represent an accurate size increase. The majority of specimens were collected from recreational fishermen at shark fishing tournaments in the United States (88% sexes combined, 91% of females, and 86% of males; Suppl. Table 1) and between June and August (94% of females and 85% of males; Table 1). No specimens of either sex were obtained in December; males and females were caught in all other months with the exception of February and March, respectively (Table 1).

## Maturity indicators

**Females** The relationships of the measurements of oviduct width, oviducal gland width, uterus diameter, ovary length, ovary width, ovary weight, and follicle diameter to FL indicate a sharp increase in size of ~250–270 cm FL<sub>OTB</sub>, as exemplified by the relationship between the oviducal gland width and FL (Fig. 2, Suppl. Fig. 2). Only the relationship between FL and uterus length is essentially linear, indicating that growth of the uterus is relatively constant over ontogeny, rather than being indicative of size at maturity.

**Immature females** On the basis of organ measurements and the visual assessment used to assign status at dissection (full dissection:  $n=170$ ; total:  $n=325$ ), immature females ranged in length from 70.6 to 291.0 cm FL<sub>OTB</sub>. Immature females have undeveloped ovaries with small follicles with little or no yolk; most follicles appear white to clear (Table 2). Maximum follicle size is generally  $\leq 1$  mm at this stage. Immature ovaries are embedded in epigonal tissue that progressively thins out in the larger immature females, ultimately becoming a thin, transparent sheath around the main ovary as the female matures. The immature uterus appears narrow and constricted with the oviducal gland appearing as a slight widening of the oviduct. Female shortfin makos  $>250$  cm FL<sub>OTB</sub> are starting to mature, and this transition to maturity is first observed in the development of the ovary. By the time a female is 250 cm FL<sub>OTB</sub>, the ovary is clearly increasing

<sup>6</sup> Campana, S. E., J. Gibson, J. Brazner, L. Marks, and W. Joyce. 2008. Status of basking sharks in Atlantic Canada. Can. Sci. Adv. Secr. Res. Doc. 2008/004, 56 p. [Available from [website](#).]

**Table 2**

Size ranges of measurements and descriptions of organs used to determine maturity stages of female shortfin makos (*Isurus oxyrinchus*) captured in the western North Atlantic Ocean between 1971 and 2018. Sharks in the size ranges associated with the immature and mature stages generally conform to those assignments (unless otherwise noted), whereas sharks in the transitional range can be either immature or mature. Follicles classified as uncertain could indicate a specimen is transitional or mature. Table format adapted from Walker (2005). *n*=number of specimens.

Organ	Index	Size range of measurements	Description	Maturity classification
Upper oviduct				
<i>n</i> =175	UO-1	≤7 mm	Thin tubular structure	Immature
	UO-2	>7 to ≥15 mm		Transitional
	UO-3	>15 mm	Thickened tubular structure	Mature
Oviducal gland				
<i>n</i> =168	OG-1	≤11 mm	Undifferentiated from oviduct	Immature
	OG-2	>11 to ≤35 mm	Increased width distinguishable from oviduct	Probably immature
	OG-3	>35 mm	Enlarged and bulbous	Probably mature
	OG-4	>49 mm	Enlarged and bulbous	Mature
Ovarian follicles				
<i>n</i> =111	OF-1	≤1 mm	Small and white	Immature
	OF-2	>1 mm	Larger with yolk	Uncertain
Ovary length				
<i>n</i> =166	OL-1	≤160 mm	Clear follicles barely distinguishable from epigonal	Immature
	OL-2	>160 to ≤210 mm	White or opaque follicles distinguishable; thinning epigonal	Transitional
	OL-3	>210 mm	Thin epigonal surrounding cream- to yellow-colored yolked follicles <sup>†</sup>	Mature
Ovary width				
<i>n</i> =171	OW-1	≤50 mm	Thin; follicles barely distinguishable from epigonal	Immature
	OW-2	>50 to ≤110 mm	Widening area of distinguishable follicles	Transitional
	OW-3	>110 mm	Wide area of follicles surrounded by thin epigonal	Mature
Uterus length				
<i>n</i> =112	UL-1	≤280 mm	Thin tubular structure indistinguishable from upper oviduct	Immature
	UL-2	>280 to ≤470 mm <sup>‡</sup>	Elongated tube, distinguishable from lower oviduct	Transitional
	UL-3	>470 mm	Large, often flaccid tubular structure	Mature
Uterus width				
<i>n</i> =181	UW-1	≤38 mm <sup>§</sup>	Thin tubular structure	Immature
	UW-2	>38 to ≤70 mm	Widening tube distinguishable from upper oviduct	Transitional
	UW-3	>70 mm	Large, distended tubular structure	Mature

<sup>†</sup> Mature and transitional ovaries can appear similar.

<sup>‡</sup> One specimen had a size larger than this range as a juvenile.

<sup>§</sup> One specimen had a size smaller than this range as an adult.

**Table 3**

Size ranges of measurements and descriptions of organs used to determine maturity stages of male shortfin makos (*Isurus oxyrinchus*) captured in the western North Atlantic Ocean between 1971 and 2018. Sharks in the size ranges associated with the immature and mature stages generally conform to those assignments, whereas sharks in the transitional range can be either immature or mature. Table format adapted from Walker (2005).  $n$ =number of specimens.

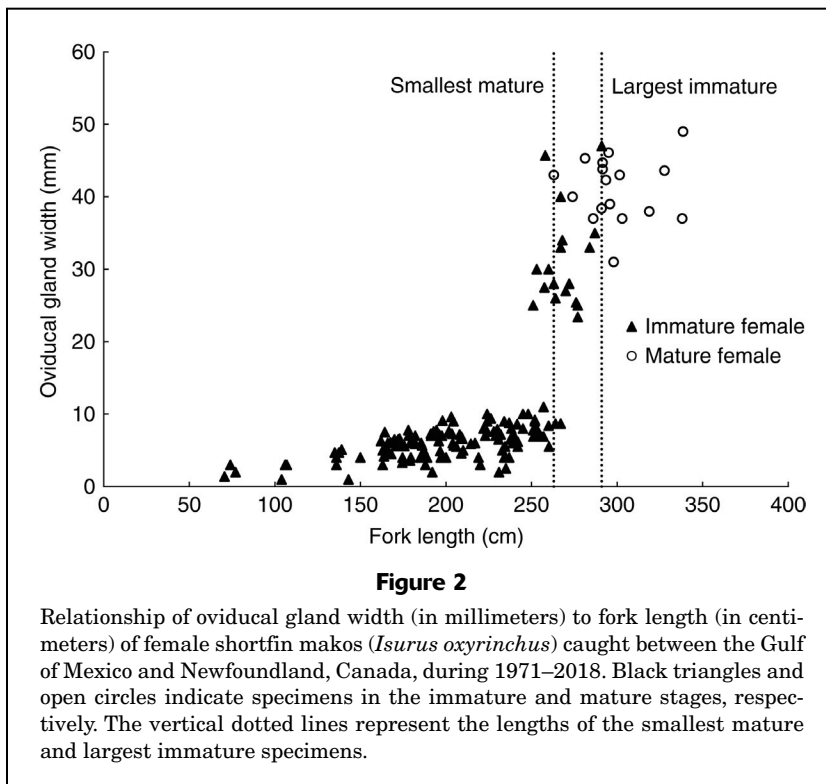
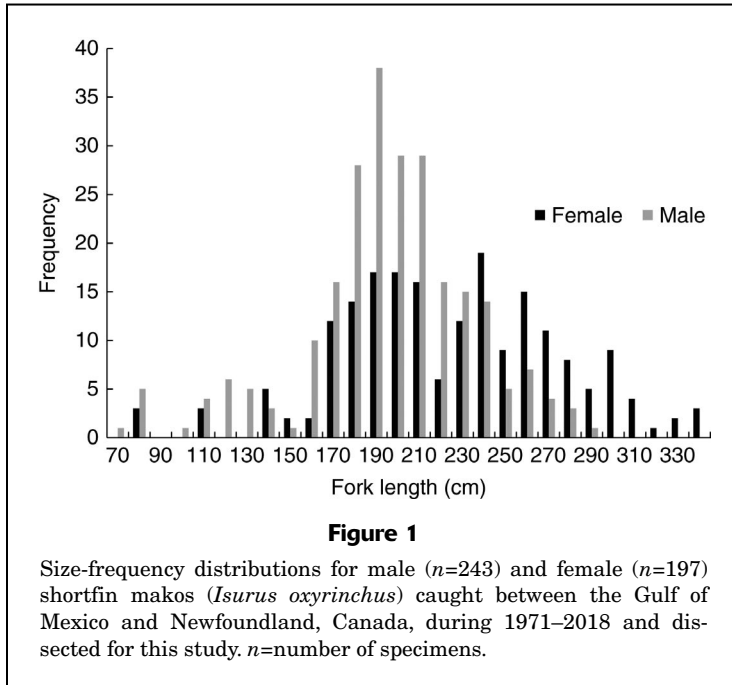
Organ	Index	Size range of measurements	Description	Maturity classification
<b>Left clasper length</b>				
$n=237$	LCL-1	$\leq 185$ mm	Soft, do not freely rotate, do not extend beyond pelvic fins, tip does not flex	Immature
	LCL-2	$>85$ to $\leq 221$ mm	Soft to plastic, starting to rotate and extend beyond pelvic fins, tip does not flex	Transitional
	LCL-3	$>221$ mm	Rigid, freely rotate and flex at tip, extend beyond pelvic fins	Mature
<b>Testis diameter</b>				
$n=209$	TD-1	$\leq 20$ mm	Small testis encased in epigonal	Immature
	TD-2	$>20$ to $\leq 42$ mm	Larger testis, epigonal decreasing in proportion	Transitional
	TD-3	$>42$ mm	Large testis with minimal epigonal	Mature
<b>Testis length</b>				
$n=209$	TL-1	$\leq 70$ mm	Thin testis encased in epigonal	Immature
	TL-2	$>70$ to $\leq 120$ mm	Elongated testis, distinguishable from epigonal	Transitional
	TL-3	$>120$ mm	Long, distended testis from epigonal	Mature
<b>Testis weight</b>				
$n=80$	TW-1	$\leq 45$ g		Immature
	TW-2	$\geq 45$ to $90 \leq$ g		Transitional
	TW-3	$>90$ g		Mature

in size, particularly in length (Fig. 3). An increase in size of all other organs can be seen in female shortfin makos  $>250$  cm  $FL_{OTB}$  (Suppl. Fig. 2).

The transitional length range, where individuals are approaching maturity, is bracketed by the smallest mature and largest immature female (263.0 and 291.0 cm  $FL_{OTB}$ , respectively). In this range, organ measurements in an individual may or may not be in the mature size range. The majority of immature sharks (92%) examined had a membrane separating the urogenital sinus from the cloaca. Of the 8% that did not, the majority (70%) were approaching the transitional length range. In general, the transitional ovary is larger and contains larger follicles than the smaller immature ovaries; however, in most cases, the follicles are not as large as in the mature stages. In smaller transitional individuals, reproductive organs are in various stages of development. However, by the time a female is 260 cm  $FL_{OTB}$ , organs are beginning to mature, as indicated by the marked increase in most morphometric measurements during the transitional

length range (Fig. 2, Suppl. Fig. 3). In and of itself, this increase in growth does not demonstrate maturity because most individuals are still immature until  $\sim 275$  cm  $FL_{OTB}$ .

**Mature females** Adult females ranged from 263.0 to 338.5 cm  $FL_{OTB}$  ( $n=26$ ). Of those sampled, 3 were pregnant, 4 were postpartum, and 18 were staged as resting. The maturity stage of 1 specimen (either newly mature or resting) could not be determined with available information. The 3 pregnant females were 270.4, 285.0, and 301.0 cm  $FL_{OTB}$  and were caught in January, February, and November, respectively, in the Gulf of Mexico. The largest trophonemata measured in this study (5 and 10 mm) were taken from 2 of the pregnant females. The postpartum females ranged in length from 289.0 to 325.0 cm  $FL_{OTB}$ . A recently postpartum female was caught in February in the Gulf of Mexico, and 3 specimens that had given birth within the season but had begun to recover were caught off Long Island in the summer (June:  $n=2$ ; August:  $n=1$ ).



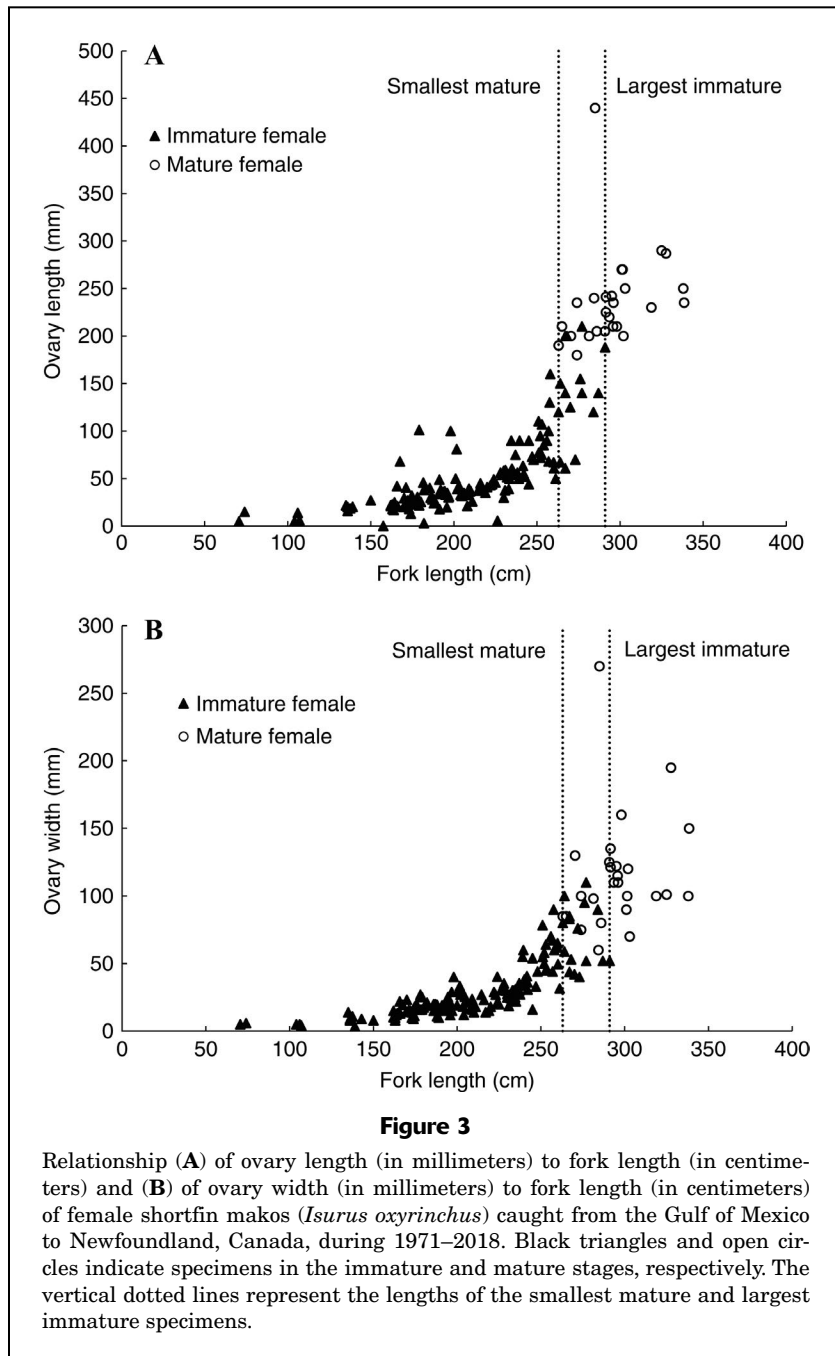
The large range of follicle sizes observed in the resting stage (1.5–5.9 mm) is most likely indicative of the amount of time the individuals had been recovering from their most recent parturition. Although females with follicles of 3.6 mm are usually mature (Table 2), it is difficult to classify these stages on the basis of appearance of the ovary

alone, because of the similarity of some resting ovaries to some immature ovaries. Stage must be determined in combination with other organ characteristics, particularly follicle and uterus size and condition (Natanson and Gervelis, 2013). Resting stage females have expanded but recovered uteri indicating that they have previously given birth; some have small trophonemata (0.0–1.5 mm), and the condition of their ovaries indicates they had not given birth in the current season.

**Males** On the basis of organ measurements and the visual assessment used to assign status at dissection (full dissection:  $n=241$ ; total:  $n=379$ ), immature males ranged in length from 70.0 to 187.1 cm  $FL_{OTB}$  (Suppl. Table 1). Measurements of clasper length (Fig. 4) verified visual accounts of the morphology during dissection, and a strong change in clasper growth rate at maturity was observed. Testis diameter, length, and weight as well as siphon sac size had approximately linear relationships with shark length, particularly after ~150 cm  $FL_{OTB}$  (Fig. 5, Suppl. Fig. 3).

Clasper length, testis diameter, length, and weight, and siphon sac length show a rapid increase in growth at ~150 cm  $FL_{OTB}$  (Figs. 4 and 5, Suppl. Fig. 3), which levels off at ~175 cm FL for clasper length (Fig. 4). Siphon sacs are undeveloped and short in immature males, usually not extending far past the pelvic fins. There is a marked increase in growth once an animal reaches ~150 cm  $FL_{OTB}$  (Suppl. Fig. 3), and the siphon sacs expand anteriorly along the abdomen but do not reach the level of the pectoral fins by the time they fully develop. The degree of rigidity of the claspers is the best overall indicator of maturity. Mature males have rigid claspers, with the ability of the clasper to rotate freely and of the rhipidion to splay, whereas immature males do not have these qualities (Table 3). There were very few exceptions ( $n=7$ ) in which males did not have fully rigid claspers but had all other organs in the mature range, indicating that these males were approaching maturity. These specimens ranged in  $FL_{OTB}$  from 175.0 to 221.0 cm, with the larger 3 males (200.0–221.0 cm  $FL_{OTB}$ ) having claspers that were partially rigid with sperm present and the smaller 4 specimens (175.0–187.4 cm  $FL_{OTB}$ ) having claspers that were soft and flexible. The latter fish were at the transitional size for male maturity (172.8–187.1 cm  $FL_{OTB}$ ). Immature males with rigid claspers ( $n=4$ ) ranged in size from 176.0 to 187.0 cm





FL<sub>OTB</sub>, lengths that are also in the transitional range for maturity. Although individual variation exists in body length and in the order that organ development takes place, clasper calcification appears to be the last phase of maturation.

**Median length and weight at maturity**

The estimated  $L_{50}$  for females was 279.8 cm FL<sub>OTB</sub> (95% confidence interval [CI]: 273.8–286.6), and the estimated  $WT_{50}$  for females was 274.8 kg (95% CI: 255.4–274.0; Fig. 6). For males, the estimated  $L_{50}$  was 181.6 cm FL<sub>OTB</sub>

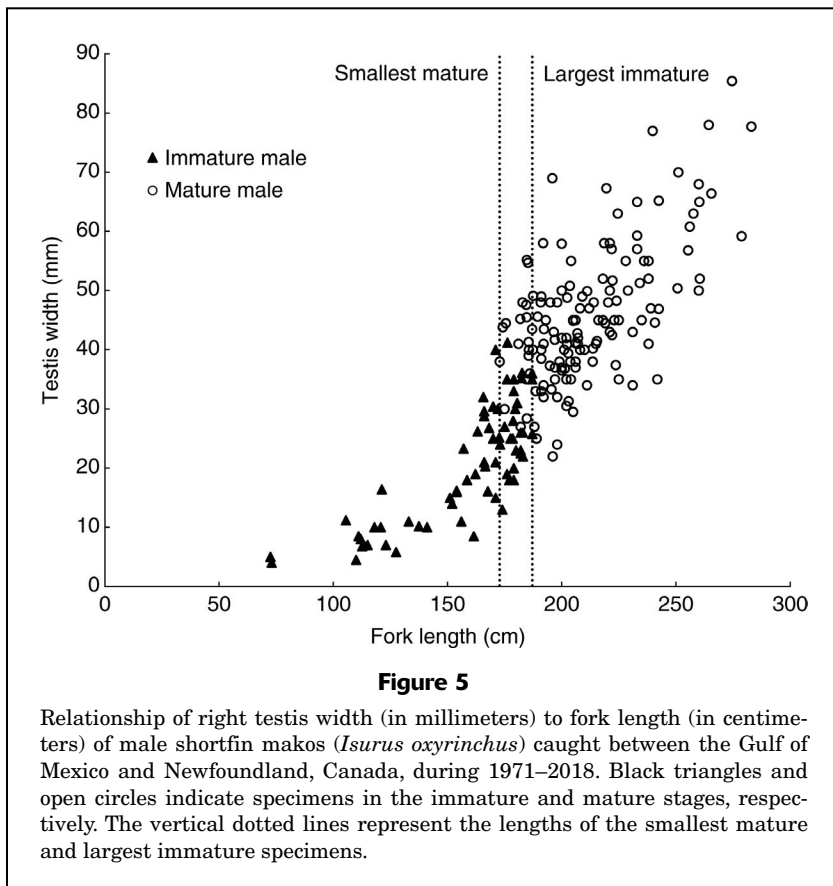
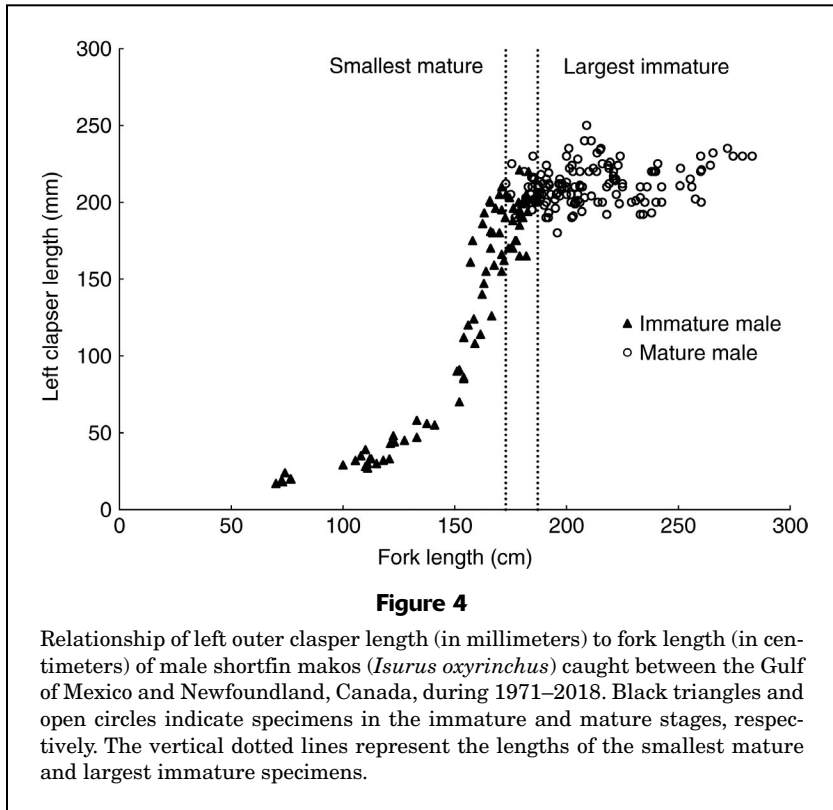
(95% CI: 179.9–188.4) and the  $WT_{50}$  was 63.8 kg (95% CI: 62.0–74.0; Fig. 6). Converting both  $L_{50}$  estimates into FL<sub>S</sub> for comparison with the catch data resulted in 274.2 cm FL<sub>S</sub> for females and 178.0 cm FL<sub>S</sub> for males.

**Demographic structure**

On the basis of the estimated median size at maturity, 88% of the specimens were classified as immature; of these, immature females outnumbered immature males and mature males outnumbered mature females in all seasons (Table 1). Mature as well as immature animals of both sexes were caught in similar areas in all months, with the exception of mature females, which were not caught in June and October (Figs. 7 and 8, Suppl. Figs. 4 and 5). These movements could be related to shifts in the fishing fleets, but some generalizations can be made by season and sex. Although there were few captures of mature females, catches occurred in the Gulf of Mexico in fall and winter, shifting slightly onto the continental shelf in spring and summer. Young-of-the-year and neonate sharks were found primarily on the western side of the North Atlantic Ocean from the Gulf of Mexico up to the Flemish Cap with a small concentration in the northern Gulf of Mexico (Figs. 7 and 8).

**Discussion**

The reproductive parameters estimated in this study provide improved sex-specific inputs for stock assessment of shortfin makos in the North Atlantic Ocean. Our sampling was done throughout a vast geographical range and resulted in a data set that was an order of magnitude larger than those of previous studies on male or female reproduction. Although our sampling was concentrated in the west, it is representative of the entire region, given the strong evidence for one population in the North Atlantic Ocean. Conventional tag and recapture data from 1148 shortfin makos indicate 1) mixing of individuals tagged in Europe and in the United States in an area west of the Azores of Portugal; 2) movement from the western to the eastern Atlantic Ocean; and 3) movement into and out of the Gulf of Mexico and the Caribbean Sea (Kohler and Turner, 2019). Our estimate of female  $L_{50}$  (279.8 cm FL<sub>OTB</sub>, 274.2 cm FL<sub>S</sub>\*) is slightly larger than the previous estimate by Mollet et al. (2000) (275 cm FL<sub>OTB</sub>\*), although their value

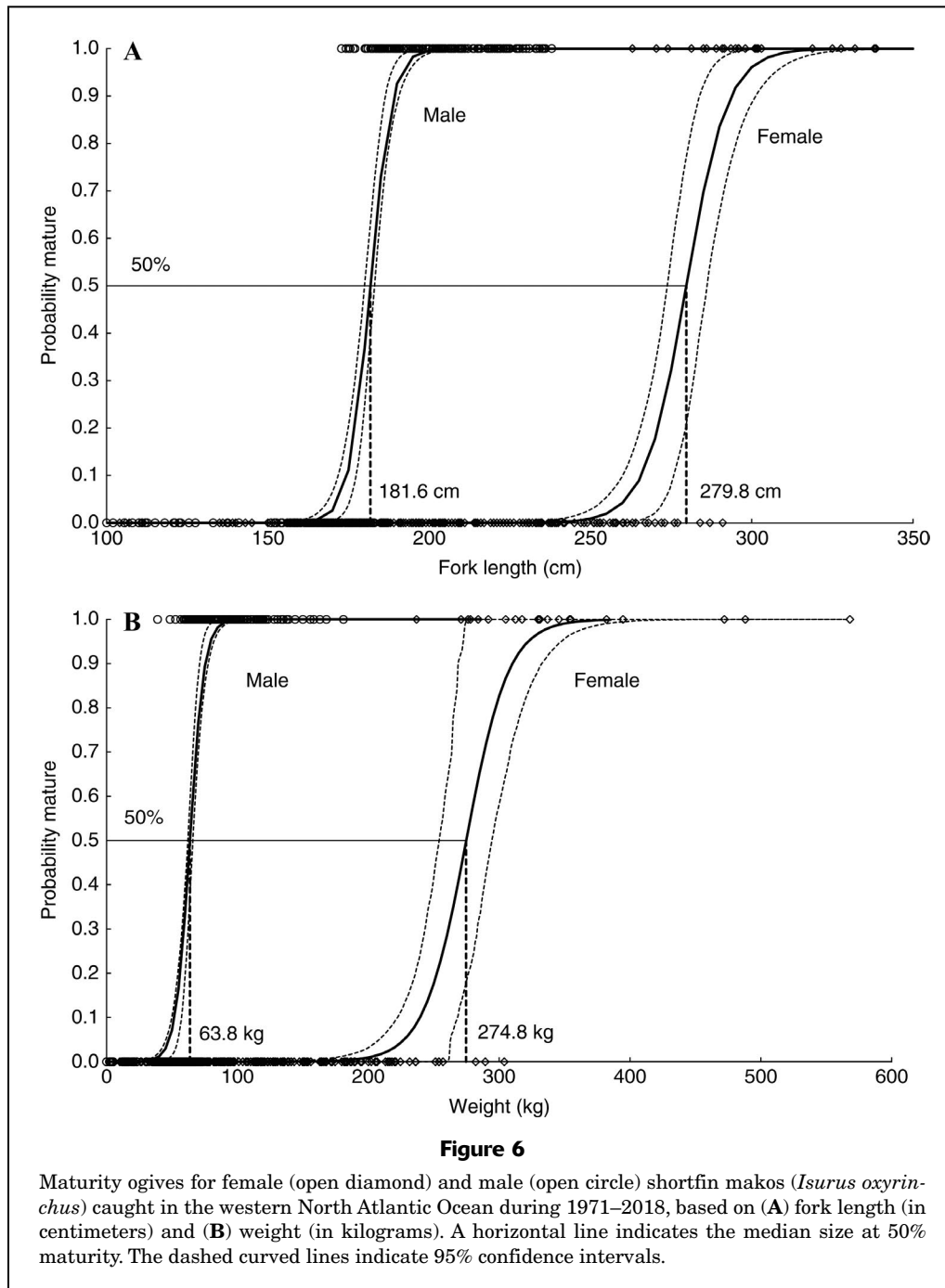


is within the 95% CI of this study. Our estimate for male  $L_{50}$  (181.6 cm  $FL_{OTB}$ , 178.0 cm  $FL_S^*$ ) is similar to the previous estimate from a study in waters of Portugal in the eastern North Atlantic Ocean (180 cm  $FL_{OTB}$ ; Maia et al., 2007).

On the basis of existing age–length relationships, age at  $L_{50}$  were estimated for males at 7.5 years (Natanson et al., 2006; Rosa et al.<sup>7</sup>); the estimate for females was slightly over 19 years, when following Natanson et al. (2006), and 22 years, when following Rosa et al.<sup>7</sup> The dissection data provide a comprehensive view of the maturity of this species for the western North Atlantic Ocean, and the evidence for one stock supports the use of these data for characterizing maturity of the entire population in the North Atlantic Ocean. The fact that maturity estimates have not changed markedly over time increases our confidence in their accuracy, making our updated values the best available to describe maturity and to inform age- and sex-structured models used for stock assessment (ICCAT<sup>4</sup>).

The growth patterns of individual reproductive organs indicate increased energetic investment in reproduction in advance of maturity in both male and female shortfin makos, although not all organs are as useful for distinguishing between immature and mature individuals. With the exception of uterus length, which grew gradually relative to length, measurements of internal reproductive organs of females increased sharply as sharks matured. Similar to Mollet et al. (2000), we found that uterus width and oviducal gland growth were suitable for distinguishing between immature and mature females and reproductive stage. Although the maximum follicle diameter also increases with FL (Mollet et al., 2000), there is overlap in follicle size between all maturity stages because of the nature of the lamnid ovary and mode of embryonic nutrition, indicating that follicle diameter alone is not useful for determining stage of maturity.

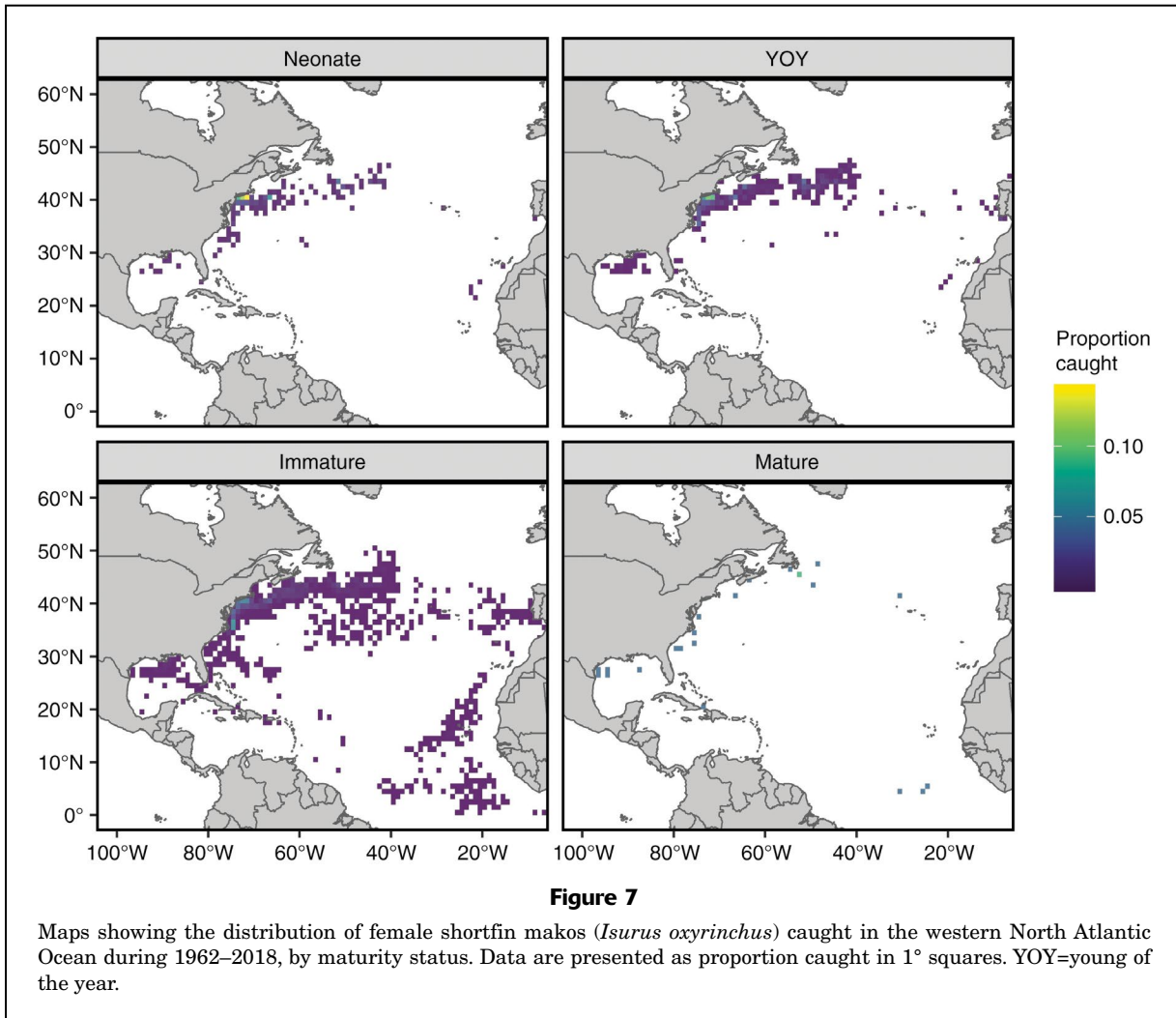
<sup>7</sup> Rosa, D., F. Mas, A. Mathers, L. J. Natanson, A. Domingo, J. Carlson, and R. Coelho. 2017. Age and growth of shortfin mako in the north Atlantic, with revised parameters for consideration to use in the stock assessment. Int. Comm. Conserv. Atlantic Tunas, ICCAT SCRS/2017/111, 22p. [Working paper.]



For males, clasper length and calcification are the most accurate means of determining maturity. It is not uncommon in elasmobranchs that the secondary sexual characteristics (including clasper rigidity, rotation, and the ability of the rhipidion to splay open) develop after the primary sexual organs and are the defining criteria for maturity (Clark and von Schmidt, 1965). At a minimum, future studies on the reproductive dynamics of shortfin makos should combine comprehensive visual assessments (e.g., presence or absence of embryos and condition of ovaries and uterus) with morphometric measurements (on

the organs that show the most rapid growth to body size in females and on clasper length and rigidity in males) to accurately assign maturity stage.

The overlap observed in the demographic structure in the seasonal distributions of the 2 sexes as well as among the different life history stages of shortfin makos were unexpected, given that habitat partitioning and sex and size segregation is common in sharks (Haulsee et al., 2018). Immature males, adult males, immature females, and adult females were found together in every month, with the exception of June and October when mature

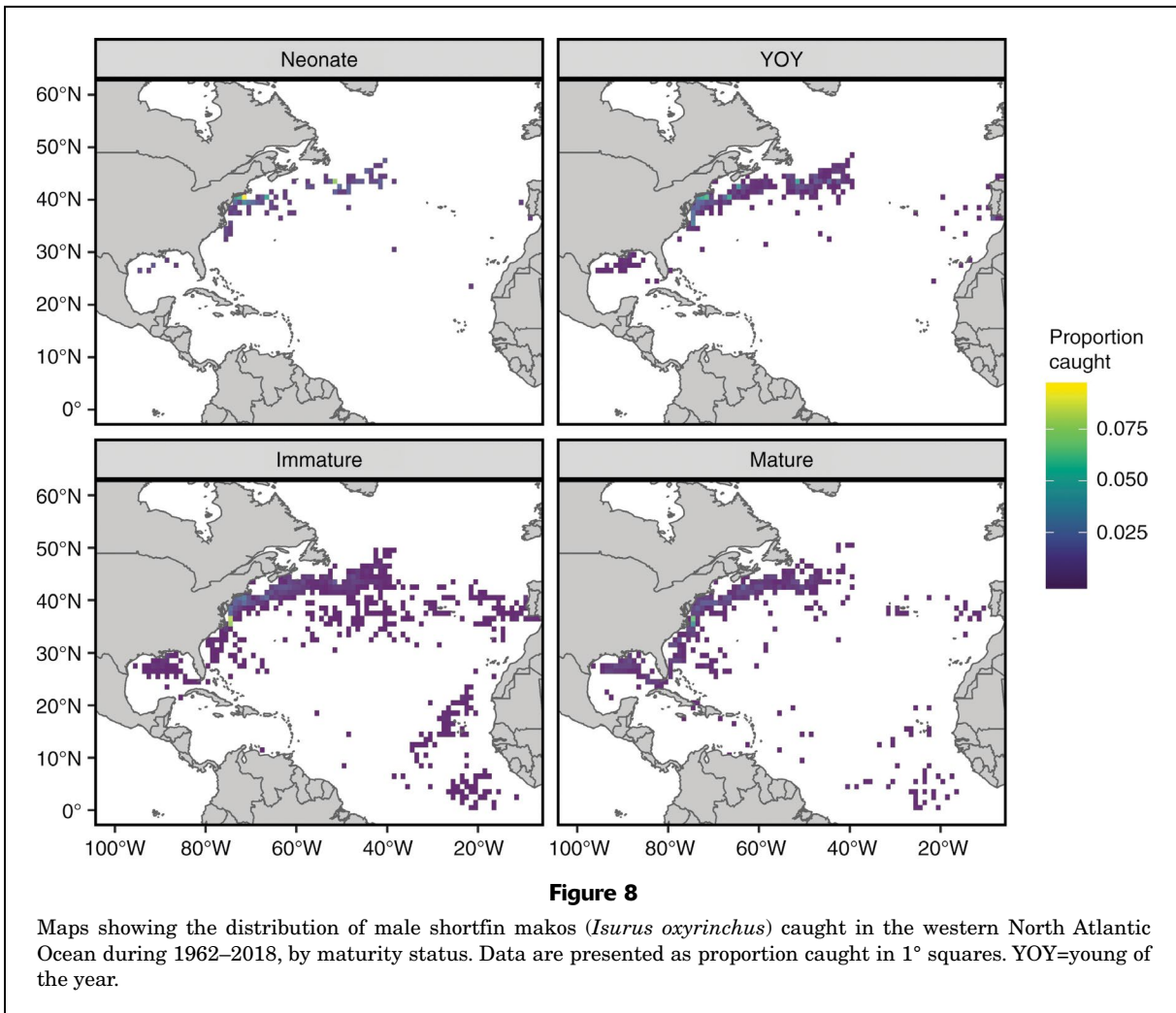


females were not caught. Segregation in space and in particular by depth has been previously reported for shortfin makos in the South Pacific Ocean, with males being predominantly found in the west and females in the east and with larger fish spending time at greater depths than smaller fish (Mucientes et al., 2009). Similar to Mucientes et al. (2009), more mature males were captured than mature females in our study, possibly as a result of mature females being absent from the areas targeted by commercial fishing operations or remaining at depths that are out of the range of the fishing gear.

Although the distribution data used in this study were spatially and temporally dependent on fishing effort, the same is true for the majority of data used in other studies to describe the distributions of pelagic sharks (Mucientes et al., 2009; Heupel et al., 2018). Some gear configuration changes (Federal Register, 2004; Coelho and Muñoz-Lechuga, 2019) may have influenced the catchability of sharks over time (Reinhardt et al., 2018), but no management or systematic changes in the distribution of fishing effort would have affected the geographic range of the catch data used. The majority of the catch data used to

infer distributions, however, originated from the western North Atlantic Ocean (87% came from west of longitude 45°W); therefore, there remains the possibility that spatial segregation occurs at a larger geographical scale. The fact that immature shortfin makos in our data were predominantly female but that Maia et al. (2007) found the majority of specimens taken off the coast of Portugal to be male is consistent with this hypothesis. Incorporating more distribution data from the Northeast Atlantic Ocean is needed to fully understand demographic structure and seasonal movement patterns of shortfin makos in the North Atlantic Ocean.

The identification of pupping and nursery areas for sharks is crucial to protect vulnerable life stages and support conservation goals (Heupel et al., 2007; Kinney and Simpfendorfer, 2009; Heupel et al., 2018). Unless movement following birth is substantial, the distribution of the youngest age classes should delineate potential birthing and nursery areas. Although the distribution data of mature females from this study and others (Branstetter, cited in Depperman, 1953; Branstetter, 1981; Gilmore, 1993; Mollet et al., 2000) indicates that the Gulf of Mexico is a possible



gestation and parturition area from winter to spring, the distribution of neonates is much more widespread along the coast of North America and largely overlaps with the distribution of older immature sharks and adults. Neonate and YOY shortfin makos have also been found off Africa and Portugal (Maia et al., 2007), in waters that may prove to be important birthing or nursery areas with more intensive sampling in the Northeast Atlantic Ocean.

The suggestion of a nursery ground of some degree off Portugal is supported by Maia et al. (2007), who reported captures of birth-size individuals (<70 cm  $FL_{OTB}$ ) in May and July. Maia et al. (2007) question the probability of pups swimming against the current to migrate from a southern pupping ground to Portugal. However, the new evidence of northern pupping on the western side of the Atlantic Ocean indicates that there could also be pupping on the northern area of the eastern Atlantic Ocean or that pups may be using northern surface currents to move from the western to the eastern Atlantic Ocean. Because the coastal areas off Portugal are considered unattractive to sharks (Maia et al., 2007), portions of the western North Atlantic Ocean, which are productive and the location of

many shark nursery grounds (Castro, 1993), may be the main parturition and nursery areas for shortfin makos. Data from long-term tracking studies also indicate considerable use of the shelf between South Carolina and Nova Scotia, Canada, by primarily juvenile shortfin makos (Byrne et al., 2017), but additional fishery-independent data are needed to define these boundaries.

The updated reproductive and maturity estimates for both sexes and spatiotemporal patterns in the distribution of life history stages from this study can be used to improve the reliability of science-based advice, as well as to evaluate the likely effect of conservation measures such as size limits. Conservation measures to protect the shortfin mako have been implemented in commercial and recreational fisheries following the ICCAT<sup>5</sup> recommendations. For example, in an initial effort to limit mortality and reduce overfishing by recreational fishermen, the United States imposed size limits for 2019 of 210 cm  $FL_S$  and 180 cm  $FL_S$  for female and male shortfin makos, respectively. The female size limit is below the new  $L_{50}$  and the male limit is just below the new  $L_{50}$ , indicating that these management measures will reduce but not



remove fishing pressure on mature individuals. Both the United States and Canada have banned the retention of live shortfin makos by commercial fleets, and Canada prohibited all retention of shortfin makos in recreational fisheries (COSEWIC, in press; Federal Register, 2019). Such measures are timely given that updated projections from the North Atlantic Ocean assessment model indicate continued population declines (ICCAT<sup>4</sup>). However, there is still a need to better understand the seasonality and segregation of mature females, gestation, and parturition activities in the Gulf of Mexico and along the continental shelf, to develop mitigation options and aid in stock recovery. Ideally, future work on shortfin makos would rely on increased collection of fishery-independent data from sparsely sampled areas.

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