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Update of Age and sex specific Natural mortality of the blue shark (*Prionace glauca*) in the North Pacific Ocean

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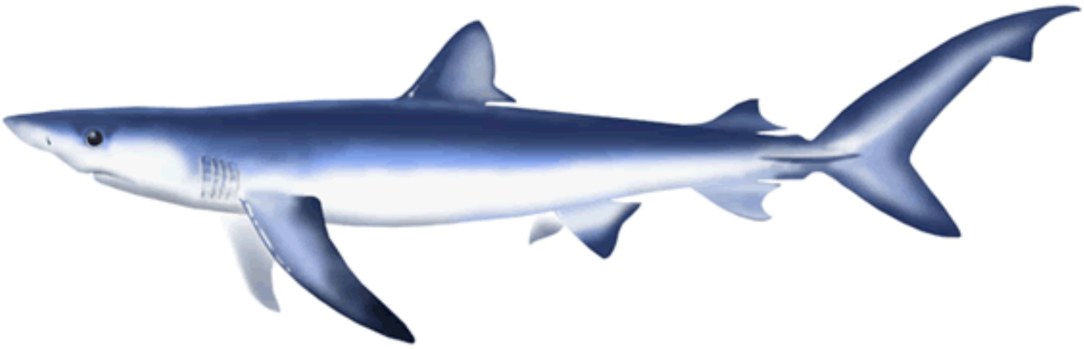

Introduction

In the last stock assessment of blue shark (*Prionace glauca*) in the North Pacific, age and sex-specific natural mortality (indicated as "M" hereafter) of this stock was used as the input data for Stock Synthesis model (Rice et al. 2014). In Rice and Semba (2014), the estimator by Peterson and Wroblewski (1984) and Chen and Watanabe (1986) and the growth equation by Nakano (1994) and Hsu et al. (2011) were used. The estimator of M applied is divided into weight-based (Peterson and Wroblewski 1984) and age-based (Chen and Watanabe 1986). The age and sex-specific M based on the former estimator was adopted in the stock assessment with the assumption of maximum age of 30. However, in the calculation by Rice and Semba (2014), the coefficient assigned for the dry weight (1.92) was mistakenly applied to wet weight of North Pacific blue shark, instead of that for the wet weight (1.28), which needs to be corrected in the upcoming stock assessment.

While the weight-based estimator has been widely applied in the stock assessment of fishery resources, the effect of variance of weight among individual is suggested to be large compared to that of body length. For example, large difference in weight would be expected between pregnant female and adult male with same age. In this context, we show the age and sex-specific M based on the length-based method used in the stock assessment of Atlantic yellowfin tuna (*Thunnus albacares*) this year (Method 2 in Walter et al. 2016) as well as the modified M by Peterson and Wroblewski (1984). In addition, we calculated the age and sex-specific M based on another estimators included in the review by Kenchington (2014) for comparison. Regarding growth curve necessary for the estimation of M, von Bertalanffy growth curve (VBGC) by Nakano (1994) and Hsu et al. (2011) are used for the sake of consistency with the past estimates. In addition, the estimates based on VBGC by Fujinami et al. (2016) is also indicated for reference.

Methods

Basic equation

We show several equations necessary to estimate of natural mortality-at-age, below (i.e. growth curve, weight-length relationship, conversion equation between total length (TL) and precaudal length (PCL)). The parameter of VBGC (eq. 1) for each sex from Nakano (1994), Hsu et al. (2011), and Fujinami et al. (2016) is indicated below.

Growth curve (von Bertalanffy (1938))

$$L_t\ (cm) = L_\infty(1 - \exp(-K(t - t_0)) \qquad (1)$$

1. Nakano (1994)

$$PCL: L_\infty = 289.7, K = 0.129, t_0 = -0.756 \quad Male$$

$$PCL: L_\infty = 243.3, K = 0.144, t_0 = -0.849 \quad Female$$

2. Hsu et al. (2011)

$$TL: L_\infty = 375.8, K = 0.121, t_0 = -1.554 \ \ Male$$

$$TL: L_\infty = 317.4, K = 0.172, t_0 = -1.123 \ \ Female$$

3. Fujinami et al. (2016)

$$PCL: L_\infty = 284.8, K = 0.117, t_0 = -1.34 \ \ Male$$

$$PCL: L_\infty = 256.3, K = 0.147, t_0 = -0.97 \ \ Female$$

,where L_t, L_∞, K and t_0 denote body length at age t, asymptotic length, von Bertalanffy growth coefficient and theoretical age at which the organism was 0 length, respectively.

Body length used Nakano (1994) and Fujinami et al. (2016) is PCL, while that used in Hsu et al. (2011) is TL. For unifying the body length, TL and PCL was converted using the conversion equation (eq. 2a, b) below;

Length (PCL)-length (TL) (Nakano 1985)

$$PCL\ (cm) = 0.762 * TL(cm) - 0.2505 \qquad (2a)$$

$$TL\ (cm) = (PCL + 0.2505)/0.762 \qquad (2b)$$

Sex-specific conversion equation between wet body weight (kg) and PCL (eq. 3) was cited from Nakano (1994) as follows;

Wet weight (kg)-body length(PCL) relationship (Nakano 1994)

$$W\ (kg) = 5.388 * 10^{-6}\ PCL^{3.102}\ (cm)\ \ Male \qquad (3a)$$

$$W\ (kg) = 3.293 * 10^{-6}\ PCL^{3.225}\ (cm)\ Female \qquad (3b)$$

,where W is body weight.

Mortality estimator

As empirical and theoretical estimator for age specific M commonly used, we focused on the method by Lorenzen (1996), Gislason et al. (2010) and Charnov et al. (2013) as well as that by Peterson and Wroblewski (1984) and Chen and Watanabe (1989). Regarding Peterson and Wroblewski (1984), the previous study used the dry weight (eq. 4), but this study used the wet weight (eq. 5).

1. Peterson and Wroblewski (1984)

$$M\ (year^{-1}) = 1.92 * W^{-0.25}\ (g)\ \ Dry\ weights \qquad (4)$$

$$M\ (year^{-1}) = 1.28 * W^{-0.25}\ (g)\ \ Wet\ weights \qquad (5)$$

2. Chen and Watanabe (1989)

$$M\ (year^{-1}) = \begin{cases} \dfrac{K}{1 - e^{-K(t-t_0)}} & (t \leq t_M) \\ \dfrac{K}{1 - e^{-K(t_M-t_0)} + (t - t_M)Ke^{-K(t_M-t_0)} - 0.5 * (t - t_M)^2 K^2 e^{-K(t_M-t_0)}} & (t \geq t_M) \end{cases} \qquad (6)$$

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

, where t_M is age at end of reproductive span, i.e. age at the intersection of the stable and senescent growth phases.

3. Lorenzen (1996)

$$M\ (year^{-1}) = 3.00 * W^{-0.288}\ (g) \qquad (7)$$

4. Gislason et al. (2010)

$$M\ (year^{-1}) = 1.73 * TL^{-1.61}(cm) * L_{\infty}^{1.44} * K \qquad (8)$$

5. Charnov et al. (2012)

$$M\ (year^{-1}) = (TL\ (cm)/L_{\infty})^{-1.5} * K \qquad (9)$$

6. Method 2 in Walter et al. (2016)

$$M\ (year^{-1}) = \frac{M_T(t_{max} - t_c)}{\ln\left(\frac{l_c}{l_c + L_{\infty}\left(\exp\left(K(t_{max} - t_c)\right) - 1\right)}\right)} \ln\left(\frac{l_t}{l_t + L_{\infty}(\exp(K) - 1)}\right) \qquad (10)$$

, where M_T is Target M defined as the M as obtained from an external study (Walter et al. 2016) and t_c is the age at first full recruitment, l_c is the body length at t_c, l_t is body length at age t, and t_{max} is the maximum age. As the base case here, we set Target M as 0.23 (Campana et al. 2004), t_c as 0 (discussed later), t_{max} as 30 (Rice and Semba 2014, Rice et al. 2014). The concept of this method and derivation of equation (10) is described in Appendix 1.

Throughout all estimators, growth parameter (L_{∞}, K, t_0) were used from equation by Nakano (1994), Hsu et al. (2011), and Fujinami et al. (2016) indicated above.

Given the uncertainty associated with the interpretation of t_c, age and sex-specific M by six different t_c (0~5) was calculated for the growth curve by Nakano (1994) and Fujinami et al. (2016).

In addition, to check the effect of t_{max}, we also calculated age and sex-specific M by (1) six different t_c (0~5) assuming t_{max}=20 for the growth curve by Nakano (1994) and (2) three different t_{max} (20,24,30) for three VBGC (Nakano 1994, Hsu et al. 2011, Fujinami et al. 2016) assuming t_c=0 .

Results

Sex-specific growth curve based on Nakano (1994), Hsu et al. (2011) and Fujinami et al. (2016) indicated slight difference in growth rate between studies for female but almost same growth rate for male (Figure 1, Table 1).

The revised M based on Peterson and Wroblewski (1984) was lower than the past estimates in both sex and growth curve. This is reasonable considering that the corrected coefficient (1.28) is smaller than that used in the past report (1.92).

Estimates of age and sex-specific M based on growth curve by Nakano (1994) were indicated in Table 2 and Figure2. In both sexes, M at age 0 is the highest in the estimates based on Charnov et al. (2012) and the second highest in that by Gislason et al. (2010). In general, M by length-based estimators were higher than those by weight-based estimators, while M by Chen and Watanabe (1989) and Walter et al. (2016) were intermediate, especially before M reaches at plateau. M at age 0 declined most steeply from a high of 0.37~4.50 (male) and 0.36~3.65 (female) to approximately 0.20~1.40 (male) and 0.21~1.27 (female) at age 1. Thereafter M declined gradually for both sex by age at maturity to 0.10~0.34 (age 5 for male) and 0.09~0.29 (age 6 for female). Subsequently, M showed slow decrease over lifetime of the fish in almost all estimators and below 0.2 for both sexes after age 10.

Estimates of age and sex-specific M based on growth curve by Hsu et al. (2011) were indicated in Table 3 and Figure3. As with the previous result, M at age 0 is the highest in the estimates based on Charnov et al. (2012) and the second highest in that by Gislason et al. (2010) in both sexes, but the absolute value was smaller than those based on Nakano (1994)'s growth curve. Relative relationship between length-based and weight-based estimates were similar with the case in the growth curve by Nakano (1994). M at age 0 declined most steeply from a high of

0.23~1.70 (male) and 0.26~2.34 (female) to approximately 0.16~0.88 (male) and 0.17~1.02 (female) at age 1. Thereafter M declined gradually for both sex by age at maturity to 0.09~0.30 (age 5 for male) and 0.08~0.29 (age 6 for female). Subsequently, male M showed slow decrease and stabilized around 0.1 after age 20 in all estimators. Female M showed similar trend with males but estimates based on Chen and Watanabe (1989) showed increasing trend from 0.20 to 0.55 after age 20.

The effect of t_c in the method by Walter et al. (2016) was shown in Figure 4 and calculated value is indicated in Appendix 2. M with assumption of $t_c = 0$ is the lowest and that of t_c=5 is the highest of all estimate in both sexes. Especially, estimates with assumption of $t_c = 4$ and $t_c = 5$ was closely similar, while difference of t_c between 0 and 2 was moderate in both sexes.

If t_{max} changed from 30 to 20, M got smaller in every t_c for both sexes (Figure 5). The estimates for three different t_{max} for 3 VBGC with t_c=0 is shown in Appendix 3.

Discussion

Regardless of sex and growth curve used, estimates by Charnov et al. (2012) and Gislason et al. (2010) were much higher than other estimates. These are length-based estimates and also based on the regression between empirical value of M and length from variety of organism (e.g., sand eel, herring, and seahorse). Application of empirical value from taxa totally different from shark might affect this high M observed in early ages. Although empirical information on M at early ages in blue shark is lacking, M at age 0 by Charnov et al. (2012) and Gislason et al. (2010), indicating 1.7~4.5 in the former and 1.3~3.7 in the latter, would be unrealistic, given the empirical estimate of M at age 0 for bluefin tuna (1.6), yellowfin tuna (lower than 0.8 except for M in 21-30 cm folk length) and bigeye tuna (0.15 - 0.9 for size classes >40 cm folk length) (Hampton 2000, Mangel et al. 2010). Although M in later age was low and similar among estimators, unrealistically high M at earlier age might influence the result of stock assessment.

The moderate M observed in estimator of Chen and Watanabe (1989) and Walter et al. (2016) might because they are length-based method with theoretical approach (not affected by empirical value). Regarding Chen and Watanabe (1989), the high value obtained from after age 20 in female for Hsu et al. (2011) was suggested to be unlikely and disregarded in Rice and Semba (2014). Although increase of M due to senescence has been widely discussed, the degree of increase indicated here contain large uncertainly because long lived elasmobranchs are expected to have a relatively low M, particularly once they reach larger sizes (Rice and Semba 2014). Estimates by Walter et al. (2016) ranges from 0.7 and 1.0 depending on the growth curve used and do not show increasing trend observed in Chen and Watanabe (1989). Thus, within length-based estimator, method by Walter et al. (2016) may provide reasonable estimates of M.

Weight-based estimator provided relatively low M and revised estimates from Peterson and Wroblewski (1984) was the lowest of all estimates. Mean M across ages (i.e., constant M) from revised Peterson and Wroblewski (1984) and Lorenzen (1996) is 0.08-0.09 for Nakano (1994) and 0.08 for Hsu et al. (2011) in the former estimator and 0.14 for Nakano (1994) and 0.13 for Hsu et al. (2011) in the latter estimator, respectively. This is lower than constant M estimated for *Lamna nasus* (0.18, Aasen 1963), which seems unlikely given the life history parameter and fecundity of *L. nasus*. Given that estimator by Peterson and Wroblewski (1984) also relies upon the empirical value of M and weight for a wide variety of animals including chaetognatha and larval fish and most data consists of dry weight lighter than 1 kg, the application of this estimator might increase uncertainty on the M of blue shark.

In application of Walter's method, we set M_T as 0.23 and t_c as 0. RegardingM_T, we regarded that constant M from meta-analysis by Campana et al. (2004) would be reasonable because it covers various parameter of this species and several estimators of M. Although we did not check the target age/size for which each estimator in this meta-analysis covered, we selected t_c=0, given the situation that constant M has been applied to all ages in the stock assessment in practice. If the estimator included in this meta-analysis only cover adult or juvenile, our assumption (i.e., t_c=0) may affect the results. Considering the room for discussion on the value of t_c, arising from the original definition in Walter et al. (2016), we showed the M on various t_c (0~5) in the appendix2 and 4. Although the effect of t_c and t_{max} was not so large, the assumption of M_T is suggested to have impacts on the results.

In this document, we reviewed the previous estimator of age and sex-specific M and compared the estimates based on length- and weight- based estimators. The estimator based on regression analysis for empirical value would cause over or under estimation for M when applied to group which is not covered in the original data. Given the discussion above, we suggest that age and sex-specific M based on method2 in Walter et al. (2016) is worth to be discussed when inputted into stock synthesis modelling. Regarding the growth curve to be used for the estimation, it is suggested that Fujinami et al. (2016) equation provided plausible estimates throughout the life span of the North Pacific blue shark, when applied to Walter's method with t_c=0. As there are room for discussion over both estimator and parameter such as t_c and t_{max}, we hope this document is used as the tool for further discussion for the upcoming stock assessment of this stock.

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Table 1. Length at age by sex for growth curve by Nakano (1994), Hsu et al.(2011), and Fujinami et al. (2016). Body length is converted into PCL.

Age	Nakano (1994) Male	Nakano (1994) Female	Hsu et al. (2011) Male	Hsu et al. (2011) Female	Fujinami et al. (2016) Male	Fujinami et al. (2016) Female
0	26.9	28.0	48.8	42.2	41.3	34.1
1	58.7	56.9	75.9	73.7	68.2	64.4
2	86.7	81.9	99.8	100.3	92.1	90.7
3	111.2	103.5	121.1	122.6	113.4	113.3
4	132.8	122.3	139.9	141.4	132.3	132.9
5	151.8	138.5	156.5	157.2	149.2	149.7
6	168.5	152.6	171.3	170.6	164.1	164.3
7	183.2	164.7	184.4	181.8	177.5	176.9
8	196.1	175.3	196.0	191.2	189.3	187.7
9	207.4	184.4	206.3	199.2	199.9	197.1
10	217.4	192.3	215.4	205.9	209.2	205.2
11	226.1	199.1	223.4	211.5	217.6	212.2
12	233.8	205.1	230.6	216.3	225.0	218.2
13	240.6	210.2	236.9	220.3	231.6	223.4
14	246.5	214.6	242.5	223.7	237.5	227.9
15	251.7	218.5	247.5	226.5	242.7	231.8
16	256.3	221.8	251.9	228.9	247.3	235.1
17	260.4	224.7	255.8	230.9	251.5	238.0
18	263.9	227.2	259.2	232.6	255.2	240.5
19	267.0	229.3	262.3	234.0	258.4	242.7
20	269.8	231.2	265.0	235.2	261.3	244.6
21	272.2	232.8	267.4	236.2	263.9	246.2
22	274.3	234.2	269.5	237.1	266.2	247.5
23	276.2	235.5	271.4	237.8	268.3	248.7
24	277.8	236.5	273.1	238.4	270.1	249.8
25	279.3	237.4	274.6	238.9	271.7	250.7
26	280.5	238.2	275.9	239.3	273.2	251.4
27	281.6	238.9	277.1	239.7	274.5	252.1
28	282.6	239.5	278.1	240.0	275.6	252.7
29	283.5	240.0	279.0	240.2	276.6	253.2
30	284.2	240.4	279.8	240.5	277.5	253.6

Table 2. Natural mortality-at-age by sex for each estimator, based on the growth curve by Nakano (1994).

	Nakano (1994)															
	Male								Female							
Age	Rev. Peterson &Wroblewski (1984)	Gislason et al. (2010)	Chen & Watanabe (1989)	Lorenzen (1996)	Charnov et al. (2012)	Previous (Peterson & Wroblewski 1984)	Walter et al. (2016) tc=0	Fujinami et al. (2016) male (Walters:tc=0)	Rev. Peterson &Wroblewski (1984)	Gislason et al. (2010)	Chen & Watanabe (1989)	Lorenzen (1996)	Charnov et al. (2012)	Previous (Peterson & Wroblewski 1984)	Walter et al. (2016) tc=0	Fujinami et al. (2016) female (Walters:tc=0)
0	0.3676	3.6766	1.3883	0.7127	4.4974	0.5514	1.0072	0.7877	0.3640	2.9986	1.2513	0.7046	3.6454	0.5348	0.9093	0.8436
1	0.2007	1.0558	0.6364	0.3550	1.4064	0.3011	0.5744	0.5321	0.2056	0.9651	0.6160	0.3648	1.2677	0.3087	0.5421	0.5252
2	0.1484	0.5653	0.4312	0.2507	0.7859	0.2226	0.4195	0.4139	0.1532	0.5379	0.4279	0.2601	0.7354	0.2327	0.4038	0.3977
3	0.1223	0.3786	0.3359	0.2006	0.5410	0.1835	0.3395	0.3458	0.1268	0.3691	0.3384	0.2092	0.5177	0.1940	0.3310	0.3292
4	0.1066	0.2847	0.2813	0.1712	0.4148	0.1599	0.2910	0.3017	0.1109	0.2825	0.2865	0.1792	0.4036	0.1705	0.2865	0.2866
5	0.0961	0.2297	0.2461	0.1520	0.3396	0.1441	0.2585	0.2710	0.1003	0.2312	0.2530	0.1596	0.3349	0.1548	0.2566	0.2579
6	0.0886	0.1943	0.2218	0.1384	0.2905	0.1329	0.2354	0.2486	0.0928	0.1980	0.2297	0.1459	0.2898	0.1436	0.2354	0.2373
7	0.0831	0.1699	0.2040	0.1285	0.2564	0.1246	0.2183	0.2315	0.0872	0.1750	0.2127	0.1359	0.2583	0.1353	0.2197	0.2221
8	0.0788	0.1523	0.1906	0.1209	0.2315	0.1182	0.2052	0.2182	0.0830	0.1584	0.1999	0.1283	0.2354	0.1290	0.2077	0.2104
9	0.0755	0.1391	0.1802	0.1150	0.2128	0.1132	0.1949	0.2075	0.0796	0.1460	0.1900	0.1224	0.2182	0.1240	0.1983	0.2013
10	0.0728	0.1290	0.1719	0.1103	0.1984	0.1091	0.1867	0.1989	0.0770	0.1364	0.1822	0.1177	0.2049	0.1200	0.1908	0.1940
11	0.0706	0.1211	0.1653	0.1065	0.1870	0.1058	0.1800	0.1919	0.0748	0.1290	0.1759	0.1139	0.1944	0.1168	0.1848	0.1882
12	0.0688	0.1147	0.1598	0.1033	0.1779	0.1031	0.1745	0.1860	0.0731	0.1230	0.1709	0.1109	0.1861	0.1142	0.1799	0.1834
13	0.0672	0.1096	0.1553	0.1007	0.1704	0.1009	0.1700	0.1810	0.0717	0.1183	0.1667	0.1083	0.1793	0.1120	0.1759	0.1795
14	0.0660	0.1054	0.1516	0.0985	0.1643	0.0990	0.1662	0.1768	0.0705	0.1143	0.1632	0.1063	0.1738	0.1102	0.1725	0.1762
15	0.0649	0.1019	0.1484	0.0967	0.1592	0.0974	0.1630	0.1733	0.0695	0.1111	0.1604	0.1045	0.1692	0.1087	0.1697	0.1735
16	0.0640	0.0990	0.1458	0.0952	0.1550	0.0960	0.1603	0.1702	0.0686	0.1085	0.1580	0.1031	0.1654	0.1074	0.1673	0.1712
17	0.0632	0.0965	0.1435	0.0938	0.1514	0.0949	0.1579	0.1676	0.0679	0.1062	0.1561	0.1018	0.1622	0.1064	0.1653	0.1693
18	0.0626	0.0944	0.1416	0.0927	0.1483	0.0939	0.1560	0.1653	0.0673	0.1044	0.1547	0.1008	0.1596	0.1055	0.1637	0.1676
19	0.0620	0.0927	0.1400	0.0918	0.1457	0.0930	0.1543	0.1634	0.0668	0.1028	0.1537	0.0999	0.1573	0.1047	0.1622	0.1663
20	0.0615	0.0911	0.1386	0.0909	0.1435	0.0923	0.1528	0.1617	0.0663	0.1014	0.1530	0.0992	0.1554	0.1040	0.1610	0.1651
21	0.0611	0.0898	0.1375	0.0902	0.1416	0.0917	0.1515	0.1602	0.0660	0.1003	0.1528	0.0985	0.1538	0.1035	0.1600	0.1641
22	0.0607	0.0887	0.1366	0.0896	0.1400	0.0911	0.1504	0.1589	0.0657	0.0993	0.1529	0.0980	0.1524	0.1030	0.1591	0.1632
23	0.0604	0.0878	0.1359	0.0890	0.1386	0.0906	0.1495	0.1577	0.0654	0.0985	0.1535	0.0975	0.1512	0.1026	0.1583	0.1625
24	0.0601	0.0869	0.1355	0.0886	0.1374	0.0902	0.1487	0.1567	0.0651	0.0978	0.1544	0.0971	0.1502	0.1022	0.1577	0.1619
25	0.0599	0.0862	0.1353	0.0882	0.1363	0.0899	0.1479	0.1559	0.0649	0.0972	0.1558	0.0968	0.1494	0.1019	0.1571	0.1613
26	0.0597	0.0856	0.1353	0.0878	0.1354	0.0895	0.1473	0.1551	0.0648	0.0967	0.1576	0.0965	0.1486	0.1017	0.1566	0.1609
27	0.0595	0.0851	0.1356	0.0875	0.1346	0.0893	0.1468	0.1544	0.0646	0.0962	0.1598	0.0962	0.1480	0.1014	0.1562	0.1605
28	0.0594	0.0846	0.1360	0.0872	0.1339	0.0890	0.1463	0.1538	0.0645	0.0959	0.1626	0.0960	0.1475	0.1012	0.1558	0.1602
29	0.0592	0.0842	0.1367	0.0870	0.1333	0.0888	0.1459	0.1533	0.0644	0.0955	0.1659	0.0958	0.1470	0.1011	0.1555	0.1599
30	0.0591	0.0838	0.1376	0.0868	0.1327	0.0886	0.1455	0.1528	0.0643	0.0953	0.1698	0.0956	0.1466	0.1009	0.1553	0.1596
Mean	0.0868	0.2859	0.2303	0.1389	0.3916	0.1302	0.2273	0.2275	0.0912	0.2674	0.2382	0.1466	0.3648	0.1405	0.2276	0.2277

Table 3. Natural mortality-at-age by sex for each estimator, based on the growth curve by Hsu et al. (2011).

	Hsu et al. (2011)															
	Male								Female							
Age	Rev. Peterson &Wroblewski (1984)	Gislason et al. (2010)	Chen & Watanabe (1989)	Lorenzen (1996)	Charnov et al. (2012)	Previous (Peterson & Wroblewski 1984)	Walter et al. (2016) tc=0	Fujinami et al. (2016) male (Walters:tc=0)	Rev. Peterson &Wroblewski (1984)	Gislason et al. (2010)	Chen & Watanabe (1989)	Lorenzen (1996)	Charnov et al. (2012)	Previous (Peterson & Wroblewski 1984)	Walter et al. (2016) tc=0	Fujinami et al. (2016) female (Walters:tc=0)
0	0.2316	1.3070	0.7059	0.4186	1.7050	0.3591	0.7191	0.7877	0.2613	1.8384	0.9792	0.4810	2.3365	0.3662	0.7274	0.8436
1	0.1646	0.6448	0.4552	0.2824	0.8828	0.2451	0.5069	0.5321	0.1667	0.7525	0.5623	0.2866	1.0166	0.2454	0.4788	0.5252
2	0.1330	0.4151	0.3462	0.2210	0.5856	0.1945	0.4025	0.4139	0.1301	0.4595	0.4139	0.2155	0.6420	0.1954	0.3730	0.3977
3	0.1145	0.3045	0.2856	0.1860	0.4388	0.1658	0.3406	0.3458	0.1107	0.3326	0.3386	0.1788	0.4751	0.1679	0.3147	0.3292
4	0.1024	0.2415	0.2473	0.1635	0.3535	0.1473	0.2998	0.3017	0.0986	0.2645	0.2937	0.1566	0.3837	0.1505	0.2782	0.2866
5	0.0938	0.2015	0.2210	0.1479	0.2987	0.1344	0.2710	0.2710	0.0905	0.2230	0.2641	0.1419	0.3273	0.1387	0.2535	0.2579
6	0.0875	0.1743	0.2020	0.1364	0.2609	0.1250	0.2498	0.2486	0.0848	0.1956	0.2435	0.1315	0.2898	0.1302	0.2358	0.2373
7	0.0827	0.1549	0.1877	0.1277	0.2337	0.1178	0.2337	0.2315	0.0805	0.1766	0.2285	0.1240	0.2634	0.1238	0.2228	0.2221
8	0.0788	0.1404	0.1766	0.1210	0.2133	0.1122	0.2210	0.2182	0.0773	0.1628	0.2172	0.1183	0.2441	0.1190	0.2129	0.2104
9	0.0758	0.1293	0.1678	0.1156	0.1976	0.1078	0.2108	0.2075	0.0748	0.1524	0.2086	0.1139	0.2297	0.1152	0.2052	0.2013
10	0.0733	0.1206	0.1607	0.1112	0.1852	0.1042	0.2026	0.1989	0.0728	0.1445	0.2018	0.1104	0.2186	0.1122	0.1992	0.1940
11	0.0712	0.1137	0.1549	0.1076	0.1753	0.1012	0.1958	0.1919	0.0713	0.1384	0.1967	0.1077	0.2099	0.1098	0.1943	0.1882
12	0.0695	0.1081	0.1501	0.1046	0.1672	0.0988	0.1902	0.1860	0.0700	0.1335	0.1929	0.1055	0.2030	0.1078	0.1905	0.1834
13	0.0681	0.1035	0.1461	0.1021	0.1606	0.0967	0.1855	0.1810	0.0690	0.1297	0.1903	0.1037	0.1975	0.1062	0.1873	0.1795
14	0.0668	0.0997	0.1427	0.1000	0.1550	0.0950	0.1815	0.1768	0.0681	0.1265	0.1889	0.1023	0.1931	0.1049	0.1847	0.1762
15	0.0658	0.0965	0.1399	0.0982	0.1504	0.0935	0.1781	0.1733	0.0675	0.1240	0.1886	0.1011	0.1895	0.1038	0.1826	0.1735
16	0.0649	0.0938	0.1376	0.0967	0.1465	0.0923	0.1752	0.1702	0.0669	0.1219	0.1893	0.1001	0.1865	0.1029	0.1809	0.1712
17	0.0641	0.0915	0.1358	0.0954	0.1431	0.0912	0.1727	0.1676	0.0664	0.1202	0.1912	0.0993	0.1841	0.1021	0.1794	0.1693
18	0.0635	0.0895	0.1343	0.0942	0.1403	0.0903	0.1705	0.1653	0.0660	0.1188	0.1942	0.0986	0.1821	0.1015	0.1782	0.1676
19	0.0629	0.0879	0.1333	0.0932	0.1378	0.0895	0.1686	0.1634	0.0657	0.1177	0.1985	0.0981	0.1804	0.1010	0.1772	0.1663
20	0.0624	0.0864	0.1326	0.0924	0.1357	0.0889	0.1670	0.1617	0.0654	0.1167	0.2043	0.0976	0.1791	0.1005	0.1764	0.1651
21	0.0620	0.0852	0.1324	0.0916	0.1339	0.0883	0.1656	0.1602	0.0652	0.1159	0.2117	0.0972	0.1779	0.1002	0.1757	0.1641
22	0.0616	0.0841	0.1324	0.0910	0.1323	0.0878	0.1644	0.1589	0.0650	0.1152	0.2212	0.0969	0.1770	0.0999	0.1752	0.1632
23	0.0612	0.0832	0.1329	0.0904	0.1309	0.0873	0.1633	0.1577	0.0649	0.1147	0.2332	0.0966	0.1762	0.0996	0.1747	0.1625
24	0.0610	0.0823	0.1337	0.0899	0.1297	0.0869	0.1624	0.1567	0.0647	0.1142	0.2484	0.0964	0.1755	0.0994	0.1743	0.1619
25	0.0607	0.0816	0.1349	0.0895	0.1287	0.0866	0.1616	0.1559	0.0646	0.1138	0.2679	0.0962	0.1749	0.0992	0.1739	0.1613
26	0.0605	0.0810	0.1365	0.0891	0.1278	0.0863	0.1608	0.1551	0.0645	0.1135	0.2933	0.0960	0.1745	0.0990	0.1736	0.1609
27	0.0603	0.0805	0.1386	0.0888	0.1270	0.0860	0.1602	0.1544	0.0644	0.1132	0.3272	0.0959	0.1741	0.0989	0.1734	0.1605
28	0.0601	0.0800	0.1411	0.0885	0.1263	0.0858	0.1596	0.1538	0.0644	0.1130	0.3742	0.0958	0.1737	0.0988	0.1732	0.1602
29	0.0599	0.0796	0.1441	0.0882	0.1256	0.0856	0.1591	0.1533	0.0643	0.1128	0.4427	0.0957	0.1735	0.0987	0.1730	0.1599
30	0.0598	0.0792	0.1477	0.0880	0.1251	0.0854	0.1587	0.1528	0.0643	0.1126	0.5510	0.0956	0.1732	0.0986	0.1729	0.1596
Mean	0.0808	0.1813	0.1915	0.1262	0.2630	0.1167	0.2277	0.2275	0.0829	0.2287	0.2922	0.1302	0.3252	0.1257	0.2282	0.2277

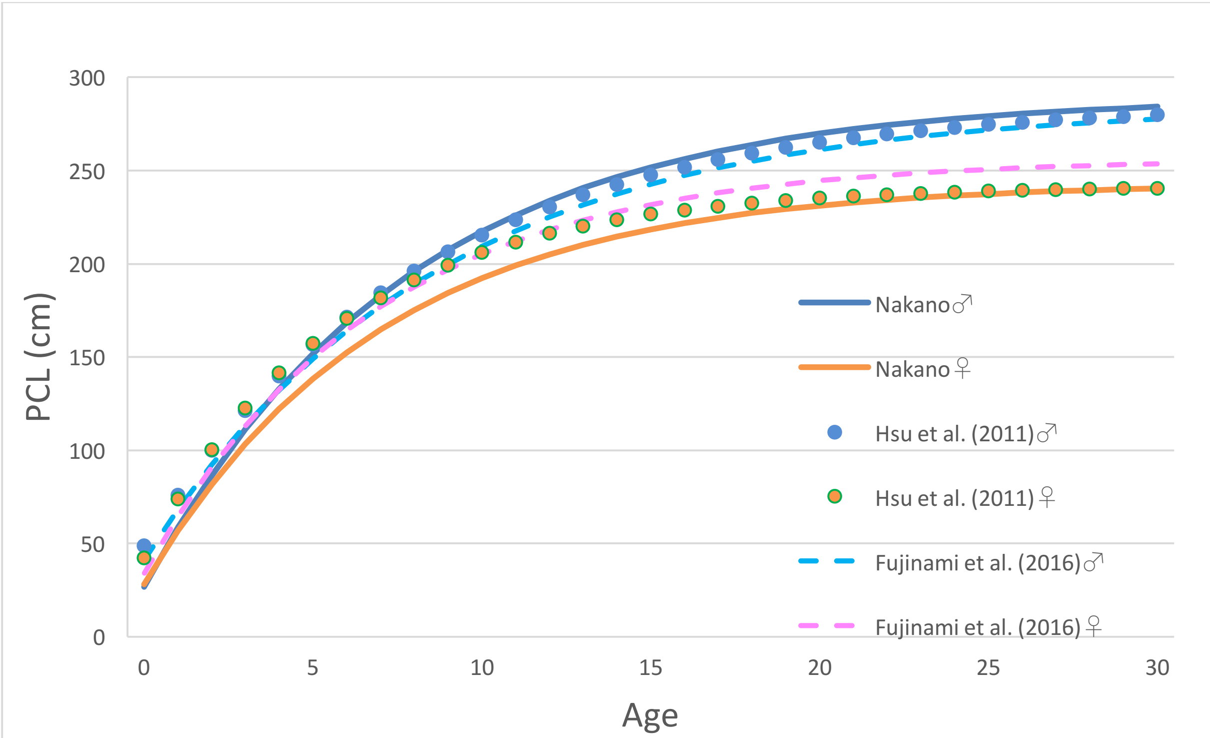

Figure 1. Growth curve by sex by Nakano (1994), Hsu et al. (2011), and Fujinami et al. (2016).

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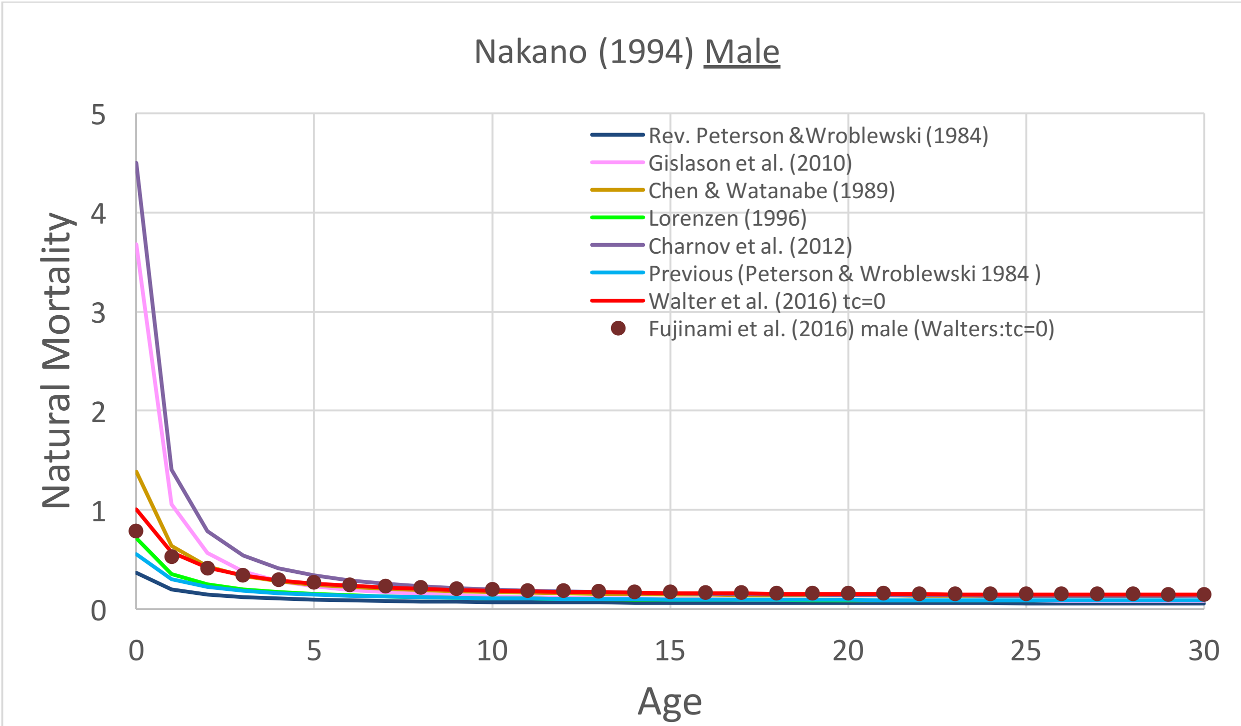

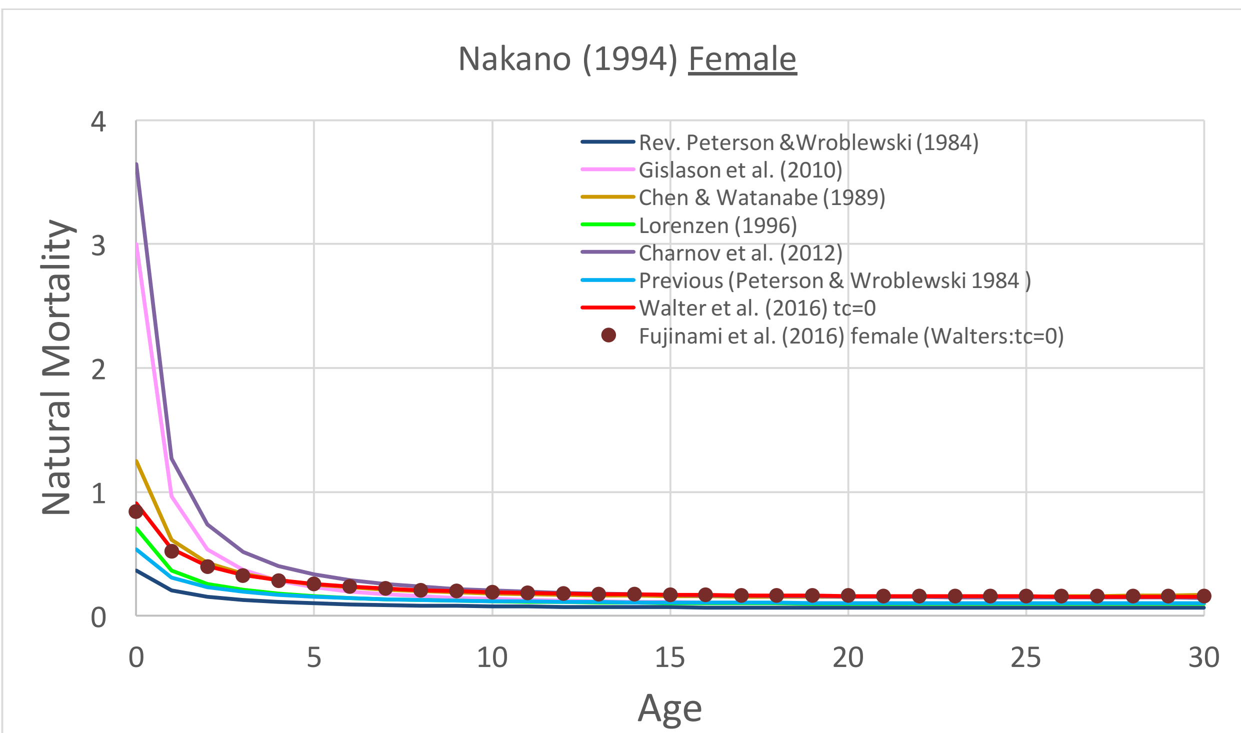

Figure 2. Natural mortality at age for male (upper) and female (below) blue shark by each estimator, based on the growth curve by Nakano (1994).

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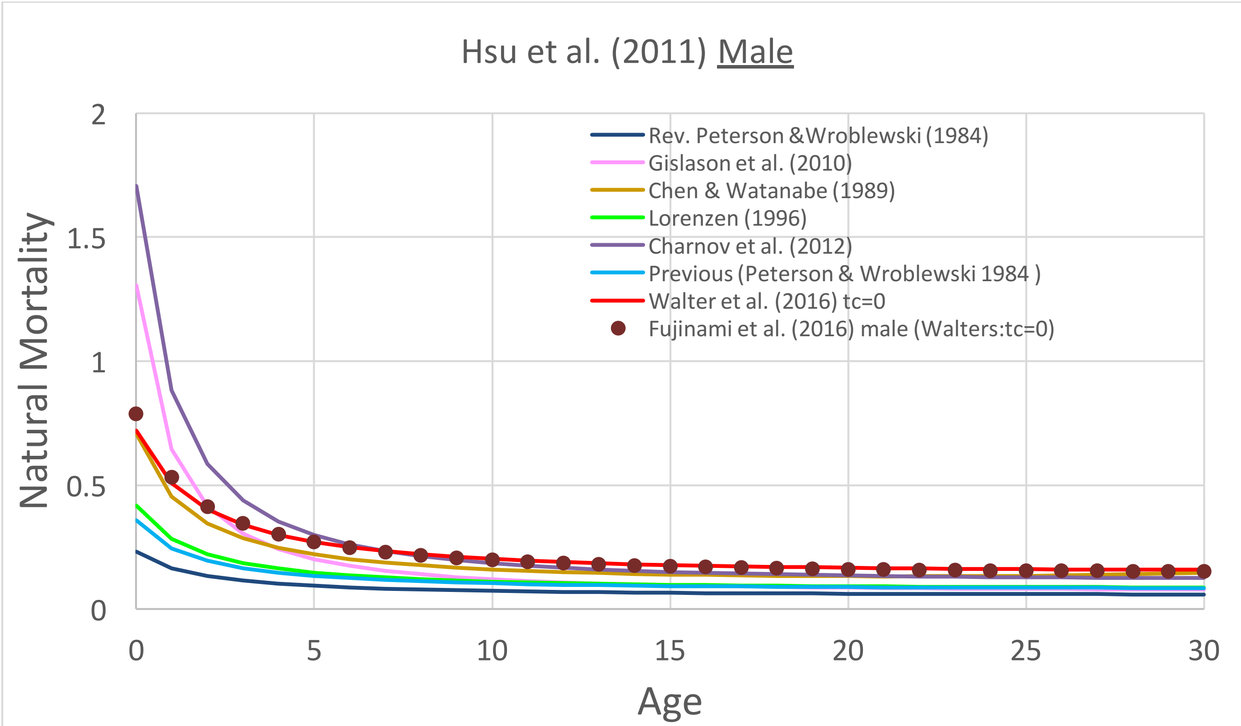


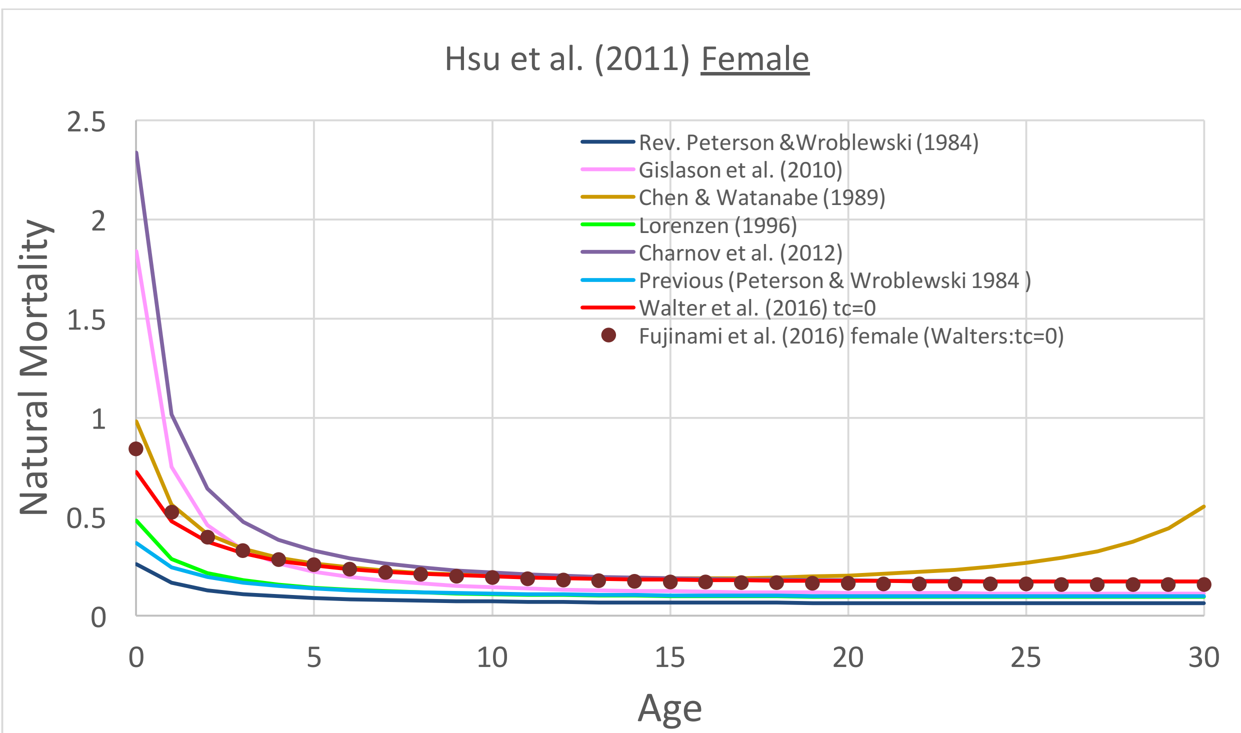
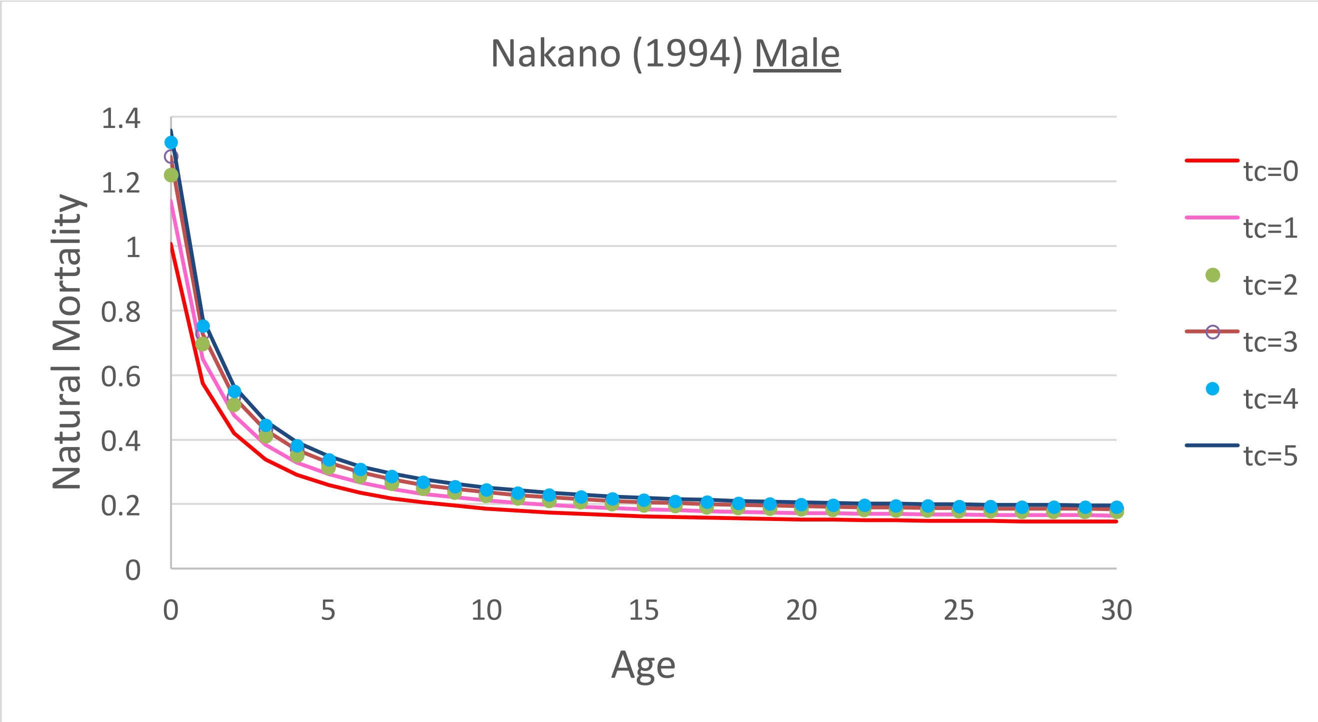


Figure 3. Natural mortality at age for male (upper) and female (below) blue shark by each estimator, based on the growth curve by Hsu et al. (2011).



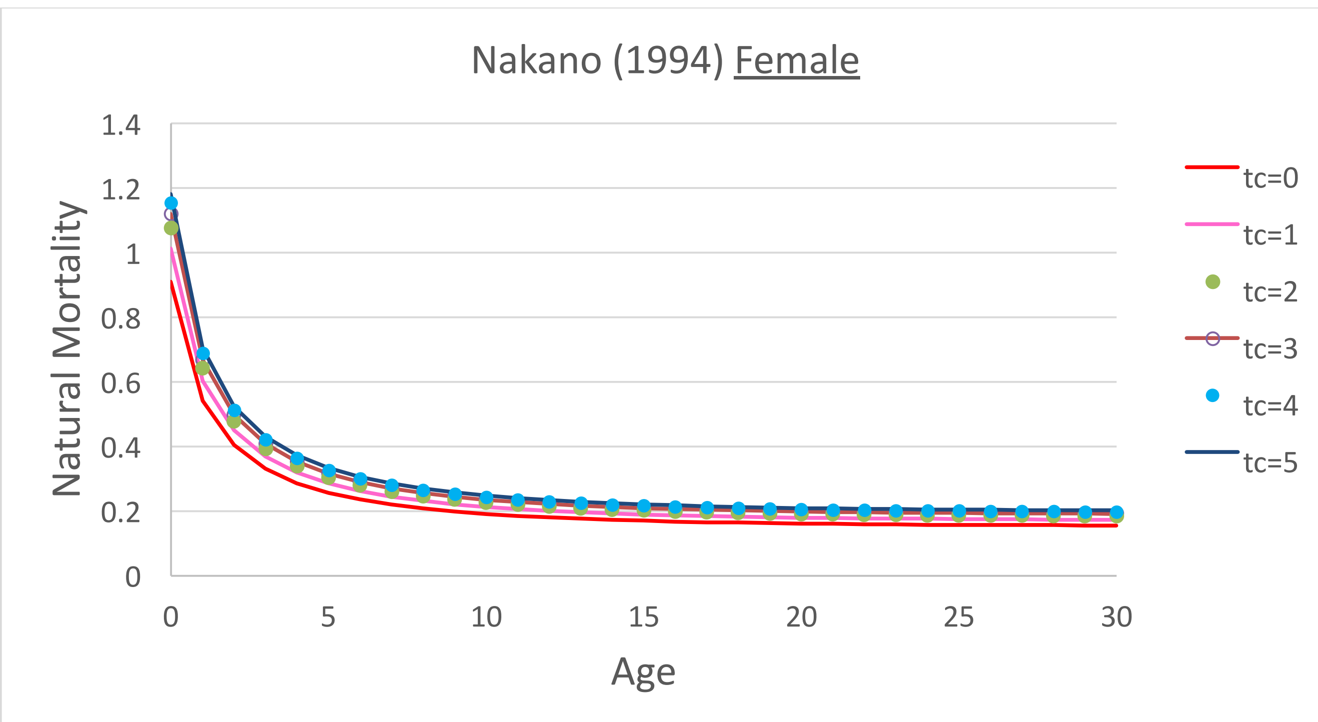
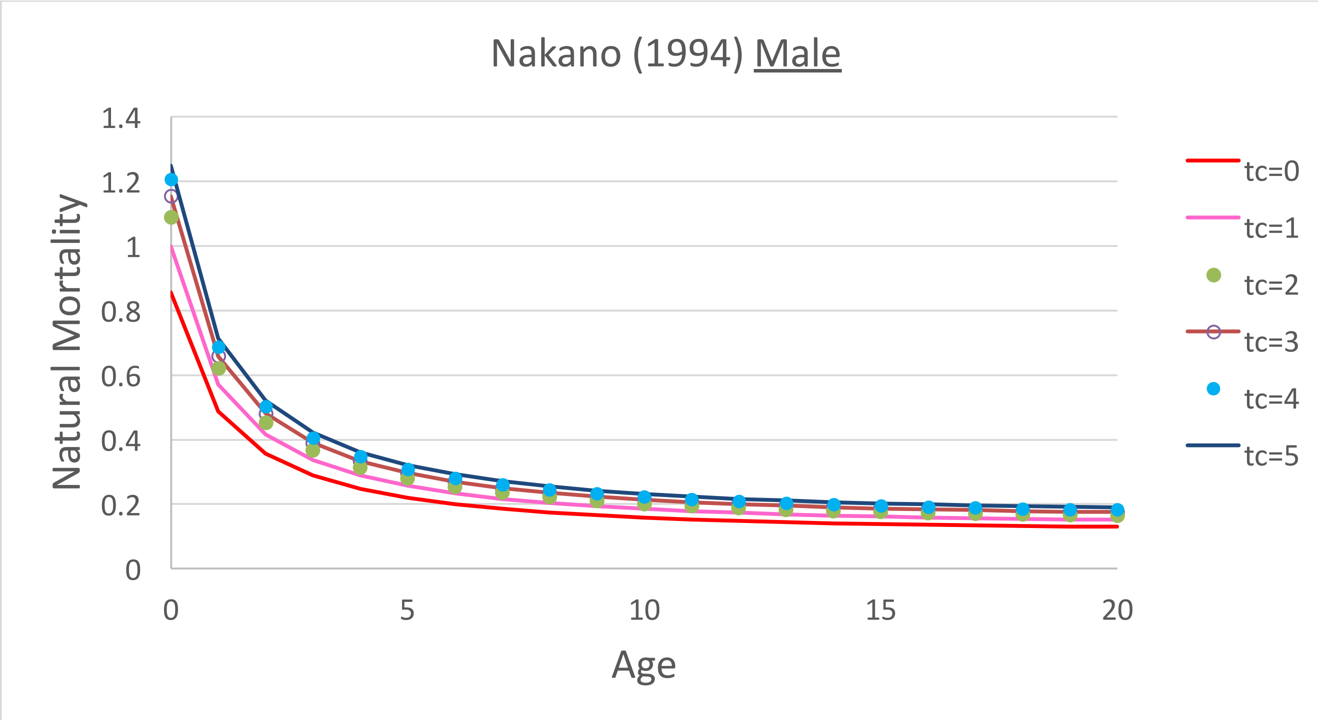


Figure 4. Natural mortality at age for male (upper) and female (below) blue shark by each t_c, based on the growth curve by Nakano (1994).



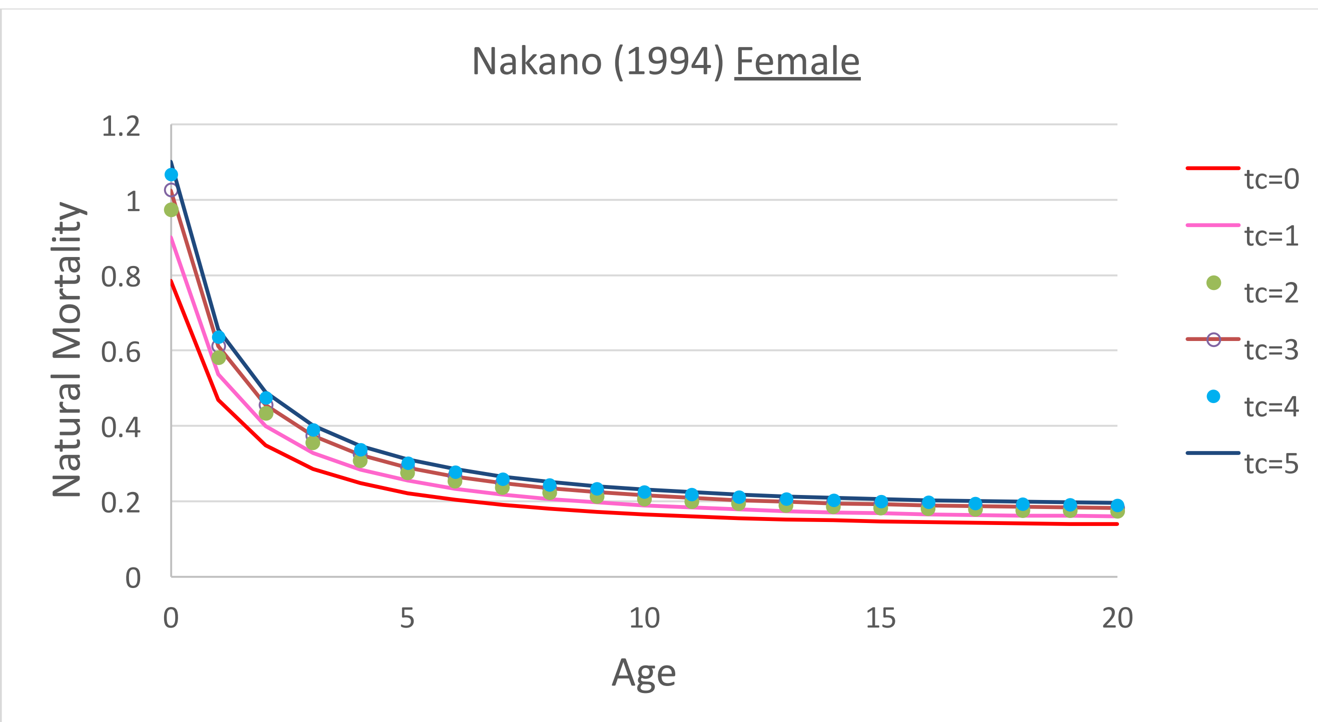


Figure 5. Natural mortality at age for male (upper) and female (below) blue shark by each t_c, based on the growth curve by Nakano (1994) with assumption of t_{max}=20.

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Appendix 1. Concept of Method 2 in Walter et al. (2016) and derivation of equation (10) in **Methods**.

Concept of Method 2 by Walter et al. (2016)

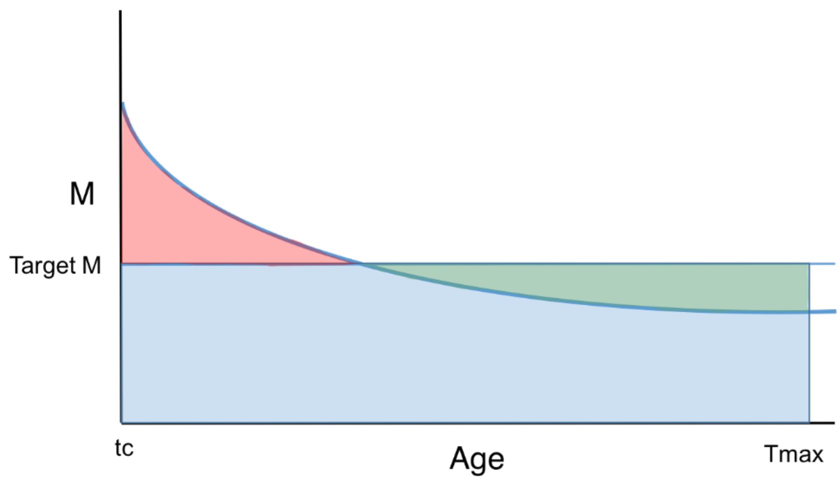
This method consists of 2 step;

Step1: M per unit length (M_unitL: theoretical value) is calculated based on Target M.

Step2: Age-specific M is estimated based on the length at age using VBGC.

M_unitL depends on t_c and t_{max}. Only VBGC is available for growth curve at present.

As geometric interpretation of this method, one can distribute the area of rectangle encompassed by Target M, t_c and t_{max} for each age (in originally meaning, length). Thus, the area of red color is equal to that of green color in the figure below. Thereby, survival rate at t_{max} is guarantee to be equal to that when Target M is applied.



Appendix Figure 1. Diagram of Method 2 in Walter et al. (2016). Solid curve is age specific M with $t_c = 0$.

Derivation of equation (10)

According to the equation for estimating M which takes into account the variation by growth (Lorenzen 2000, 2005), Survival rate (S_t) between t_c *and* t_{max} can be expressed as follows,

$$S = \left(\frac{l_c}{l_c + L_\infty(\exp(K(t_{max} - t_c)) - 1)}\right)^{\frac{M_r l_r}{L_\infty k}} \qquad (1)$$

, where L_∞ is asymptotic length, K is von Bertalanffy growth coefficient, M_r is M by unit length (l_r). l_c is the

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body length at t_c. When VBGC is substituted into l_c and then equation (1) can be transformed as follows,

$$l_c = L_\infty\left(1 - \exp\left(-\mathrm{K}(t_c - t_o)\right)\right) \qquad (2)$$

Given that mean of natural mortality between t_c and t_{max} is expressed as Target M (M_T), survival rate (S) between t_c and t_{max} is expressed as follows,

$$S = \exp\left(-M_T(t_{max} - t_c)\right) \qquad (3)$$

Assuming that survival rate (S) derived from M (equation 1) and that (S) derived from M_T (equation 3) is equal,

$$S = \exp\left(-M_T(t_{max} - t_c)\right) = \left(\frac{l_c}{l_c + L_\infty(\exp(K(t_{max} - t_c)) - 1)}\right)^{\frac{M_r l_r}{L_\infty k}} \qquad (4)$$

,which can be transformed as follows,

$$M_r l_r = \frac{-M_T L_\infty K(t_{max} - t_c)}{\ln\left(\frac{l_c}{l_c + L_\infty\left(\exp\left(K(t_{max} - t_c)\right) - 1\right)}\right)} \qquad (5)$$

Same as derivation of equation 1, survival rate (S_t) between t and $t + 1$ is expressed as

$$\mathrm{S}_t = \left(\frac{l_t}{l_t + L_\infty(\exp(K) - 1)}\right)^{\frac{M_r l_r}{L_\infty k}} \qquad (6)$$

Because the relationship between survival rate and natural mortality can be described as

$$\mathrm{S}_t = \exp(-M_t) \qquad (7)$$

, where M_t denotes natural mortality at age t. From equation (6) and (7), natural mortality is expressed as

$$M_t = \frac{-M_r l_r}{L_\infty K}\ln\left(\frac{l_t}{l_t + L_\infty(\exp(K) - 1)}\right) \qquad (8)$$

If equation (5) is substituted in equation (8),

$$M_t = \frac{M_T(t_{max} - t_c)}{\ln\left(\frac{l_c}{l_c + L_\infty\left(\exp\left(K(t_{max} - t_c)\right) - 1\right)}\right)}\ln\left(\frac{l_t}{l_t + L_\infty(\exp(K) - 1)}\right) \qquad (9)$$

is derived.

Appendix 2. Natural mortality-at-age by sex estimated by the method of Walter et al. (2016) for various t_c, based on the growth curve by Nakano (1994).

Nakano (male)						
Age	tc=0	tc=1	tc=2	tc=3	tc=4	tc=5
0	1.0072	1.1401	1.2197	1.2768	1.3211	1.3569
1	0.5744	0.6502	0.6955	0.7281	0.7534	0.7738
2	0.4195	0.4748	0.5080	0.5318	0.5502	0.5651
3	0.3395	0.3843	0.4112	0.4304	0.4453	0.4574
4	0.2910	0.3293	0.3523	0.3688	0.3816	0.3919
5	0.2585	0.2926	0.3130	0.3277	0.3390	0.3482
6	0.2354	0.2665	0.2851	0.2984	0.3088	0.3171
7	0.2183	0.2471	0.2643	0.2767	0.2863	0.2941
8	0.2052	0.2323	0.2485	0.2601	0.2691	0.2764
9	0.1949	0.2206	0.2360	0.2471	0.2557	0.2626
10	0.1867	0.2113	0.2261	0.2367	0.2449	0.2515
11	0.1800	0.2038	0.2180	0.2282	0.2361	0.2425
12	0.1745	0.1976	0.2114	0.2213	0.2289	0.2351
13	0.1700	0.1924	0.2058	0.2155	0.2230	0.2290
14	0.1662	0.1881	0.2012	0.2107	0.2180	0.2239
15	0.1630	0.1845	0.1974	0.2066	0.2138	0.2196
16	0.1603	0.1814	0.1941	0.2032	0.2102	0.2159
17	0.1579	0.1788	0.1913	0.2002	0.2072	0.2128
18	0.1560	0.1765	0.1889	0.1977	0.2046	0.2101
19	0.1543	0.1746	0.1868	0.1955	0.2023	0.2078
20	0.1528	0.1730	0.1850	0.1937	0.2004	0.2058
21	0.1515	0.1715	0.1835	0.1921	0.1988	0.2041
22	0.1504	0.1703	0.1822	0.1907	0.1973	0.2027
23	0.1495	0.1692	0.1810	0.1895	0.1961	0.2014
24	0.1487	0.1683	0.1800	0.1885	0.1950	0.2003
25	0.1479	0.1675	0.1792	0.1875	0.1941	0.1993
26	0.1473	0.1668	0.1784	0.1868	0.1932	0.1985
27	0.1468	0.1661	0.1777	0.1861	0.1925	0.1977
28	0.1463	0.1656	0.1772	0.1855	0.1919	0.1971
29	0.1459	0.1651	0.1767	0.1849	0.1913	0.1965
30	0.1455	0.1647	0.1762	0.1845	0.1909	0.1960

Nakano (Female)						
Age	tc=0	tc=1	tc=2	tc=3	tc=4	tc=5
0	0.9093	1.0124	1.0748	1.1193	1.1536	1.1810
1	0.5421	0.6036	0.6408	0.6674	0.6878	0.7041
2	0.4038	0.4495	0.4772	0.4970	0.5122	0.5244
3	0.3310	0.3686	0.3913	0.4075	0.4200	0.4299
4	0.2865	0.3190	0.3386	0.3527	0.3634	0.3721
5	0.2566	0.2857	0.3033	0.3159	0.3256	0.3333
6	0.2354	0.2621	0.2782	0.2898	0.2986	0.3057
7	0.2197	0.2446	0.2597	0.2704	0.2787	0.2853
8	0.2077	0.2312	0.2455	0.2557	0.2635	0.2697
9	0.1983	0.2208	0.2344	0.2441	0.2516	0.2576
10	0.1908	0.2125	0.2256	0.2349	0.2421	0.2479
11	0.1848	0.2058	0.2185	0.2275	0.2345	0.2400
12	0.1799	0.2003	0.2126	0.2215	0.2282	0.2337
13	0.1759	0.1958	0.2079	0.2165	0.2231	0.2284
14	0.1725	0.1921	0.2039	0.2123	0.2188	0.2240
15	0.1697	0.1889	0.2006	0.2089	0.2153	0.2204
16	0.1673	0.1863	0.1978	0.2060	0.2123	0.2173
17	0.1653	0.1841	0.1954	0.2035	0.2098	0.2147
18	0.1637	0.1822	0.1934	0.2015	0.2076	0.2126
19	0.1622	0.1806	0.1918	0.1997	0.2058	0.2107
20	0.1610	0.1793	0.1903	0.1982	0.2043	0.2091
21	0.1600	0.1781	0.1891	0.1969	0.2029	0.2078
22	0.1591	0.1771	0.1880	0.1958	0.2018	0.2066
23	0.1583	0.1763	0.1871	0.1949	0.2008	0.2056
24	0.1577	0.1755	0.1864	0.1941	0.2000	0.2048
25	0.1571	0.1749	0.1857	0.1934	0.1993	0.2040
26	0.1566	0.1744	0.1851	0.1928	0.1987	0.2034
27	0.1562	0.1739	0.1846	0.1923	0.1982	0.2029
28	0.1558	0.1735	0.1842	0.1918	0.1977	0.2024
29	0.1555	0.1732	0.1838	0.1915	0.1973	0.2020
30	0.1553	0.1729	0.1835	0.1911	0.1970	0.2017

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Appendix 3. Natural mortality-at-age by sex estimated by the method of Walter et al. (2016) for various t_{max}, based on three VBGC with assumption of t_c=0.

tmax=30			
Age	Fujinami et al. 2016	Nakano (1994)	Hsu et al. (2011)
0	0.8436	0.9093	0.7274
1	0.5252	0.5421	0.4788
2	0.3977	0.4038	0.3730
3	0.3292	0.3310	0.3147
4	0.2866	0.2865	0.2782
5	0.2579	0.2566	0.2535
6	0.2373	0.2354	0.2358
7	0.2221	0.2197	0.2228
8	0.2104	0.2077	0.2129
9	0.2013	0.1983	0.2052
10	0.1940	0.1908	0.1992
11	0.1882	0.1848	0.1943
12	0.1834	0.1799	0.1905
13	0.1795	0.1759	0.1873
14	0.1762	0.1725	0.1847
15	0.1735	0.1697	0.1826
16	0.1712	0.1673	0.1809
17	0.1693	0.1653	0.1794
18	0.1676	0.1637	0.1782
19	0.1663	0.1622	0.1772
20	0.1651	0.1610	0.1764
21	0.1641	0.1600	0.1757
22	0.1632	0.1591	0.1752
23	0.1625	0.1583	0.1747
24	0.1619	0.1577	0.1743
25	0.1613	0.1571	0.1739
26	0.1609	0.1566	0.1736
27	0.1605	0.1562	0.1734
28	0.1602	0.1558	0.1732
29	0.1599	0.1555	0.1730
30	0.1596	0.1553	0.1729

tmax=24			
Age	Fujinami et al. 2016	Nakano (1994)	Hsu et al. (2011)
0	0.7846	0.8420	0.6854
1	0.4884	0.5020	0.4511
2	0.3699	0.3739	0.3514
3	0.3061	0.3065	0.2965
4	0.2666	0.2653	0.2621
5	0.2398	0.2376	0.2388
6	0.2207	0.2180	0.2222
7	0.2066	0.2034	0.2099
8	0.1957	0.1923	0.2006
9	0.1872	0.1836	0.1933
10	0.1805	0.1767	0.1876
11	0.1750	0.1711	0.1831
12	0.1706	0.1666	0.1794
13	0.1669	0.1629	0.1765
14	0.1639	0.1597	0.1741
15	0.1613	0.1571	0.1721
16	0.1592	0.1550	0.1704
17	0.1574	0.1531	0.1691
18	0.1559	0.1516	0.1679
19	0.1546	0.1502	0.1670
20	0.1535	0.1491	0.1662
21	0.1526	0.1481	0.1656
22	0.1518	0.1473	0.1650
23	0.1511	0.1466	0.1646
24	0.1506	0.1460	0.1642

tmax=20			
Age	Fujinami et al. 2016	Nakano (1994)	Hsu et al. (2011)
0	0.7349	0.7858	0.6489
1	0.4575	0.4685	0.4271
2	0.3465	0.3489	0.3327
3	0.2867	0.2861	0.2807
4	0.2497	0.2476	0.2482
5	0.2246	0.2218	0.2261
6	0.2068	0.2034	0.2104
7	0.1935	0.1899	0.1987
8	0.1833	0.1795	0.1899
9	0.1754	0.1714	0.1831
10	0.1690	0.1649	0.1777
11	0.1639	0.1597	0.1734
12	0.1598	0.1555	0.1699
13	0.1563	0.1520	0.1671
14	0.1535	0.1491	0.1648
15	0.1511	0.1467	0.1629
16	0.1491	0.1446	0.1614
17	0.1475	0.1429	0.1601
18	0.1460	0.1414	0.1590
19	0.1448	0.1402	0.1581
20	0.1438	0.1392	0.1574

Appendix 4. Natural mortality-at-age by sex estimated by the method of Walter et al. (2016) for various t_c, based on the growth curve by Fujinami et al. (2016).

	Fujinami (male)							Fujinami (female)					
Age	tc=0	tc=1	tc=2	tc=3	tc=4	tc=5	Age	tc=0	tc=1	tc=2	tc=3	tc=4	tc=5
0	0.7877	0.8595	0.9090	0.9468	0.9771	1.0023	0	0.8436	0.9291	0.9822	1.0205	1.0501	1.0737
1	0.5321	0.5807	0.6141	0.6396	0.6601	0.6771	1	0.5252	0.5784	0.6115	0.6353	0.6537	0.6684
2	0.4139	0.4516	0.4777	0.4975	0.5134	0.5266	2	0.3977	0.4380	0.4631	0.4811	0.4951	0.5062
3	0.3458	0.3773	0.3991	0.4157	0.4290	0.4400	3	0.3292	0.3625	0.3832	0.3982	0.4097	0.4189
4	0.3017	0.3293	0.3482	0.3627	0.3743	0.3839	4	0.2866	0.3156	0.3337	0.3467	0.3567	0.3648
5	0.2710	0.2958	0.3128	0.3258	0.3362	0.3449	5	0.2579	0.2840	0.3002	0.3120	0.3210	0.3282
6	0.2486	0.2712	0.2869	0.2988	0.3083	0.3163	6	0.2373	0.2614	0.2763	0.2871	0.2954	0.3021
7	0.2315	0.2526	0.2672	0.2783	0.2872	0.2946	7	0.2221	0.2446	0.2586	0.2687	0.2764	0.2827
8	0.2182	0.2381	0.2518	0.2622	0.2706	0.2776	8	0.2104	0.2318	0.2450	0.2546	0.2619	0.2678
9	0.2075	0.2265	0.2395	0.2495	0.2575	0.2641	9	0.2013	0.2217	0.2344	0.2435	0.2506	0.2562
10	0.1989	0.2171	0.2296	0.2391	0.2468	0.2531	10	0.1940	0.2137	0.2259	0.2347	0.2415	0.2470
11	0.1919	0.2094	0.2214	0.2306	0.2380	0.2441	11	0.1882	0.2072	0.2191	0.2276	0.2342	0.2395
12	0.1860	0.2029	0.2146	0.2235	0.2307	0.2366	12	0.1834	0.2020	0.2135	0.2219	0.2283	0.2334
13	0.1810	0.1975	0.2089	0.2176	0.2246	0.2303	13	0.1795	0.1976	0.2089	0.2171	0.2234	0.2284
14	0.1768	0.1930	0.2041	0.2126	0.2194	0.2250	14	0.1762	0.1940	0.2051	0.2131	0.2193	0.2243
15	0.1733	0.1891	0.2000	0.2083	0.2150	0.2205	15	0.1735	0.1911	0.2020	0.2099	0.2159	0.2208
16	0.1702	0.1858	0.1965	0.2046	0.2112	0.2166	16	0.1712	0.1885	0.1993	0.2071	0.2131	0.2179
17	0.1676	0.1829	0.1934	0.2015	0.2079	0.2133	17	0.1693	0.1864	0.1971	0.2048	0.2107	0.2154
18	0.1653	0.1804	0.1908	0.1987	0.2051	0.2104	18	0.1676	0.1846	0.1952	0.2028	0.2087	0.2134
19	0.1634	0.1783	0.1885	0.1964	0.2027	0.2079	19	0.1663	0.1831	0.1936	0.2011	0.2069	0.2116
20	0.1617	0.1764	0.1866	0.1943	0.2006	0.2057	20	0.1651	0.1818	0.1922	0.1997	0.2055	0.2101
21	0.1602	0.1748	0.1849	0.1925	0.1987	0.2038	21	0.1641	0.1807	0.1910	0.1985	0.2042	0.2088
22	0.1589	0.1734	0.1834	0.1910	0.1971	0.2022	22	0.1632	0.1798	0.1901	0.1975	0.2032	0.2078
23	0.1577	0.1721	0.1820	0.1896	0.1957	0.2007	23	0.1625	0.1790	0.1892	0.1966	0.2023	0.2068
24	0.1567	0.1710	0.1809	0.1884	0.1944	0.1994	24	0.1619	0.1783	0.1885	0.1958	0.2015	0.2060
25	0.1559	0.1701	0.1799	0.1873	0.1933	0.1983	25	0.1613	0.1777	0.1879	0.1952	0.2008	0.2054
26	0.1551	0.1692	0.1790	0.1864	0.1924	0.1973	26	0.1609	0.1772	0.1873	0.1946	0.2003	0.2048
27	0.1544	0.1685	0.1782	0.1856	0.1915	0.1965	27	0.1605	0.1768	0.1869	0.1942	0.1998	0.2043
28	0.1538	0.1678	0.1775	0.1849	0.1908	0.1957	28	0.1602	0.1764	0.1865	0.1937	0.1993	0.2038
29	0.1533	0.1672	0.1769	0.1842	0.1901	0.1950	29	0.1599	0.1761	0.1861	0.1934	0.1990	0.2035
30	0.1528	0.1667	0.1763	0.1837	0.1895	0.1944	30	0.1596	0.1758	0.1858	0.1931	0.1987	0.2032

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