Age and Sex Specific Natural Mortality of the Blue Shark (Prionace glauca) in the North Pacific Ocean[1]

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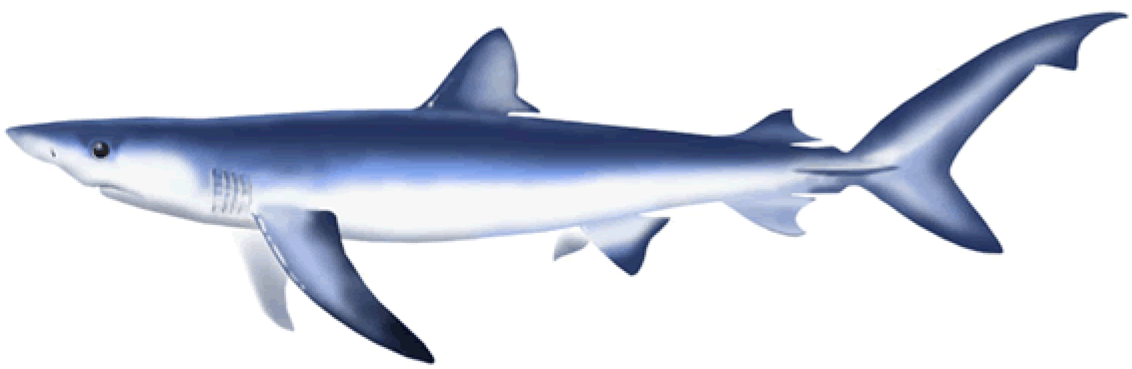

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Introduction

Biological parameters such as growth and natural mortality form the basis for the inputs for stock assessment models (Siegfried and Sanso 2013) and can be used to assess the vulnerability of the stock to fishing (Hilborn and Walters 1992). Some attempts have been made to combine gross estimates of biological change such as length or age over time, with catch data to get a rough estimate of trends in stock status (e.g. Clarke 2011). In the absence of good biological data, estimates derived from closely related populations or species can be used. However, these estimates may differ from reality and in order to encapsulate the uncertainty appropriately for use in a stock assessment, additional work is required (Cortes 2002).

This work was motivated by a desire for age and sex specific natural mortality estimates for a length based integrated stock assessment model. The ISC Shark working group (SWG) recognized the potential to develop age and sex-specific natural mortality estimates for blue shark (*Prionace glauca*) in the north Pacific Ocean based on published literature and documents submitted to the SWG. This paper documents the methods and results.

Sex specific mortality-at-age for north Pacific blue shark are estimated based on length-at-age from two different sources in the Pacific. Hsu et al. (2011) and Nakano (1994) both aged blue shark vertebrae from samples collected in the north Pacific.

Materials and Methods

Age and growth parameters from two ageing studies (Hsu et al. 2011; and Nakano 1994) for blue sharks in the north Pacific Ocean using vertebral counts were used to provide the length-at-age estimates. Length-at-age was converted to weight-at-age (g) using the length (PCL) weight relationship of Nakano (1994) (Table 1).

Natural mortality-at-age was estimated using two methods

1) Peterson and Wroblewski (1984) who estimated M-at age using:

$$M_t = 1.92{W_t}^{-0.25}$$

where W_t is weight (g)-at-age.

2) Chen and Watanabe (1986) who estimated M-at age using the von Bertalanffy parameters t_0 and K:

$$M_t = \frac{K}{\left[1-e^{-K(t-t_0)}\right]} \qquad t \leq t_M$$

$$M_t = \frac{K}{a_0 + a_1(t - t_M) + a_2 x (t - t_M)^2}, \qquad t \geq t_M$$

$$\begin{cases} a_0 = 1 - e^{-k(t_M - t_0)} \\ a_1 = ke^{-(t_M - t_0)} \\ a_2 = -\frac{1}{2}K^2 e^{-k(} t_M - t_0) \end{cases}$$

And

$$t_M = -\frac{1}{k}\ln\left|1 - e^{-kt_0}\right| + t_0$$

Where t is age, k, growth coefficient, and t_0 is an adjustment parameter in von Bertalanffy's growth equation.

The average mortality over life of fish was estimated using 3 different methods:

1) Hoenig (1983) who determined that M could be estimated as follows:

$\ln Z = 1.46 - 1.01 * \ln(t_{max})$

where t_{max} is the maximum age of the fish, and if approximately 5% of the population is still alive at the maximum age. Simpfendorfer et al. (2005) recommend to use the teleost relationship for estimating the t_{max} for sharks.

2) Hewett and Hoenig (2005) who determined that M could be estimated as follows:

$$M \approx \frac{4.22}{t_{max}}$$

t_{max} is the maximum age observed in the stock (Hewett and Hoenig 2005).

3) Jensen (1996) who estimated M using the von Bertalanffy parameter K:

$$M = 1.5K$$

For t_{max} in Hoenig (1983) and Hewett and Hownig (2005), the following equation (Cailliet et al., 1992) was used for the estimation;

$t_{max} = 5(\ln 2)/k$.

Results

The growth curves of from Hsu et al. (2011); and Nakano (1994) showed that male and female growth differed but the sex-specific growth curves from these two studies were broadly similar (Figure 1).

Due to the similarity in sex specific growth from the two data sets used, the resultant age-specific mortality estimates were broadly similar (Figure 2 and 3). However, the age-specific M values estimated from Chen and Watanabe (1986) (Figure 2) were substantially different from those estimated using the Peterson and Wroblewski (1984) (Figure 3), which by design estimates an increasing M-at-age starting at the age of sexual maturity, a feature thought to be unlikely given blue shark life history.

M-at-age estimated using Chen and Watanabe (1986) ranged from 1.39 to 0.7 for males and 0.86 to 1.25 for females at age 0. M stabilised at approximately 0.22 from ages 6 to 13 after which M-at-age began to diverge for males and females and for weight-at-age derived from Hsu et al. (2011) and Nakano (1994).

Using Peterson and Wroblewski (1984) sex specific M-at-age was almost identical for fish aged by Hsu et al. (2011) and Nakano (1994) and for both datasets declined rapidly from a high of 0.3 and 0.25 (Nakano and Hsu respectively) at age 1 to approximately 0.14 for both sexes by age 5, thereafter M declined slowly over the lifetime of the fish to approximate 0.1 for fish aged 12 and below 0.1 for older fish.

Theoretical maximum age of blue shark was estimated as 26.9 (Nakano 1994) and 28.6 (Hsu *et al*. 2011) for males and 24.1 (Nakano 1994) and 20.1 (Hsu *et al*. 2011) for females (Table 3).

The average M over life of fish estimated using the three methods are presented in Table 4. The sex-specific values estimated using Hoenig (1983) and Hewett and Hoenig (2005) were similar within sexes and slightly higher for females than for males for both models. For these two methods the average M over life of fish ranged from 0.15 to 0.16 for males and 0.17 to 0.21 for females. Estimates of M derived using the Jensen (1996) method were higher for females than for males and in all cases higher than the estimates derived using Hoenig (1983) and Hewett and Hoenig (2005).

Discussion

Two independent sources of length-at-age data (Hsu et al. (2011) and Nakano (1994)) for Pacific blue shark were used in this study. Both provide similar estimates of the length-at-age for this species despite there been only slight overlap between the sample sites of the two species. As blue sharks are highly migratory with the ability to rapidly cover ocean basins (Holdsworth 2003), this similarity in growth from different parts of the Pacific is not unexpected and provided some confidence in the results from these studies.

The M-at-age estimates obtained from the Chen and Watanabe (1986) method were high in the early and late life stages of the fish and were particularly unrealistic after age 20 in female for Hsu et al. (2011). Long lived elasmobranchs are expected to have a relatively low M particularly once they reach larger sizes. Given the very high values obtained from the Chen and Watanabe (1986) method and unlikely mortality profile over the life time of the fish this is unlikely to approximate reality for an elasmobranch and as such was disregarded.

The methods derived by Peterson and Wroblewski (1984) provided more realistic values of M-at-age where mortality was relatively high for young fish but stabilized at around 0.1 from about the age-at-50% maturity. This result was considered to be biologically plausible, and is the best available estimate at present, but further study is necessary for the estimation of accurate age-specific M.

The average M over the lifetime of the fish was assessed using three different methods (Table 3). The Jensen (1996) estimate was the highest of these three methods, and higher than the average of the estimates derived by the Peterson and Wroblewski (1984) method over the sex and study specific maximum ages (Table 2). These were considered high and were rejected. The remaining two methods (Hoenig (1983) and Hewett and Hoenig (2005)) provided similar results and as expected they approximate the average over all years (0.131 & 0.150 male and female Nakano; 0.118 & 0.138 for males and females Hsu) for the Peterson and Wroblewski (1984) results.

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Table 1: Biological parameters of blue shark (*Prionace glauca*) in the north Pacific Ocean used in this study and other studies from order Oceans.

Parameter	**Value**	**Region**	**Reference**
Length at birth	40 cm FL	North Pacific	Joung, Hsu, Liu and Wu 2011
	34-48 CM TL		Strasburg 1958
	36 PCL	North Pacific	Nakano 1994
	35-60 (units unknown)	North Pacific	Nakano & Seti 2002
	40-50 (units unknown)	Global	Wallace et al. 2006
	45 cm FL	North Atlantic	Pratt (1979)
Length at 50% maturity	M: 185 cm TL	North Pacific	Joung, Hsu, Liu and Wu 2011
	F: 193 cm TL	North Pacific	Joung, Hsu, Liu and Wu 2011
	M: 150-155 cm PCL	North Pacific	Nakano et al. 1985
	F: 159 cm PCL	North Pacific	Nakano et al. 1985
	220 cm TL	North Atlantic	Pratt (1979)
	M: 140 to 160 cm PCL (186 to 212 cm TL)	North Pacific	Nakano 1994
	F: 140 to 160 cm PCL (186 to 212 cm TL)		
Maximum length	M: 320 cm, 396 cm TL	North Atlantic	Bigelow & Schroeder 1948
	380 cm TL	North Pacific	Hart 1988
	F: 287 cm	North Atlantic	Skomal & Natanson 2003
Age at 50% maturity	M: 4-6 years	North Pacific	Nakano 1994
	F: 5-7 years	North Pacific	Nakano 1994
	M: 4-5	North Atlantic	Skomal & Natanson 2003
	F: 5 years	North Atlantic	Skomal & Natanson 2003
	6-7 years	North Pacific	Cailliet & Bedford 1983
Longevity	M: 16 years	North Atlantic	Skomal & Natanson 2003
	F: 15 years	North Atlantic	Skomal & Natanson 2003
	M: 16 years	North Pacific	Blanco-Parra et al. 2008
	F: 12	North Pacific	Blanco-Parra et al. 2008
Length conversions	FL=0.8313*TL+1.39	North Atlantic	Kohler et al. 1995
	PCL=0.9075*FL-0.3956	North Atlantic	Kohler et al. 1995
	PCL=0.762*TL-2.505	North Pacific	Nakano et al. 1985
	FL=0.829*TL-1.122	North Pacific	NOAA SWFSC
	FL=2.746*AL+11.803	North Pacific	NOAA SWFSC
	TL=0.286*AL-2.474	North Pacific	NOAA SWFSC
Reproduction	Placental viviparity		
Litter size	2-52 (mean=25.2)	North Pacific	Joung, Hsu, Liu and Wu 2011
	41	North Atlantic	Bigelow & Schroeder 1948

	25-50	Global	Wallace et al. 2006
	25-30 average (range 1-54)	North Pacific	Suda 1953, Nakano et al. 1985
Gestation	9-12 months	North Pacific & Atlantic	Cailliet & Bedford 1983, Pratt 1979
Breeding frequency	2 years	North Pacific	Joung, Hsu, Liu and Wu 2011
	1-2 years		
Sex ratio at birth	1 to 1	North Pacific	Nakano et al. 1985, Nakano 1994, Nakano & Seki 2002
Length-weight	All: $Wt(kg)=2.57 \times 10^{-5}\ TL^{3.05}$	North Pacific	Harvey 1989
	M: $Wt(kg)=3.838 \times 10^{-6}\ TL^{3.174}$	North Pacific	Nakano et al. 1985
	F: $Wt(kg)=2.328 \times 10^{-6}\ PL^{3.294}$	North Pacific	Nakano et al. 1985
	M: $Wt(kg)=3.293 \times 10^{-6}\ PL^{3.225}$	North Pacific	Nakano 1994
	F: $Wt(kg)=5.388 \times 10^{-6}\ PL^{3.102}$	North Pacific	Nakano 1994
	All: $Wt(kg)=5.009 \times 10^{-6}\ FL^{3.054}$	North Pacific	NOAA SWFSC Juvy Survey
	All: $Wt(kg)=1 \times 10^{-6}\ FL^{3.23}$	North Pacific	Joung, Hsu, Liu and Wu 2011
Growth models (VB)	VB model: $L_t= L_\infty[1-e^{-K(t-to)}]$		
	M: $TL_t= 295.3[1-e^{-0.175(t+1.113)}]$	North Pacific	Cailliet & Bedford 1983
	F: $TL_t= 241.9[1-e^{-0.251(t+0.795)}]$	North Pacific	Cailliet & Bedford 1983
	M: $PCL_t= 308.2[1-e^{-0.094(t+0.993)}]$	North Pacific	Tanaka 1984
	F: $PCL_t= 256.1[1-e^{-0.116(t+0.1.306)}]$	North Pacific	Tanaka 1984
	M: $PCL_t= 289.7[1-e^{-0.129(t+0.756)}]$	North Pacific	Nakano 1994
	F: $PCL_t= 243.3[1-e^{-0.144(t+0.849)}]$	North Pacific	Nakano 1994
	All: $FL_t =285.4[1-e^{-0.17(t+1.41)}]$	North Atlantic	Skomal & Natanson 2003
	M: $FL_t= 282.3[1-e^{-0.18(t+1.35)}]$	North Atlantic	Skomal & Natanson 2003
	F: $FL_t= 286.8[1-e^{-0.16(t+1.56)}]$	North Atlantic	Skomal & Natanson 2003
	M: $TL_t= 375.8[1-e^{-0.121(t+1.554)}]$	North Pacific	Hsu et al. 2011
	F: $TL_t= 317.4[1-e^{-0.172(t+1.123)}]$	North Pacific	Hsu et al. 2011
	M: $TL_t=299.8[1-e^{-0.10(t+2.44)}]$	NEPO (Mexico)	Blanco-Parra et al. 2008
	F: $TL_t=237.5[1-e^{-0.15(t+2.15)}]$	NEPO (Mexico)	Blanco-Parra et al. 2008
	CS: $TL_t=303.4[1^{-e^{-0.10(t+2.68)}}]$	NEPO (Mexico)	Blanco-Parra et al. 2008

Table 2. Age and sex specific natural mortality estimates (from Peterson and Wroblewski 1984).

	Nakano		Hsu	
Age	Male	Female	Male	Female
0	0.551	0.535	0.359	0.366
1	0.301	0.309	0.245	0.245
2	0.223	0.233	0.195	0.195
3	0.183	0.194	0.166	0.168
4	0.16	0.171	0.147	0.151
5	0.144	0.155	0.134	0.139
6	0.133	0.144	0.125	0.13
7	0.125	0.135	0.118	0.124
8	0.118	0.129	0.112	0.119
9	0.113	0.124	0.108	0.115
10	0.109	0.12	0.104	0.112
11	0.106	0.117	0.101	0.11
12	0.103	0.114	0.099	0.108
13	0.101	0.112	0.097	0.106
14	0.099	0.11	0.095	0.105
15	0.097	0.109	0.094	0.104
16	0.096	0.107	0.092	0.103
17	0.095	0.106	0.091	0.102
18	0.094	0.105	0.09	0.102
19	0.093	0.105	0.09	0.101
20	0.092	0.104	0.089	0.101
21	0.092	0.103	0.088	0.1
22	0.091	0.103	0.088	0.1
23	0.091	0.103	0.087	0.1
24	0.09	0.102	0.087	0.099
25	0.09	0.102	0.087	0.099
26	0.09	0.102	0.086	0.099
27	0.089	0.101	0.086	0.099
28	0.089	0.101	0.086	0.099
29	0.089	0.101	0.086	0.099
30	0.089	0.101	0.085	0.099

Table 3: Maximum age of blue shark (*Prionace glauca*) in the north Pacific Ocean estimated from t_{max} = 5(ln2)/k (Cailliet et al., 1992).

	Nakano (1994)	Hsu et al. (2011)
Male	26.866	28.642
Female	24.068	20.150

Table 4: Sex-specific population mortality estimates of blue shark (*Prionace glauca*) in the north Pacific based on the biological parameters presented in Hsu et al. (2011); and Nakano (1994), calculated using three different methods Hoening (1983), Hewett and Hoening (2005) and Jensen (1996).

	Nakano (1994)		Hsu et al. (2011)	
	Male	Female	Male	Female
Hoenig (1983)	0.155	0.173	0.145	0.207
Hewitt and Hoenig (2005)	0.157	0.175	0.147	0.209
Jensen (1996)	0.194	0.216	0.192	0.246

Figures

Figure 1: Sex specific length-at-age for north Pacific blue shark (*Prionace glauca*) from Hsu et al. (2011) and Nakano (1994).

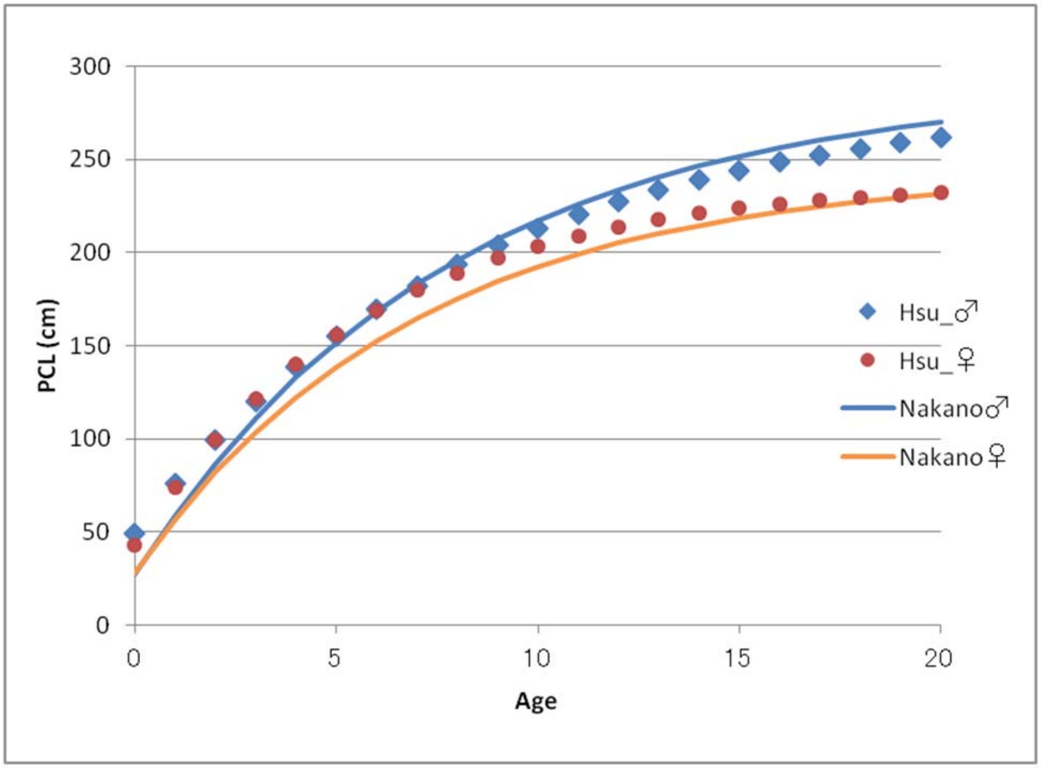

Figure 2: Age specific mortality estimates for north Pacific blue shark (*Prionace glauca*) derived from length-at-age estimates from Hsu et al. (2011) and Nakano (1994) calculated using Peterson and Wroblewski (1984).

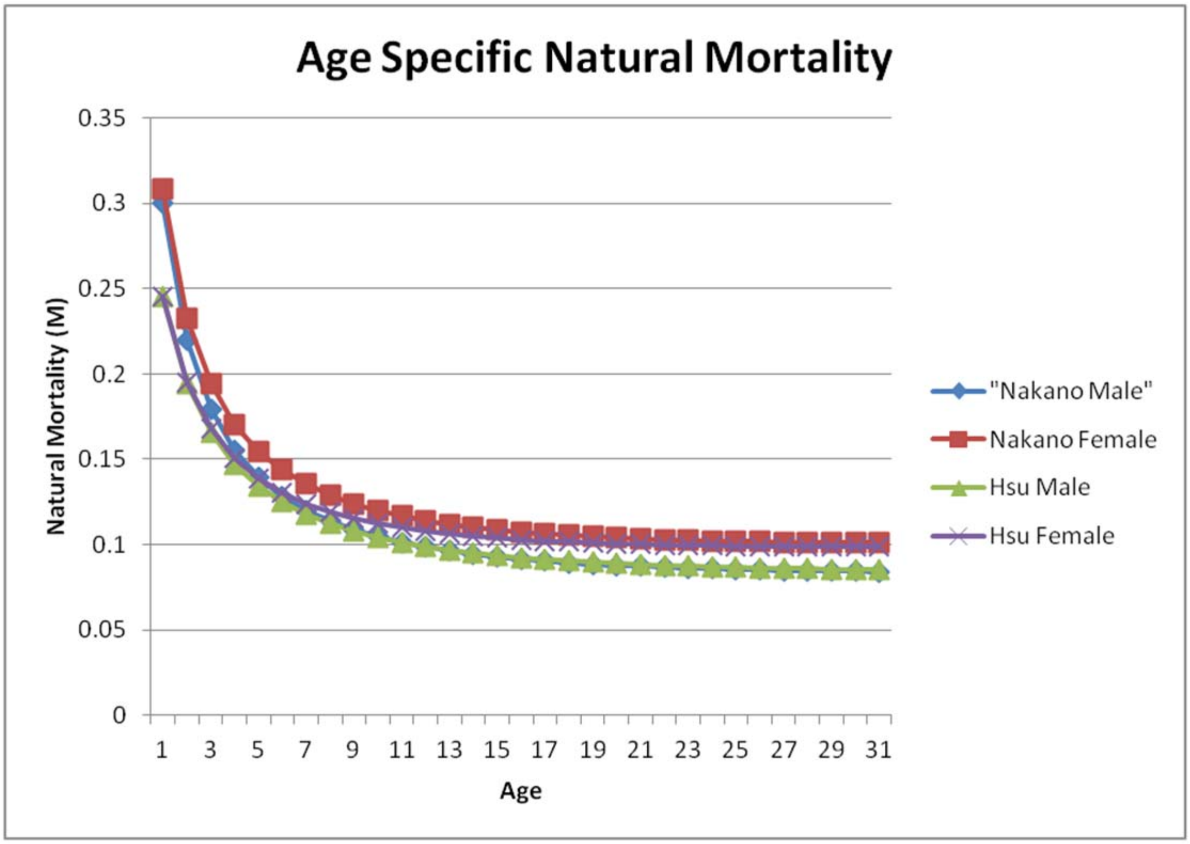

Figure 3: Age specific mortality estimates for north Pacific blue shark (*Prionace glauca*) derived from length-at-age estimates from Hsu et al. (2011) and Nakano (1994) calculated using Chen and Watanabe (1989).