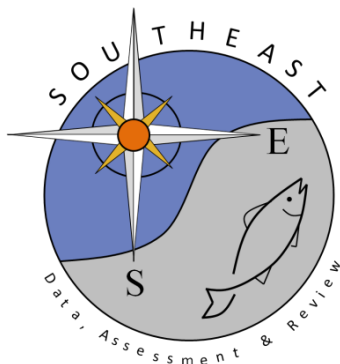


Updated reproductive parameters for sandbar sharks  
(*Carcharhinus plumbeus*) in US waters of the western North  
Atlantic Ocean

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SEDAR101-DW-27

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## Updated reproductive parameters for sandbar sharks (*Carcharhinus plumbeus*) in US waters of the western North Atlantic Ocean.

G. Walter Ingram, Jr.<sup>1</sup>, William B. Driggers III<sup>1</sup>, Bryan S. Frazier<sup>2</sup>, Annsli Hilton<sup>1</sup>, Heather Moncrief-Cox<sup>1</sup>, Lisa J. Natanson<sup>3</sup>, and Michelle S. Passerotti<sup>3</sup>.

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### Background

From 2016-2024, reproductive data were collected from 1,553 sandbar sharks during commercial fishing operations and fisheries-independent surveys. Maturity status was assigned to all but 17 individuals, including 1,019 females and 517 males. Males were considered mature if the claspers were elongated and fully calcified. Females were classified as mature if the uteri and oviducal glands were fully developed. Ovarian activity was not considered a criterion for maturity due to the uncertainty associated with the reproductive cycle. Reproductive data collected from females also included, among other measures, ovary weight, total number and diameter of the five largest vitellogenic follicles, width of one uterus in non-pregnant females, and oviducal gland width. If pregnant, the total brood size was recorded.

Length and age (see SEDAR101-DW-24) data were used in conjunction with maturity data to generate sex and region-specific ogives. Records with missing maturity classification, FL, or age were removed from the analysis to ensure a consistent, 1:1 dataset for all model comparisons. Macroscopic maturity was binarized, assigning 0 to juvenile sharks and 1 to mature sharks. Appropriate binomial models against both fork length (FL, cm) and age (years) were fitted, and Likelihood Ratio Tests (LRTs) to compare spatial and temporal parameters were conducted, generating high-resolution visualizations.

The 50% maturity inflection points ( $L_{50}$  and  $A_{50}$ ) were extracted algebraically by dividing the negative model intercept by the slope covariate. Confidence intervals (95%) were calculated natively on the link scale and back-transformed to the probability scale to produce structurally valid bounds. To definitively ascertain whether temporal shifts have occurred, sex- and area-specific ogives for each individual SEDAR assessment were constructed, followed by a statistical comparison (i.e., LRTs) encompassing all three time periods simultaneously for both length and age. R was used to construct ogives and statistically evaluate variations in parameter estimates using maximum-likelihood estimation (Ogle, 2016).

### Results

The analysis of the SEDAR 101 dataset revealed distinct differences in the size and age at which male and female sandbar sharks reach 50% maturity ( $L_{50}$  and  $A_{50}$ ).

- Length at Maturity: Females reached 50% maturity at a significantly larger fork length (147.26 cm FL) compared to males (142.87 cm FL). Likelihood Ratio Tests (LRT) confirmed that this sex-specific difference in length-based maturity is statistically

significant ( $p = 0.0464$ ). These length-at-maturity ogives are visualized in Figure 1, with associated model coefficients detailed in Table 1.

- Age at Maturity: There was a roughly one-year difference in the average age at 50% maturity, with females reaching  $A_{50}$  at 11.00 years and males at 10.05 years. However, statistical testing indicated that this difference in age at maturity between the sexes was not statistically significant ( $p = 0.1235$ ). The age-at-maturity ogives are depicted in Figure 2.

A geographic comparison of the SEDAR 101 data showed that females in the Atlantic (ATL) matured at a larger size and an older age than those in the Gulf of America (GOA).

- Length Differences: Atlantic females had an estimated  $L_{50}$  of 148.73 cm FL, whereas GOA females had an  $L_{50}$  of 143.15 cm FL. LRT confirmed this regional difference in length-based ogives is statistically significant ( $p = 0.0314$ ). These differences are modeled in Table 4 and visualized in Figure 3.
- Age Differences: Atlantic females reached  $A_{50}$  at 11.60 years, compared to 8.96 years for GOA females. This regional variation in age-based ogives was also highly significant ( $p = 0.0003$ ). The comparative age ogives are shown in Figure 4.

Similar to females, male sandbar sharks in the Atlantic generally matured at a larger size and greater age than their GOA conspecifics, though the statistical significance of these variations differed.

- Length Differences: Atlantic males reached an  $L_{50}$  of 145.17 cm FL, compared to 138.54 cm FL for GOA males. However, LRT results indicated this spatial difference in length-based maturity for males was not statistically significant ( $p = 0.1956$ ). These ogives are plotted in Figure 5, with parameters in Table 7.
- Age Differences: The  $A_{50}$  for Atlantic males was 10.65 years, while GOA males reached  $A_{50}$  at 8.65 years. As with the length analysis, this regional difference in male age-at-maturity was not statistically significant ( $p = 0.1501$ ). The male age-at-maturity ogives across regions are illustrated in Figure 6.

Analysis across different SEDAR assessment periods (21, 54, and 101) indicated substantial temporal shifts in maturity ogives for both sexes and regions (Tables 10, 11 & 12, Figures 7 & 8).

- Length-based Shifts: Significant temporal differences in  $L_{50}$  were found for all groups: Females in the ATL and GOA ( $p < 0.0001$ ), and males in the ATL and GOA ( $p < 0.0001$ ). Generally,  $L_{50}$  tended to decrease in more recent assessments; for example, GOA females dropped from 154.64 cm (SEDAR 21) to 143.15 cm (SEDAR 101).
- Age-based Shifts: Significant temporal shifts in  $A_{50}$  were also observed across all sex and area combinations ( $p < 0.0001$ ). Similar to length, the age at 50% maturity has declined over time, most notably in GOA males, where  $A_{50}$  decreased from 13.04 years (SEDAR 21) to 8.65 years (SEDAR 101).

Maturity schedules are provided in the Appendix.

## Brood size

Brood size counts from 201 female sandbar sharks were collected between 2016 and 2024. The mean brood size was 7.77 pups per brood (S.D. = 2.26), which was not statistically different from the mean brood size in data used for SEDAR 21 (mean = 7.80, S.D. = 2.47;  $t = 0.11$ ,  $p = 0.91$ ). Data from all years (i.e., 2006-2024) were combined to compare mean brood size between the Atlantic and GOA, and there was no statistical difference between regions ( $t = 0.66$ ,  $p = 0.511$ ).

## Maternal size/age and brood size relationships.

To evaluate potential relationships between brood size and maternal length/age, we analyzed brood size as count data. Because the dependent variable (brood size) consists of discrete, non-negative integers, we employed Generalized Linear Models (GLMs) specifying a Poisson distribution with a log link function.

To maximize the statistical power of the dataset while accounting for missing data in the age records, we developed two separate models. The first model evaluated maternal age as the primary predictor, along with geographic area (GOA vs. ATL) and the SEDAR assessment timeframe as covariates. The second model evaluated maternal FL as the primary predictor, utilizing the same spatial and temporal covariates.

The relationship between maternal characteristics and reproductive output was modeled using Poisson GLMs (Tables 13 & 14). Brood size was positively and significantly correlated with both maternal age and maternal length. As mothers grew older and larger, the predicted brood size increased (Figures 9 & 10). The relationship between brood size and maternal age is described by:  $\text{Brood Size} = \exp(1.630 + 0.025(\text{AGE}))$ . The relationship between brood size and maternal length is described by:  $\text{Brood size} = \exp(0.544 + 0.009(\text{FL}))$  (Tables 15 and 16). Geographic area (GOA vs. ATL) and temporal timeframe (SEDAR) did not have a statistically significant effect on brood size ( $p > 0.05$ ).

## Literature Cited

Ogle, D. H. (2016). *Introductory Fisheries Analyses with R*. Chapman & Hall/CRC, Boca Raton, FL.

**Table 1.** Length and age at maturity model coefficients & model  $p$ -values for SEDAR101 data.

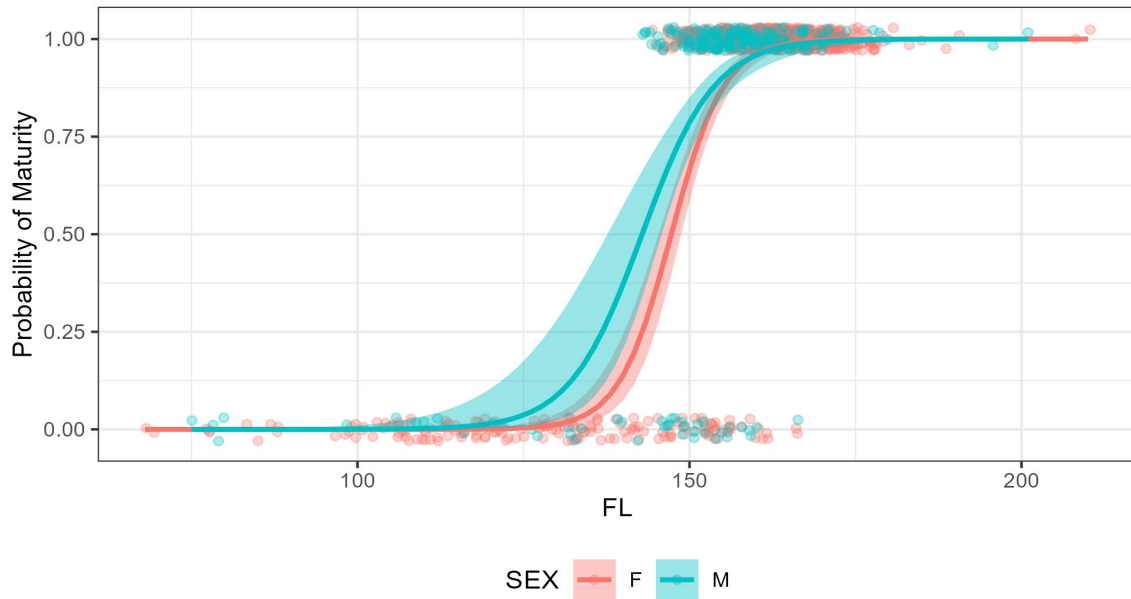
Analysis	Parameter	Estimate	LCI_95	UCI_95	Parameter $p$ -value	Model $p$ -value
Female-FL	$a$	-37.1393	-44.6201	-29.6585	<0.00001	<0.00001
	$b$	0.2522	0.2032	0.3012	<0.00001	
Male-FL	$a$	-26.1467	-35.8293	-16.4640	<0.00001	<0.00001
	$b$	0.1830	0.1189	0.2471	<0.00001	
Female-Age	$a$	-8.7015	-10.4183	-6.9848	<0.00001	<0.00001
	$b$	0.7913	0.6567	0.9259	<0.00001	
Male-Age	$a$	-5.7782	-8.0528	-3.5037	<0.00001	<0.00001
	$b$	0.5750	0.3930	0.7569	<0.00001	

**Table 2.** Sex-specific age and length at 50 % maturity (with 95 % CI) for SEDAR101 data.

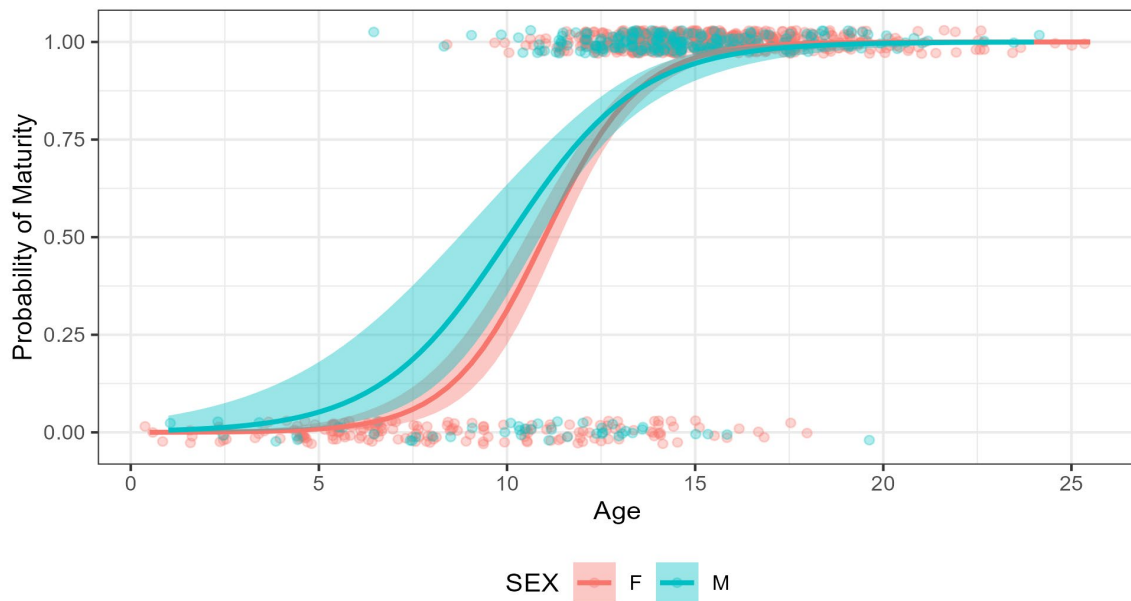
Analysis	Value	LCI_95	UCI_95
Female- $L_{50}$	147.26	145.62	148.90
Male- $L_{50}$	142.87	139.19	146.54
Female- $A_{50}$	11.00	10.55	11.44
Male- $A_{50}$	10.05	9.05	11.05

**Table 3.** Likelihood Ratio Tests for differences in sex-specific age- and length-based ogives for SEDAR101 data.

Comparison	Term	#Df	LogLik	Df	Chisq	Pr(>Chisq)
Sex-FL	1	2.0000	-205.5289			
	2	4.0000	-202.4594	2.0000	6.1390	0.0464
Sex-Age	1	2.0000	-251.9416			
	2	4.0000	-249.8503	2.0000	4.1825	0.1235



**Figure 1.** Sex-specific length-at-maturity ogives (with 95% CL) for sandbar sharks (*Carcharhinus plumbeus*) in the western North Atlantic Ocean based on SEDAR101 data.



**Figure 2.** Sex-specific age-at-maturity ogives (with 95% CL) for sandbar sharks (*Carcharhinus plumbeus*) in the western North Atlantic Ocean based on SEDAR101 data.

**Table 4.** Model Coefficients & Model *p*-values for females (ATL vs GOA) (SEDAR 101).

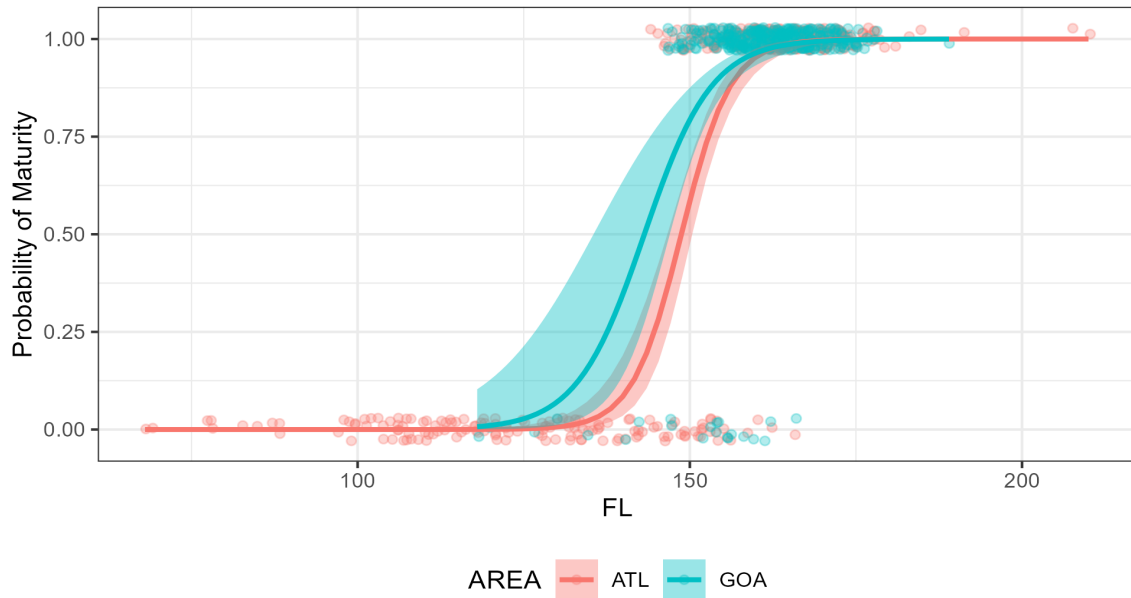
Analysis	Parameter	Estimate	LCI_95	UCI_95	Parameter <i>p</i> -value	Model <i>p</i> -value
Females ATL-Len	<i>a</i>	-40.1917	-50.4557	-29.9277	0.0000	0.0000
	<i>b</i>	0.2702	0.2029	0.3376	0.0000	0.0000
Females GOA-Len	<i>a</i>	-28.0962	-39.6899	-16.5024	0.0000	0.0000
	<i>b</i>	0.1963	0.1212	0.2713	0.0000	0.0000
Females ATL-Age	<i>a</i>	-10.0922	-12.5129	-7.6714	0.0000	0.0000
	<i>b</i>	0.8701	0.6817	1.0584	0.0000	0.0000
Females GOA-Age	<i>a</i>	-4.8184	-7.7750	-1.8618	0.0014	0.0000
	<i>b</i>	0.5376	0.3143	0.7609	0.0000	0.0000

**Table 5.** Area-specific age and length at 50 % maturity (with standard error) for females (ATL vs GOA) (SEDAR 101).

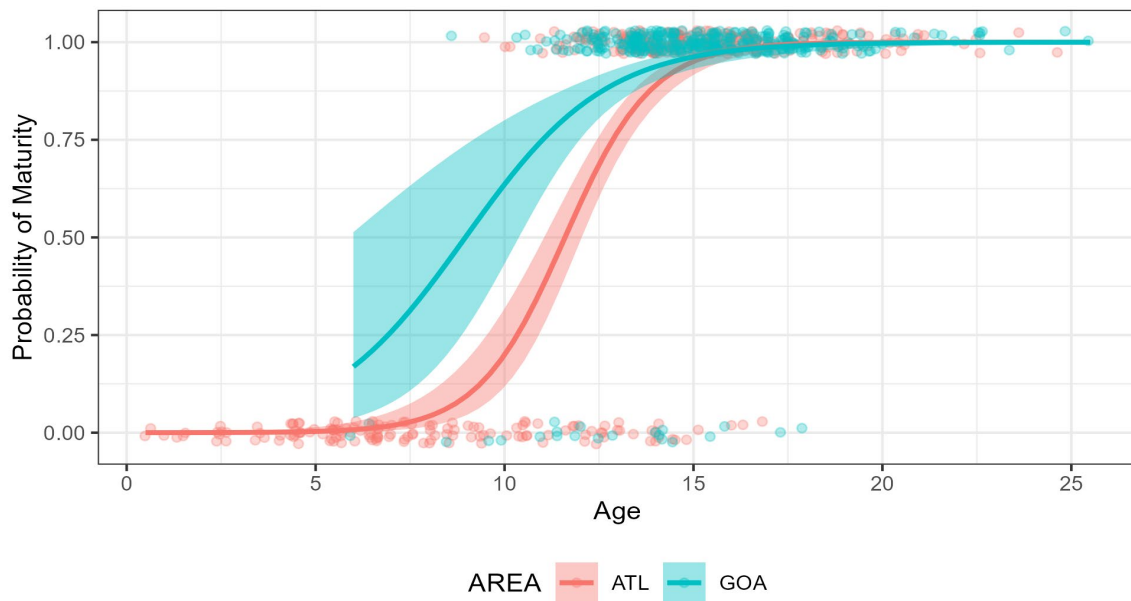
Analysis	Value	LCI_95	UCI_95
ATL Female- $L_{50}$	148.73	146.93	150.52
GOA Female- $L_{50}$	143.15	138.15	148.15
ATL Female- $A_{50}$	11.60	11.12	12.08
GOA Female- $A_{50}$	8.96	7.05	10.88

**Table 6.** Likelihood Ratio Tests for differences in age- and length-based ogives for females (ATL vs GOA) (SEDAR 101).

Comparison	Term	#Df	LogLik	Df	Chisq	Pr(>Chisq)
Females Area-FL	1	2.0000	-131.0972			
Females Area-FL	2	4.0000	-127.6353	2.0000	6.9237	0.0314
Females Area-Age	1	2.0000	-172.3278			
Females Area-Age	2	4.0000	-164.2909	2.0000	16.0739	0.0003



**Figure 3.** Female length-at-maturity ogives (with 95% CL) for sandbar sharks (*Carcharhinus plumbeus*) (ATL vs GOA) (SEDAR 101).



**Figure 4.** Female age-at-maturity ogives (with 95% CL) for sandbar sharks (*Carcharhinus plumbeus*) (ATL vs GOA) (SEDAR 101).

**Table 7.** Model Coefficients & Model *p*-values for males (ATL vs GOA) (SEDAR 101).

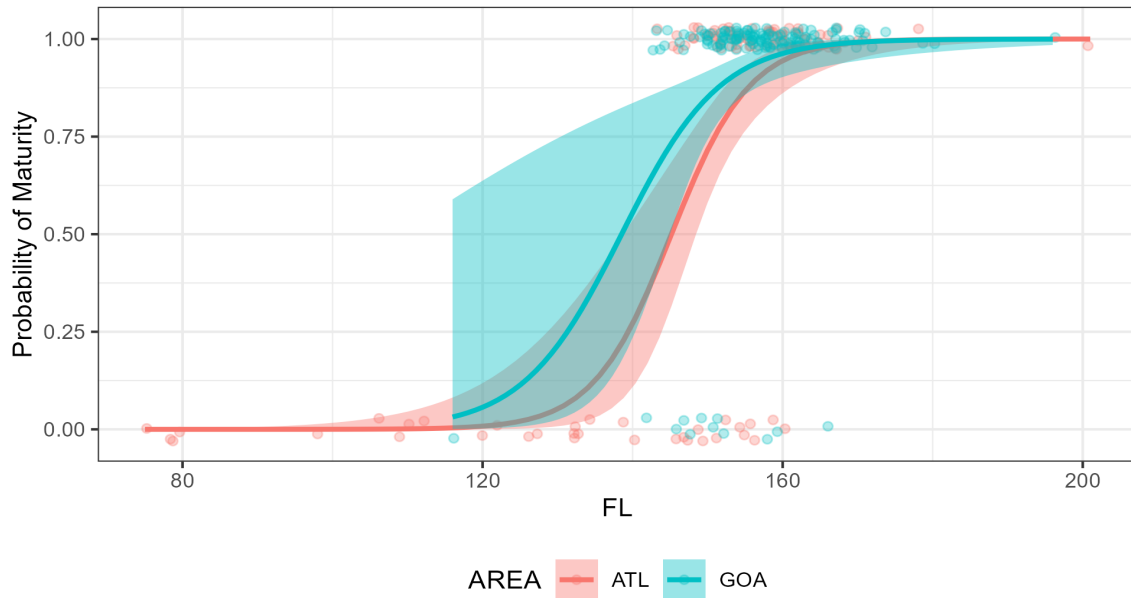
Analysis	Parameter	Estimate	LCI_95	UCI_95	Parameter <i>p</i> -value	Model <i>p</i> -value
Males ATL-Len	<i>a</i>	-27.7511	-41.1681	-14.3341	0.0001	0.0000
	<i>b</i>	0.1912	0.1023	0.2800	0.0000	0.0000
Males GOA-Len	<i>a</i>	-21.0334	-36.7370	-5.3299	0.0087	0.0002
	<i>b</i>	0.1518	0.0487	0.2550	0.0039	0.0002
Males ATL-Age	<i>a</i>	-6.0892	-9.0449	-3.1334	0.0001	0.0000
	<i>b</i>	0.5718	0.3313	0.8124	0.0000	0.0000
Males GOA-Age	<i>a</i>	-4.2092	-7.9573	-0.4611	0.0277	0.0001
	<i>b</i>	0.4865	0.1973	0.7758	0.0010	0.0001

**Table 8.** Area-specific age and length at 50 % maturity (with standard error) for males (ATL vs GOA) (SEDAR 101).

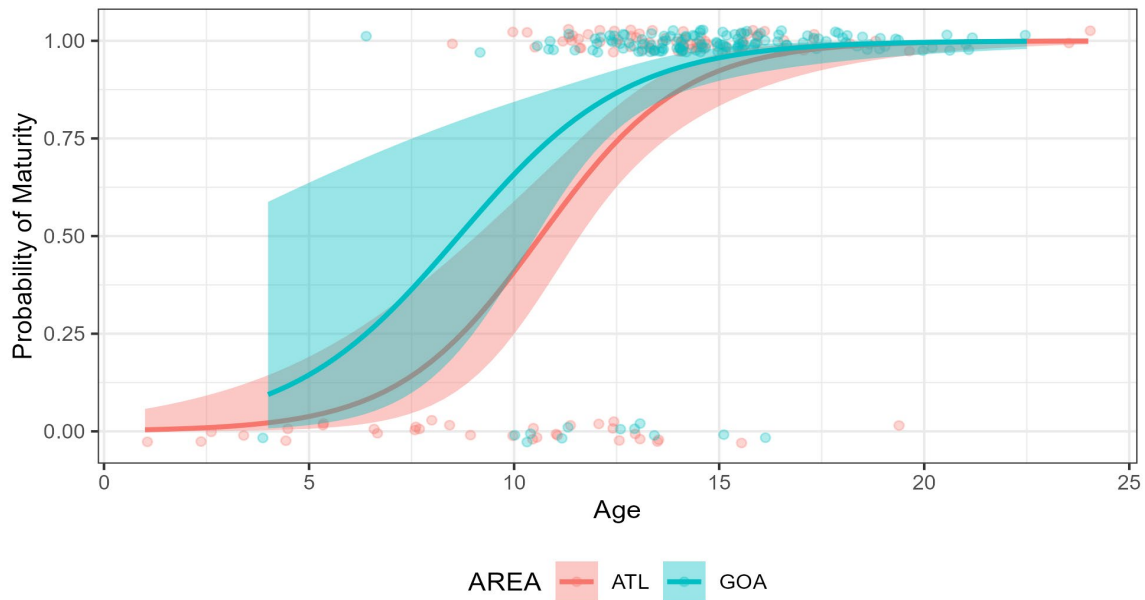
Analysis	Value	LCI_95	UCI_95
ATL Male- $L_{50}$	145.17	141.11	149.23
GOA Male- $L_{50}$	138.54	128.37	148.70
ATL Male- $A_{50}$	10.65	9.54	11.76
GOA Male- $A_{50}$	8.65	5.87	11.44

**Table 9.** Likelihood Ratio Tests for differences in area-specific age- and length-based ogives for males (ATL vs GOA) (SEDAR 101).

Comparison	Term	#Df	LogLik	Df	Chisq	Pr(>Chisq)
Males Area-FL	1	2.0000	-71.3622			
Males Area-FL	2	4.0000	-69.7306	2.0000	3.2631	0.1956
Males Area-Age	1	2.0000	-77.5225			
Males Area-Age	2	4.0000	-75.6261	2.0000	3.7929	0.1501



**Figure 5.** Length-at-maturity ogives (with 95% CL) for male sandbar sharks (*Carcharhinus plumbeus*) (ATL vs GOA) (SEDAR 101).



**Figure 6.** Age-at-maturity ogives (with 95% CL) for male sandbar sharks (*Carcharhinus plumbeus*) (ATL vs GOA) (SEDAR 101).

**Table 10.** Sex-, area- and SEDAR-specific age and length at 50 % maturity (with standard error).

SEX	AREA	SEDAR	<i>n</i>	<i>L</i> <sub>50</sub> (cm)	<i>L</i> <sub>50</sub> SE	<i>A</i> <sub>50</sub> (year)	<i>A</i> <sub>50</sub> SE
F	ATL	21	439	154.66	0.68	14.14	0.24
F	ATL	54	277	149.71	0.57	12.19	0.25
F	ATL	101	427	148.73	0.92	11.60	0.25
F	GOA	21	279	154.64	0.74	13.86	0.25
F	GOA	54	168	149.94	0.80	10.57	0.51
F	GOA	101	339	143.15	2.55	8.96	0.98
M	ATL	21	209	151.54	0.84	13.15	0.26
M	ATL	54	149	149.49	55.54	11.87	0.27
M	ATL	101	109	145.17	2.07	10.65	0.57
M	GOA	21	316	151.47	0.63	13.04	0.23
M	GOA	54	71	147.90	0.99	10.90	0.64
M	GOA	101	140	138.54	5.18	8.65	1.42

**Table 11.** Likelihood Ratio Tests for differences in area-, sex-, and SEDAR-specific length-based ogives.**Females ATL**

<b>Model</b>	<b>#Df</b>	<b>LogLik</b>	<b>Df</b>	<b>Chisq</b>	<b>Pr(&gt;Chisq)</b>
1	2.0000	-291.3999			
2	6.0000	-256.5750	4.0000	69.6498	0.0000

**Females GOA**

<b>Model</b>	<b>#Df</b>	<b>LogLik</b>	<b>Df</b>	<b>Chisq</b>	<b>Pr(&gt;Chisq)</b>
1	2.0000	-196.1576			
2	6.0000	-159.5947	4.0000	73.1257	0.0000

**Males ATL**

<b>Model</b>	<b>#Df</b>	<b>LogLik</b>	<b>Df</b>	<b>Chisq</b>	<b>Pr(&gt;Chisq)</b>
1	2.0000	-140.1170			
2	6.0000	-104.8927	4.0000	70.4487	0.0000

**Males GOA**

<b>Model</b>	<b>#Df</b>	<b>LogLik</b>	<b>Df</b>	<b>Chisq</b>	<b>Pr(&gt;Chisq)</b>
1	2.0000	-137.3033			
2	6.0000	-114.3604	4.0000	45.8857	0.0000

**Table 12.** Likelihood Ratio Tests for differences in area-, sex-, and SEDAR-specific age-based ogives.**Females ATL**

<b>Model</b>	<b>#Df</b>	<b>LogLik</b>	<b>Df</b>	<b>Chisq</b>	<b>Pr(&gt;Chisq)</b>
1	2.0000	-442.3593			
2	6.0000	-394.2728	4.0000	96.1730	0.0000

**Females GOA**

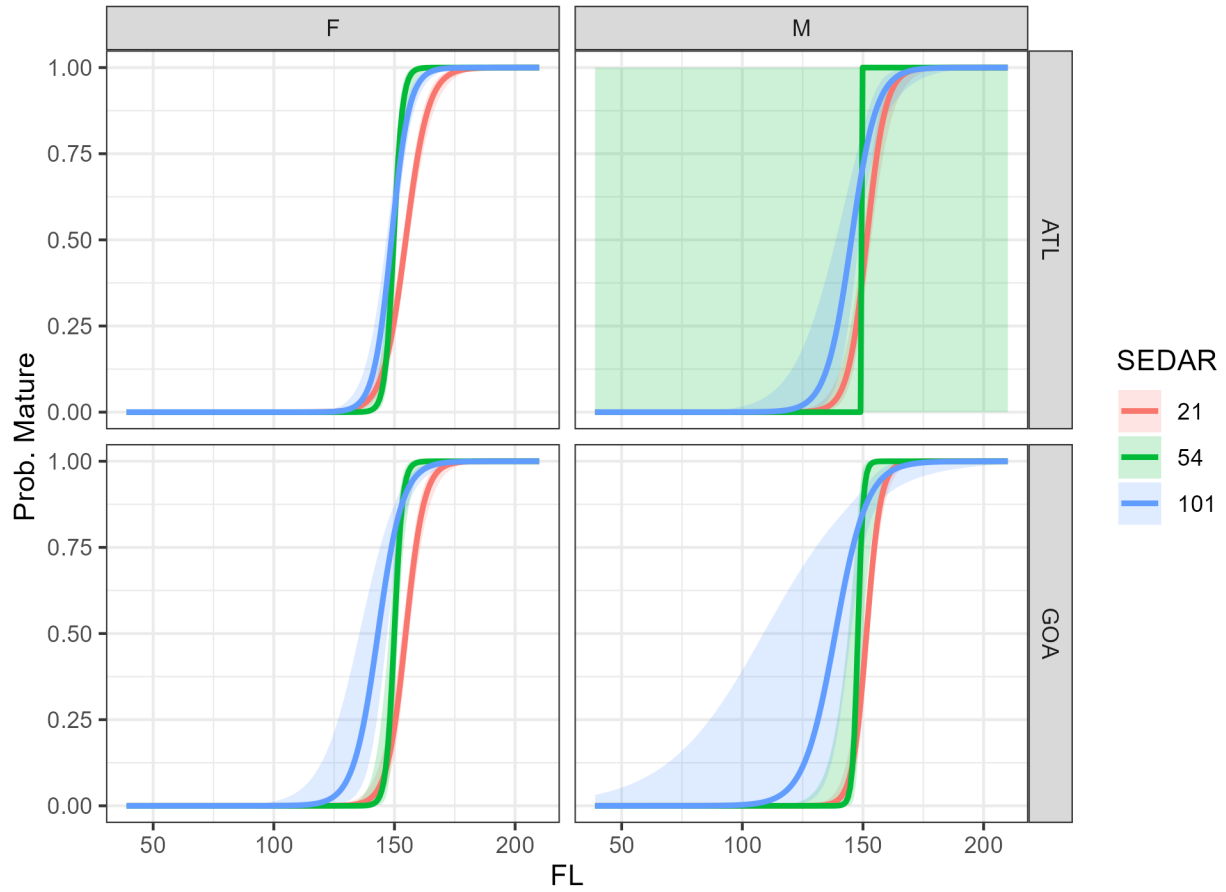
<b>Model</b>	<b>#Df</b>	<b>LogLik</b>	<b>Df</b>	<b>Chisq</b>	<b>Pr(&gt;Chisq)</b>
1	2.0000	-270.9931			
2	6.0000	-211.3839	4.0000	119.2184	0.0000

**Males ATL**

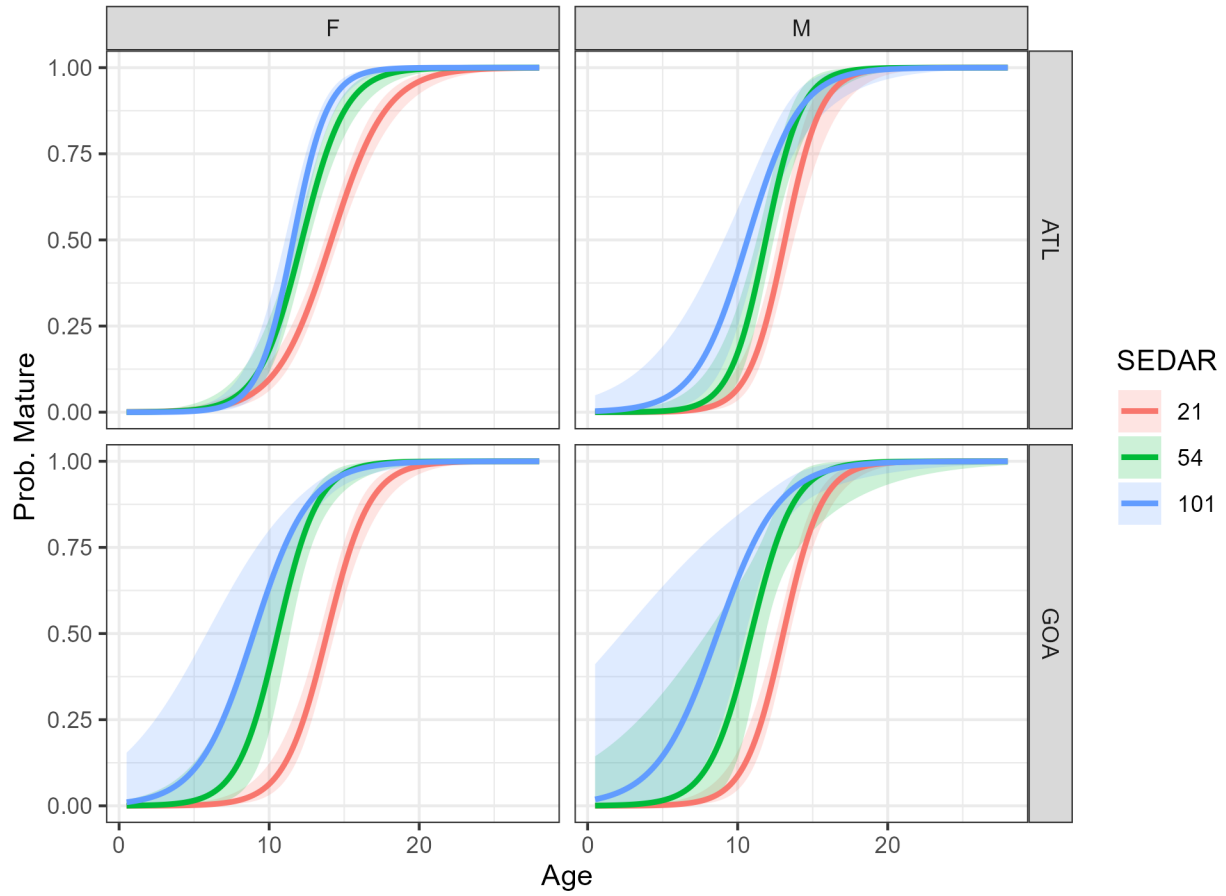
<b>Model</b>	<b>#Df</b>	<b>LogLik</b>	<b>Df</b>	<b>Chisq</b>	<b>Pr(&gt;Chisq)</b>
1	2.0000	-196.1945			
2	6.0000	-181.1964	4.0000	29.9961	0.0000

**Males GOA**

<b>Model</b>	<b>#Df</b>	<b>LogLik</b>	<b>Df</b>	<b>Chisq</b>	<b>Pr(&gt;Chisq)</b>
1	2.0000	-192.0629			
2	6.0000	-167.4078	4.0000	49.3103	0.0000



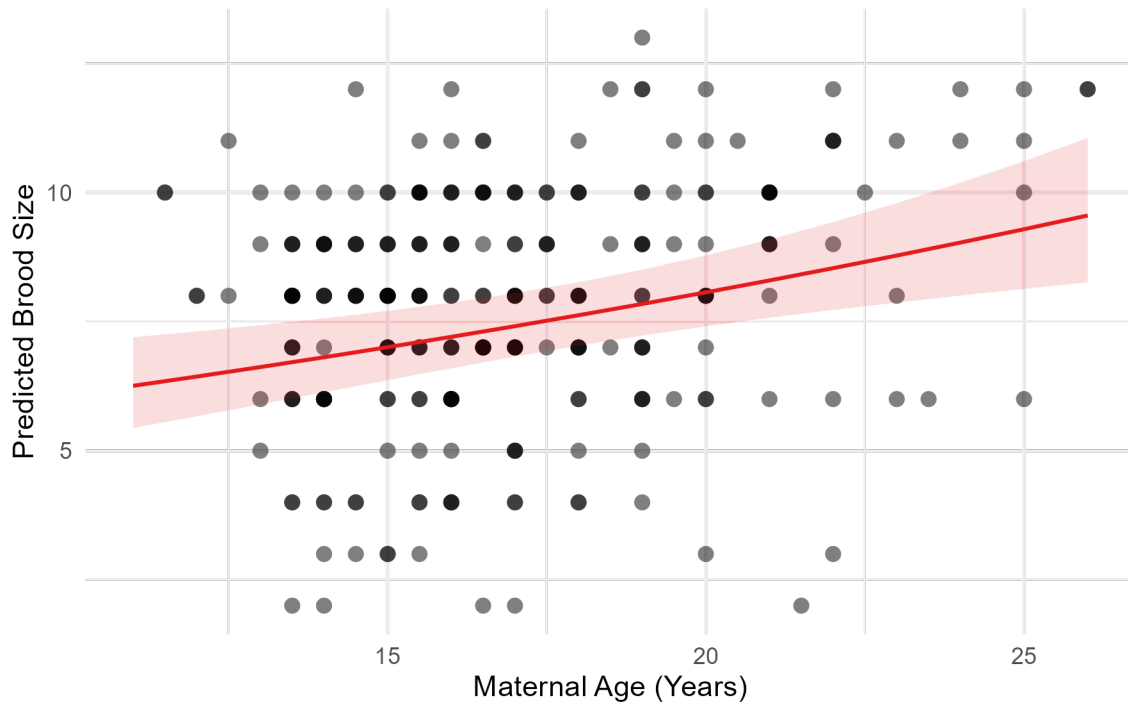
**Figure 7.** Area-, sex-, and SEDAR-specific length-at-maturity ogives (with 95% CL) for sandbar sharks (*Carcharhinus plumbeus*) in the western North Atlantic Ocean.



**Figure 8.** Area-, sex-, and SEDAR-specific age-at-maturity ogives (with 95% CL) for sandbar sharks (*Carcharhinus plumbeus*) in the western North Atlantic Ocean.

**Table 13.** Model parameter evaluation with maternal age as the primary predictor and geographic area (GOA vs. ATL) and the SEDAR assessment timeframe as covariates.

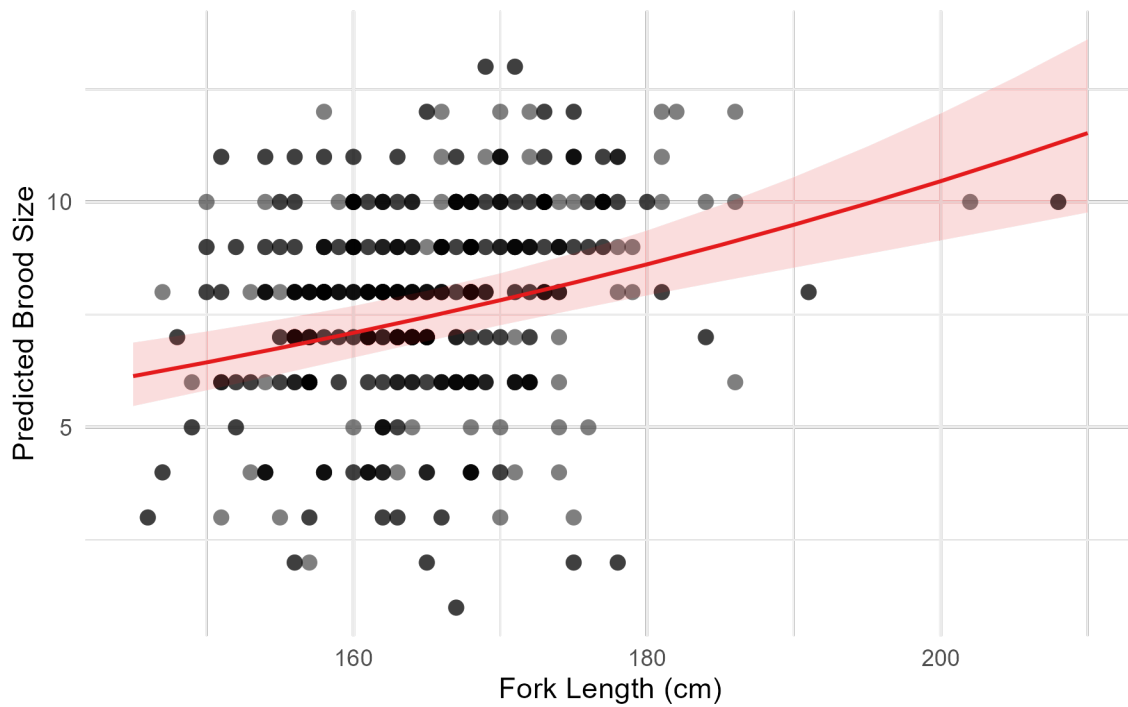
term	estimate	std.error	statistic	p.value	conf.low	conf.high
(Intercept)	1.523	0.152	10.010	0.000	1.225	1.822
AGE	0.028	0.008	3.522	0.000	0.012	0.044
AREAGOA	0.040	0.046	0.879	0.380	-0.049	0.130
SEDAR101	0.052	0.049	1.079	0.281	-0.043	0.148



**Figure 9.** Relationship between brood size and maternal age for sandbar sharks (*Carcharhinus plumbeus*) in US waters of the western North Atlantic Ocean based on the Poisson GLM (with 95 % CL). Brood size =  $\exp(1.630 + 0.025(\text{Age}))$ .

**Table 14.** Model parameter evaluation with maternal FL as the primary predictor and geographic area (GOA vs. ATL) and the SEDAR assessment timeframe as covariates.

term	estimate	std.error	statistic	p.value	conf.low	conf.high
(Intercept)	0.407	0.316	1.288	0.198	-0.210	1.028
FL	0.010	0.002	5.230	0.000	0.006	0.013
AREAGOA	0.051	0.033	1.556	0.120	-0.013	0.116
SEDAR101	0.013	0.039	0.339	0.735	-0.062	0.089



**Figure 10.** Relationship between brood size and maternal fork length (FL) for sandbar sharks (*Carcharhinus plumbeus*) in US waters of the western North Atlantic Ocean based on the Poisson GLM (with 95 % CL). Brood Size =  $\exp(0.544 + 0.009(FL))$ .

**Table 15.** Reduced Maternal Age Model: Model Equation:  $\ln(\text{Brood Size}) = 1.630 + 0.025(\text{AGE})$ , Overall Model  $p$ -value =  $< 0.001$ .

<b>Predictor</b>	<b>Estimate</b>	<b>Standard Error</b>	<b>Z-Value</b>	<b>P-Value</b>	<b>95% CI Lower</b>	<b>95% CI Upper</b>
(Intercept)	1.630	0.131	12.476	0.000	1.374	1.887
AGE	0.025	0.007	3.340	0.001	0.010	0.040

**Table 16.** Reduced Maternal Length (FL) Model: Model Equation:  $\ln(\text{Brood Size}) = 0.544 + 0.009(\text{FL})$ ,

Overall Model  $p$ -value =  $< 0.001$ .

<b>Predictor</b>	<b>Estimate</b>	<b>Standard Error</b>	<b>Z-Value</b>	<b>P-Value</b>	<b>95% CI Lower</b>	<b>95% CI Upper</b>
(Intercept)	0.544	0.300	1.810	0.07	-0.043	1.135
FL	0.009	0.002	5.037	0.00	0.006	0.013

## Appendix

Table A1. Predicted Proportions Mature by Sex for SEDAR 101 Combined Areas.

<b>FL (cm)</b>	<b>Female</b>	<b>Male</b>	<b>Age (years)</b>	<b>Female</b>	<b>Male</b>
50	0	0	0	0	0
60	0	0	0.5	0	0
70	0	0	1.5	0	0.01
80	0	0	2.5	0	0.01
90	0	0	3.5	0	0.02
100	0	0	4.5	0.01	0.04
110	0	0	5.5	0.01	0.07
120	0	0.01	6.5	0.03	0.11
130	0.01	0.09	7.5	0.06	0.19
140	0.14	0.37	8.5	0.12	0.29
150	0.67	0.79	9.5	0.23	0.42
160	0.96	0.96	10.5	0.4	0.56
170	1	0.99	11.5	0.6	0.7
180	1	1	12.5	0.77	0.8
190	1	1	13.5	0.88	0.88
200	1	1	14.5	0.94	0.93
210	1	1	15.5	0.97	0.96
			16.5	0.99	0.98
			17.5	0.99	0.99
			18.5	1	0.99
			19.5	1	1
			20.5	1	1

**Table A2.** Predicted Proportions Mature by Sex for SEDAR 101 for ATL.

<b>FL (cm)</b>	<b>Female</b>	<b>Male</b>	<b>Age (years)</b>	<b>Female</b>	<b>Male</b>
50	0	0	0	0	0
60	0	0	0.5	0	0
70	0	0	1.5	0	0.01
80	0	0	2.5	0	0.01
90	0	0	3.5	0	0.02
100	0	0	4.5	0	0.03
110	0	0	5.5	0	0.05
120	0	0.01	6.5	0.01	0.09
130	0.01	0.05	7.5	0.03	0.14
140	0.09	0.27	8.5	0.06	0.23
150	0.59	0.72	9.5	0.14	0.34
160	0.95	0.94	10.5	0.28	0.48
170	1	0.99	11.5	0.48	0.62
180	1	1	12.5	0.69	0.74
190	1	1	13.5	0.84	0.84
200	1	1	14.5	0.93	0.9
210	1	1	15.5	0.97	0.94
			16.5	0.99	0.97
			17.5	0.99	0.98
			18.5	1	0.99
			19.5	1	0.99
			20.5	1	1

**Table A3.** Predicted Proportions Mature by Sex for SEDAR 101 for GOA.

<b>FL (cm)</b>	<b>Female</b>	<b>Male</b>	<b>Age (years)</b>	<b>Female</b>	<b>Male</b>
50	0	0	0	0.01	0.01
60	0	0	0.5	0.01	0.02
70	0	0	1.5	0.02	0.03
80	0	0	2.5	0.03	0.05
90	0	0	3.5	0.05	0.08
100	0	0	4.5	0.08	0.12
110	0	0.01	5.5	0.13	0.18
120	0.01	0.06	6.5	0.21	0.26
130	0.07	0.21	7.5	0.31	0.36
140	0.35	0.56	8.5	0.44	0.48
150	0.79	0.85	9.5	0.57	0.6
160	0.96	0.96	10.5	0.7	0.71
170	0.99	0.99	11.5	0.8	0.8
180	1	1	12.5	0.87	0.87
190	1	1	13.5	0.92	0.91
200	1	1	14.5	0.95	0.95
210	1	1	15.5	0.97	0.97
			16.5	0.98	0.98
			17.5	0.99	0.99
			18.5	0.99	0.99
			19.5	1	0.99
			20.5	1	1