Shark SEDAR Data Workshop Document

Indirect estimates of natural mortality for sandbar (*Carcharhinus plumbeus*) and blacktip (*Carcharhinus limbatus*) sharks in the western North Atlantic

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Summary

This document presents indirect estimates of instantaneous natural mortality and annual survivorship rates for sandbar and blacktip sharks in the Gulf of Mexico and U.S. South Atlantic Ocean. The aim is to provide a range of estimates of natural mortality that can be used as guidance for developing Bayesian priors for this parameter. A total of ten indirect estimation methods in the form of equations that predict natural mortality based on other life history traits were used. Additionally, an average survival at age was calculated using the results from these methods, and survival at age was further predicted by assuming a linear rate of change in M with age.

1. Introduction

Natural mortality is incorporated either explicitly or implicitly in models describing the population dynamics of a given species and is thus a key parameter in conducting fisheries stock assessments. Multiple direct and indirect estimation methods have been proposed to estimate natural mortality or, more generally, total mortality (see Vetter [1988] for a general review and Simpfendorfer et al. [2004] and Cortés [2004] for reviews of applications to elasmobranchs). Here we concentrate on producing estimates of natural mortality based on indirect methods only. The data required for application of direct estimation methods of total mortality, such as catch curves or tag-recapture analysis, were not available.

2. Materials and Methods

We used a total of ten estimation methods. Five of these methods yield a single estimate of natural mortality (Hoenig 1983, Pauly 1980, two from Jensen 1996, Rikhter and Efanov 1976), whereas the other five methods (Peterson and Wroblewski 1984 and a variant proposed by Cortés (2002) for sharks, Lorenzen (1996) based on weight, Lorenzen (2000) based on length, and Chen and Watanabe 1989) yield age- or size-specific values. Details of the rationale in developing and using these methods can be found in the original documents, and more discussion on their application to elasmobranchs in Cortés (2004) and Simpfendorfer et al. (2004). Here we only provide the equations we applied and a brief description of the parameters used. The life history parameter estimates we used corresponded to females in all cases and were obtained from Carlson et al. (2005) for blacktip shark and various published documents for sandbar shark (Sminkey and Musick 1995, Kohler et al. 1995). Table 1 lists all values used.

Hoenig's (1983) method—We used the relationship between Z (total instantaneous mortality rate) and t_{max} (longevity) for 84 teleost stocks:

$$\ln Z = 1.46 - 1.01 \ln t_{\max} \tag{1}$$

where t_{max} = 30 yr for sandbar, 12.5 yr for blacktip in the Gulf of Mexico (GOM), and 15.5 yr for blacktip in the U.S. South Atlantic. The values of t_{max} used correspond to maximum ages obtained through ageing studies, not to theoretical estimates.

Pauly's (1980) method—We used the relationship based on length and assuming a mean environmental temperature (T) of 20 °C:

$$\log M = -0.0066 - 0.279 \log L_{\infty} + 0.6543 K + 0.4634 \log T \tag{2}$$

Jensen's (1996) methods—We used the relationships between age at maturity (t_{mat}) and M, and between K and M derived by this author:

$$M = \frac{1.65}{t_{mat}} \tag{3}$$

$$M = 1.5 K \tag{4}$$

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where t_{mat} = 15.5 yr for sandbar, 5.7 yr for blacktip in the Gulf of Mexico (GOM), and 6.7 yr for blacktip in the U.S. South Atlantic.

Rikhter and Efanov's (1976) method—We used another relationship between age at maturity (t_{mat}) and M derived by these authors:

$$M = \frac{1.521}{t_{mat}^{\ 0.72}} - 0.155 \tag{5}$$

Chen and Watanabe's (1989) method—These authors postulated that M could be described by two relationships: one for the early and middle life stages that varies with age, and a second, constant relationship for later "senescent" ages, defined as ages greater than a_s (Roff 1992):

$$a_s = -\frac{1}{K}\ln\left|1 - e^{Kt_0}\right| + t_0 \tag{6}$$

Prior to this age, M at age a is estimated as:

$$M_a = \frac{K}{1 - e^{-K(a - t_0)}} \tag{7}$$

And M is given by the following equation during the period of stable mortality, which spans from a_{s+1} to maximum age (a_{max}):

$$\overline{M}(a_{s+1}, a_{\max}) = \frac{1}{(a_{\max} - a_{s+1})}\ln\left(\frac{e^{Ka_{\max}} - e^{Kt_0}}{e^{Ka_{s+1}} - e^{Kt_0}}\right) \tag{8}$$

Peterson and Wroblewski's (1984) method—We used the relationship between M and dry weight (in g) proposed by these authors:

$$M_w = 1.92W^{-0.25} \tag{9}$$

To make the estimates of M age-specific, weight was obtained from length-weight relationships, and length from age through the von Bertalanffy growth function (VBGF). Dry weight was obtained assuming that it makes up 30% of wet weight (as found for lemon sharks, *Negaprion brevirostris*; Cortés and Gruber 1994). Wet weight was also used as suggested by Cortés (2002).

Lorenzen's (1996 and 2000) methods—Lorenzen (1996) first presented a predictive equation of M based on weight for ocean systems:

$$M_w = 3.69W^{-0.305} \tag{10}$$

As with eq. (9), to make the estimates of M age-specific, weight was obtained from length-weight relationships, and length from age through the VBGF. Lorenzen (2000) later developed a similar relationship based on length, wherein estimates of M at length are derived assuming that M is inversely proportional to length:

$$M_l = M_r \frac{l_r}{l} \tag{11}$$

where l_r is the reference length and M_r is the natural mortality rate at the reference length, which was taken as length at birth and thus M_r=M_0 (mortality rate at age 0), with M_0 taken from eq. (10).

We also calculated an average survivorship at age by averaging the values of M at age obtained through the ten methods and expressing M as an annual survival (S_a=e^{-Ma}). Additionally, we assumed that the rate of change in M with age is linear to predict mortality, such that:

$$\frac{dM}{da} = -cM \tag{12}$$

which gives

$$M_a = M_0 e^{-c*a} \tag{13}$$

where M_0 is age-0 natural mortality and a is age. Values of M_a were obtained by minimizing the sum of the squared differences between the average natural mortality and eq. (13) to solve for c (exponent in eq. [13]).

3. Results and Discussion

Annual survivorship estimates for sandbar shark and blacktip shark in the Gulf of Mexico and U.S. South Atlantic, respectively, obtained with the ten methods are depicted in Figure 1. The average and predicted survivorships at age are also shown.

For the sandbar shark, with the exception of the estimate obtained with the Rikhter and Efanov (1976) method, all other estimates fell within a relatively narrow range. All the methods that yield age-specific estimates produced similar results, with the exception of the Peterson and Wroblewski (1984) method based on dry weight, which consistently yielded lower estimates than the other methods (Fig. 1, top panel). All estimates are presented in Table 2.

For the blacktip shark in the Gulf of Mexico, the methods that make use of parameters from the VBGF yielded considerably lower estimates than the methods that produce age-specific estimates based on size (Fig. 1, middle panel). This is a result of the relatively fast growth dynamics of this population. The methods that yield age-specific estimates based on size all produced similar results, again with the exception of the Peterson and Wroblewski (1984) method based on dry weight, which consistently yielded lower estimates than the other three methods (Fig. 1, middle panel). All estimates are presented in Table 3.

The same general trend was obtained for the blacktip shark in the U.S. South Atlantic, but the difference in predictions between the methods that make use of parameters from the VBGF and those that produce age-specific estimates based on size was smaller than for blacktip sharks in the Gulf of Mexico (Fig. 1, bottom panel), probably as a result of the somewhat slower growth dynamics of this population when compared to the Gulf of Mexico population. The Chen and Watanabe (1989) and Peterson and Wroblewski (1984) method based on dry weight produced more similar estimates for this population than in the other cases (Fig. 1, bottom panel). All estimates are presented in Table 4.

For reference, during the 2002 Stock Evaluation Workshop (SEW) and subsequent stock assessment (Cortés et al. 2002), the following distributions were agreed upon and used for the age-structured stock assessment models: for sandbar shark, M from age 1 to maximum age was described by a lognormal distribution with mean=0.18, CV=0.25, lower bound (LB)=0.10 and upper bound (UB)=0.40 ($M_{1,tmax}$ ~ LN(0.18,0.25,0.10,0.40)) and first-year (age 0) survivorship by a normal distribution with mean=0.60, CV=0.15, LB=0.30, and UB=0.80 (S_0 ~ N(0.60,0.15,0.30,0.80)); for blacktip shark, the distributions used were $M_{1,tmax}$ ~ LN(0.22,0.35,0.12,0.40) and S_0 ~ N(0.52,0.35,0.35,0.75). Figures 2 and 3 depict these distributions for sandbar and blacktip sharks, respectively. Note that the x-axis and the probability have been rescaled to the interval defined by the lower and upper bounds of each distribution.

The values of S_0 used in the 2002 SEW were based in part on empirical estimates obtained for lemon sharks (Manire and Gruber 1993) and blacktip sharks (Heupel and

Simpfendorfer 2002), and were lower than the values obtained herein using indirect estimation methods. Mean values of M for ages 1 to maximum correspond to an annual survival of 0.835 for sandbar shark and 0.80 for blacktip shark. Average values of annual survivorship for sandbar sharks age 1+ ranged from 0.79 to 0.89 (Table 2), and from 0.70 to 0.78 (Table 3) and 0.75 to 0.82 (Table 4) for blacktip sharks age 1+ in the Gulf of Mexico and U.S. South Atlantic, respectively. The main discrepancy in survivorship values for sharks age 1+ between the 2002 SEW and the present estimates thus corresponds to blacktip sharks in the Gulf of Mexico, which would experience lower survivorship than predicted in the 2002 SEW.

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Table 1. Life history parameter values used to estimate natural mortality of sandbar and blacktip sharks.

Species	Age and growth					Length-weight relationship		Length to length relationship
	L_{inf}	K	t_0	t_{mat}	t_{max}	a	b	
Sandbar	263 (cm TL)	0.086	-3.9	15.5	30	0.000010885	3.0124	FL=0.8175*TL+2.5675
Blacktip (GOM)	141.6 (cm FL)	0.240	-2.18	5.7	12.5	0.00001	3.0549	
Blacktip (SA)	158.5 (cm FL)	0.16	-3.43	6.7	15.5	2.512E-09	3.1253	FL (mm)=0.8301*TL-29.0042

Table 2. Estimates of annual survival for sandbar shark obtained with eleven different methods.

Age x	Length	Weight	P&W (wet weight)	P&W (dry weight)	Hoenig	Pauly	Chen & Watanabe	Jensen (tmat)	Jensen (K)	Rikhter& Efanov (tmat)	(weight) Lorenzen	(length) Lorenzen	Ave Surv at age	Pred. Surv at age
0	65	1.973	0.75	0.68	0.87	0.85	0.74	0.90	0.88	0.95	0.69	0.69	0.79	0.79
1	90	5.143	0.80	0.74	0.87	0.85	0.78	0.90	0.88	0.95	0.76	0.77	0.83	0.80
2	105	7.875	0.82	0.76	0.87	0.85	0.81	0.90	0.88	0.95	0.79	0.80	0.84	0.80
3	118	11.111	0.83	0.78	0.87	0.85	0.83	0.90	0.88	0.95	0.81	0.82	0.85	0.81
4	130	14.768	0.84	0.79	0.87	0.85	0.84	0.90	0.88	0.95	0.82	0.83	0.86	0.81
5	141	18.763	0.85	0.80	0.87	0.85	0.85	0.90	0.88	0.95	0.83	0.85	0.86	0.82
6	151	23.011	0.86	0.81	0.87	0.85	0.86	0.90	0.88	0.95	0.84	0.85	0.87	0.82
7	160	27.435	0.86	0.82	0.87	0.85	0.87	0.90	0.88	0.95	0.85	0.86	0.87	0.83
8	168	31.964	0.87	0.82	0.87	0.85	0.87	0.90	0.88	0.95	0.86	0.87	0.87	0.83
9	176	36.537	0.87	0.83	0.87	0.85	0.88	0.90	0.88	0.95	0.86	0.87	0.87	0.84
10	183	41.099	0.87	0.83	0.87	0.85	0.88	0.90	0.88	0.95	0.87	0.88	0.88	0.84
11	190	45.607	0.88	0.84	0.87	0.85	0.89	0.90	0.88	0.95	0.87	0.88	0.88	0.85
12	196	50.023	0.88	0.84	0.87	0.85	0.90	0.90	0.88	0.95	0.87	0.89	0.88	0.85
13	202	54.319	0.88	0.84	0.87	0.85	0.90	0.90	0.88	0.95	0.88	0.89	0.88	0.85
14	207	58.471	0.88	0.85	0.87	0.85	0.90	0.90	0.88	0.95	0.88	0.89	0.88	0.86
15	211	62.464	0.89	0.85	0.87	0.85	0.90	0.90	0.88	0.95	0.88	0.89	0.88	0.86
16	215	66.283	0.89	0.85	0.87	0.85	0.90	0.90	0.88	0.95	0.88	0.90	0.89	0.86
17	219	69.923	0.89	0.85	0.87	0.85	0.90	0.90	0.88	0.95	0.88	0.90	0.89	0.87
18	223	73.378	0.89	0.85	0.87	0.85	0.90	0.90	0.88	0.95	0.89	0.90	0.89	0.87
19	226	76.647	0.89	0.86	0.87	0.85	0.90	0.90	0.88	0.95	0.89	0.90	0.89	0.87
20	229	79.731	0.89	0.86	0.87	0.85	0.90	0.90	0.88	0.95	0.89	0.90	0.89	0.88
21	232	82.633	0.89	0.86	0.87	0.85	0.90	0.90	0.88	0.95	0.89	0.90	0.89	0.88
22	235	85.356	0.89	0.86	0.87	0.85	0.90	0.90	0.88	0.95	0.89	0.90	0.89	0.88
23	237	87.908	0.89	0.86	0.87	0.85	0.90	0.90	0.88	0.95	0.89	0.90	0.89	0.89
24	239	90.294	0.90	0.86	0.87	0.85	0.90	0.90	0.88	0.95	0.89	0.91	0.89	0.89
25	241	92.521	0.90	0.86	0.87	0.85	0.90	0.90	0.88	0.95	0.89	0.91	0.89	0.89
26	243	94.596	0.90	0.86	0.87	0.85	0.90	0.90	0.88	0.95	0.89	0.91	0.89	0.90
27	245	96.527	0.90	0.86	0.87	0.85	0.90	0.90	0.88	0.95	0.89	0.91	0.89	0.90
28	246	98.323	0.90	0.86	0.87	0.85	0.90	0.90	0.88	0.95	0.90	0.91	0.89	0.90
29	247	99.990	0.90	0.86	0.87	0.85	0.90	0.90	0.88	0.95	0.90	0.91	0.89	0.90
30	249	101.536	0.90	0.86	0.87	0.85	0.90	0.90	0.88	0.95	0.90	0.91	0.89	0.91

Table 3. Estimates of annual survival for blacktip shark in the Gulf of Mexico obtained with eleven different methods.

Age x	Length	Weight	P&W (wet weight)	P&W (dry weight)	Hoenig	Pauly	Chen & Watanabe	Jensen (tmat)	Jensen (K)	Rikhter& Efanov (tmat)	(weight) Lorenzen	(length) Lorenzen	Ave Surv at age	Pred. Surv at age
0	58	2.398	0.76	0.69	0.71	0.68	0.55	0.75	0.70	0.76	0.71	0.71	0.70	0.70
1	76	5.477	0.80	0.74	0.71	0.68	0.64	0.75	0.70	0.76	0.77	0.77	0.73	0.71
2	90	9.230	0.82	0.77	0.71	0.68	0.68	0.75	0.70	0.76	0.80	0.80	0.75	0.72
3	101	13.176	0.84	0.78	0.71	0.68	0.75	0.75	0.70	0.76	0.82	0.82	0.75	0.72
4	109	16.976	0.85	0.80	0.71	0.68	0.75	0.75	0.70	0.76	0.83	0.83	0.76	0.73
5	116	20.437	0.85	0.80	0.71	0.68	0.75	0.75	0.70	0.76	0.84	0.84	0.77	0.74
6	122	23.472	0.86	0.81	0.71	0.68	0.75	0.75	0.70	0.76	0.84	0.85	0.77	0.75
7	126	26.062	0.86	0.82	0.71	0.68	0.75	0.75	0.70	0.76	0.85	0.85	0.77	0.75
8	129	28.229	0.86	0.82	0.71	0.68	0.75	0.75	0.70	0.76	0.85	0.86	0.77	0.76
9	132	30.017	0.86	0.82	0.71	0.68	0.75	0.75	0.70	0.76	0.85	0.86	0.77	0.77
10	134	31.475	0.87	0.82	0.71	0.68	0.75	0.75	0.70	0.76	0.85	0.86	0.77	0.77
11	136	32.655	0.87	0.82	0.71	0.68	0.75	0.75	0.70	0.76	0.86	0.86	0.78	0.78
12	137	33.604	0.87	0.83	0.71	0.68	0.75	0.75	0.70	0.76	0.86	0.87	0.78	0.79
13	138	34.364	0.87	0.83	0.71	0.68	0.75	0.75	0.70	0.76	0.86	0.87	0.78	0.79

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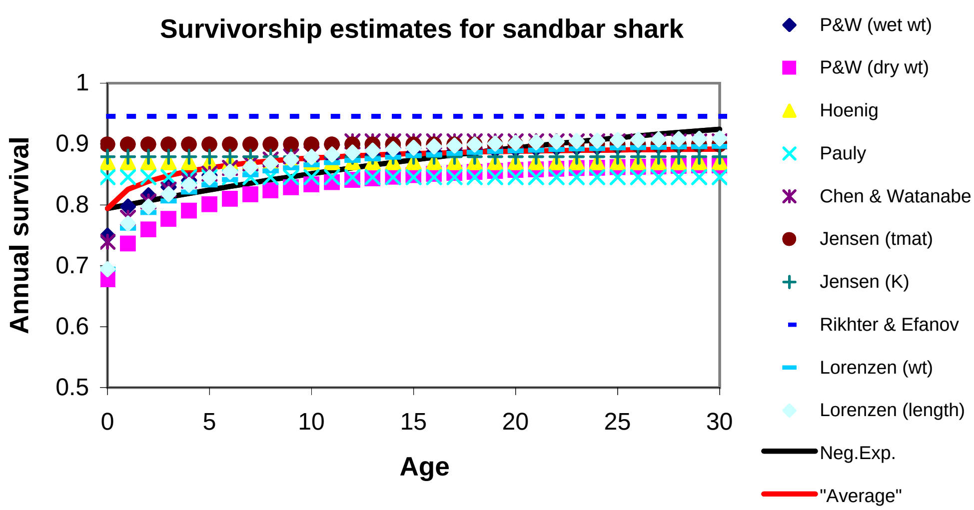
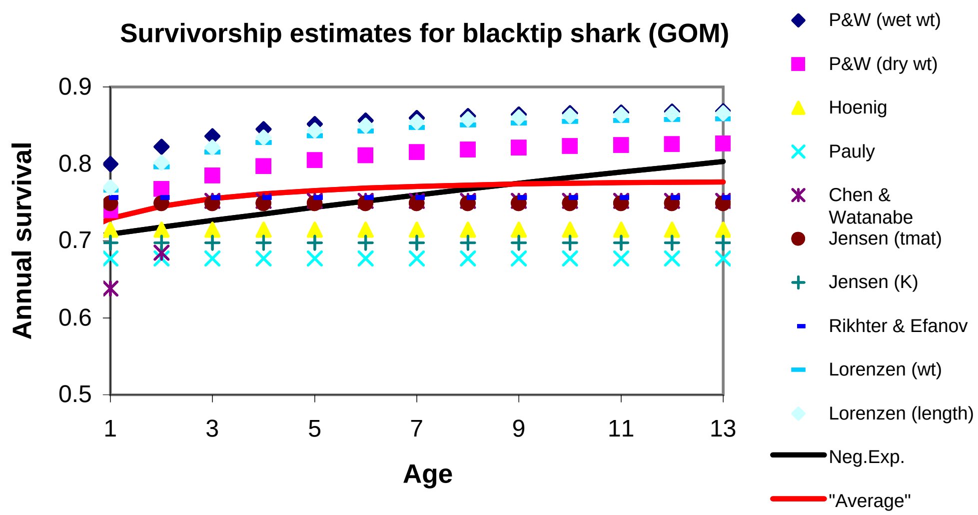
Table 4. Estimates of annual survival for blacktip shark in the U.S. South Atlantic obtained with eleven different methods.

Age x	Length	Weight	P&W (wet weight)	P&W (dry weight)	Hoenig	Pauly	Chen & Watanabe	Jensen (tmat)	Jensen (K)	Rikhter& Efanov (tmat)	(weight) Lorenzen	(length) Lorenzen	Ave Surv at age	Pred. Surv at age
0	67	3.480	0.78	0.71	0.76	0.75	0.68	0.78	0.79	0.79	0.74	0.74	0.75	0.75
1	80	6.053	0.80	0.75	0.76	0.75	0.73	0.78	0.79	0.79	0.77	0.77	0.77	0.76
2	92	9.075	0.82	0.77	0.76	0.75	0.76	0.78	0.79	0.79	0.80	0.80	0.78	0.76
3	102	12.348	0.83	0.78	0.76	0.75	0.82	0.78	0.79	0.79	0.81	0.82	0.79	0.77
4	110	15.705	0.84	0.79	0.76	0.75	0.82	0.78	0.79	0.79	0.82	0.83	0.80	0.77
5	117	19.014	0.85	0.80	0.76	0.75	0.82	0.78	0.79	0.79	0.83	0.84	0.80	0.78
6	123	22.185	0.85	0.81	0.76	0.75	0.82	0.78	0.79	0.79	0.84	0.85	0.80	0.78
7	129	25.155	0.86	0.81	0.76	0.75	0.82	0.78	0.79	0.79	0.85	0.85	0.81	0.79
8	133	27.890	0.86	0.82	0.76	0.75	0.82	0.78	0.79	0.79	0.85	0.86	0.81	0.79
9	137	30.375	0.86	0.82	0.76	0.75	0.82	0.78	0.79	0.79	0.85	0.86	0.81	0.80
10	140	32.609	0.87	0.82	0.76	0.75	0.82	0.78	0.79	0.79	0.86	0.86	0.81	0.80
11	143	34.597	0.87	0.83	0.76	0.75	0.82	0.78	0.79	0.79	0.86	0.87	0.81	0.80
12	145	36.356	0.87	0.83	0.76	0.75	0.82	0.78	0.79	0.79	0.86	0.87	0.81	0.81
13	147	37.902	0.87	0.83	0.76	0.75	0.82	0.78	0.79	0.79	0.86	0.87	0.81	0.81
14	149	39.254	0.87	0.83	0.76	0.75	0.82	0.78	0.79	0.79	0.86	0.87	0.81	0.82
15	150	40.431	0.87	0.83	0.76	0.75	0.82	0.78	0.79	0.79	0.86	0.87	0.81	0.82
16	151	41.453	0.87	0.83	0.76	0.75	0.82	0.78	0.79	0.79	0.87	0.87	0.82	0.82





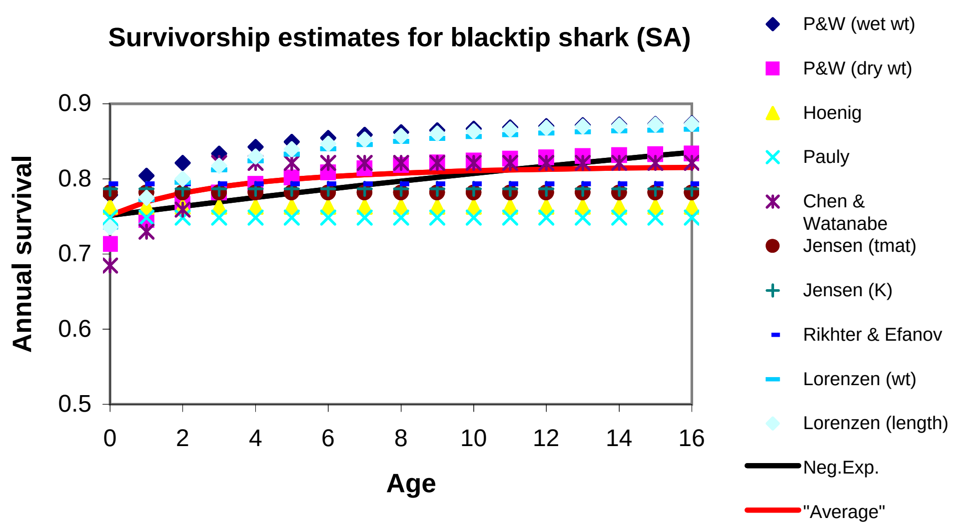


Figure 1. Estimates of annual survival ($S=e^{-M}$) for sandbar shark, blacktip shark in the Gulf of Mexico, and blacktip shark in the U.S. South Atlantic obtained with eleven different equations.

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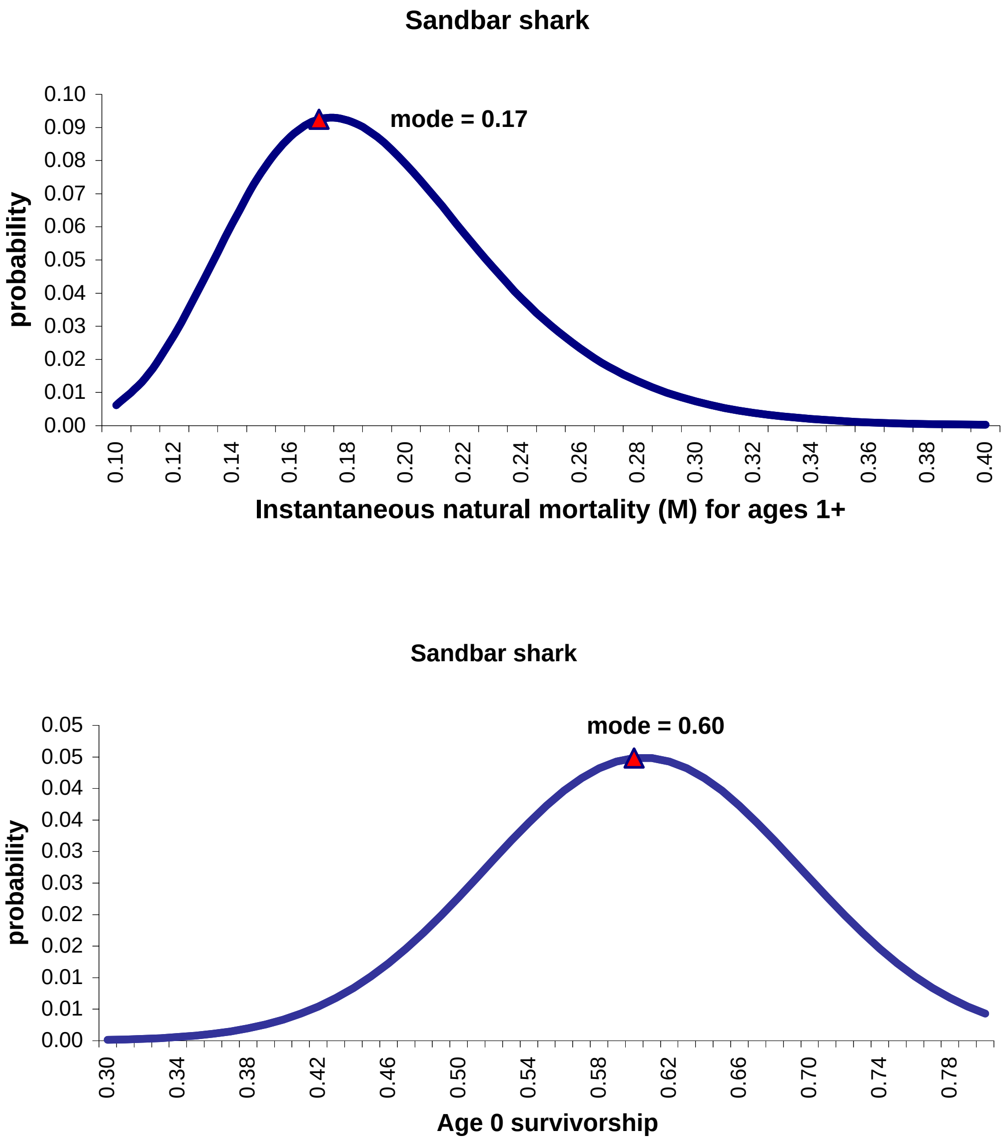
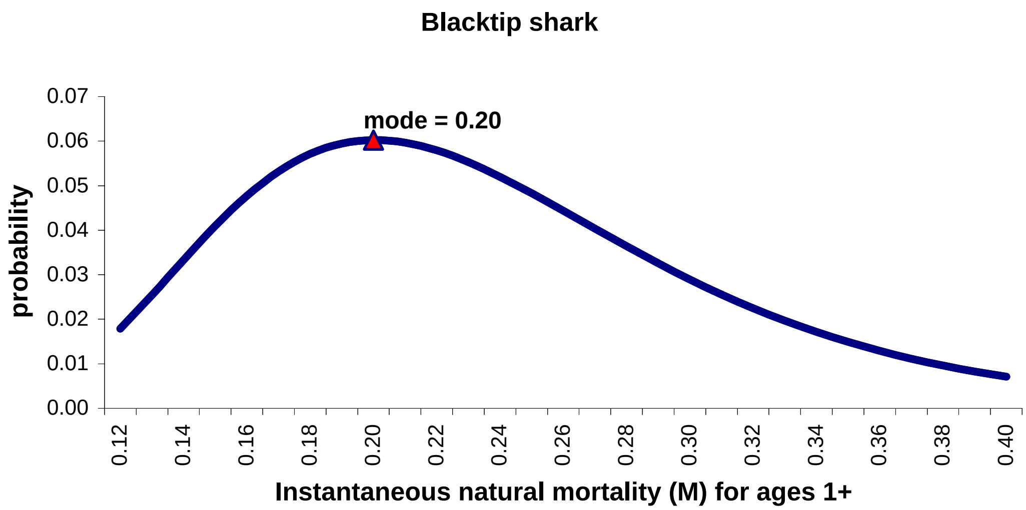


Figure 2. Lognormal pdf for natural mortality rate (ages 1 to maximum; top panel) and normal pdf for age-0 survival (bottom panel) for sandbar shark used as priors in the 2002 shark stock assessment. The probability for each prior was scaled to the interval defined by the lower and upper bounds, such that the area under each curve sums to 1.



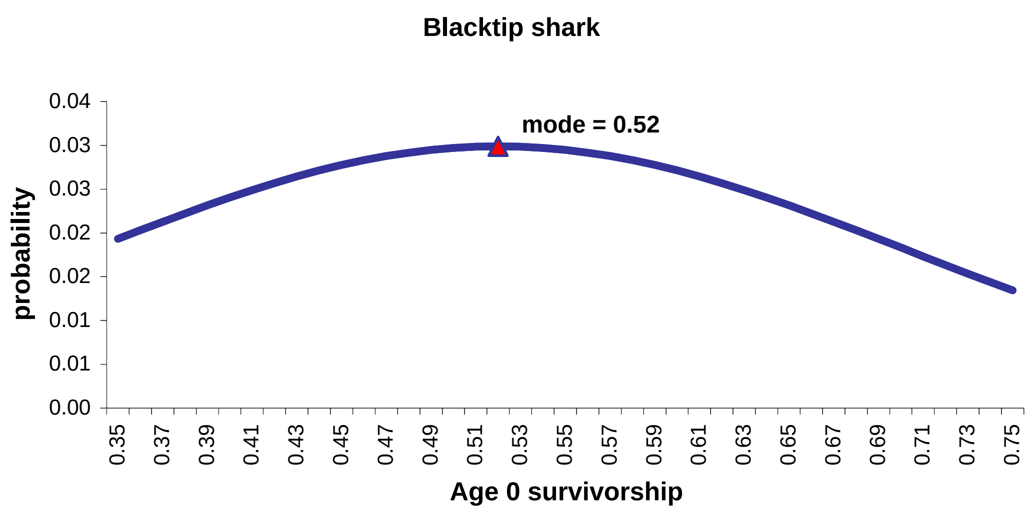


Figure 3. Lognormal pdf for natural mortality rate (ages 1 to maximum; top panel) and normal pdf for age-0 survival (bottom panel) for blacktip shark used as priors in the 2002 shark stock assessment. The probability for each prior was scaled to the interval defined by the lower and upper bounds, such that the area under each curve sums to 1.

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