Review on the Indian Ocean albacore biological parameters for stock assessments (update)

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Abstract

IOTC will conduct stock assessments for ALB (albacore) in the WPTmP08 (July 25-29, 2022). Before the July assessment meeting, IOTC will take place the on-line "data preparatory meeting (April 13-15, 2022)" and will discuss input data for stock assessments. In this regard, I reviewed the updated information on the stock structure and seven biological parameters of ALB to be used for the stock assessments. Seven types of biological parameters are (1) sex ratio, (2) LW relation, (3) growth equation, (4) life span (plus group), (5) natural mortality, (6) fecundity and (7) maturity-at-age. In this review, I referred to parameters used in ICCAT, WCPFC, ISC and IOTC. Then plausible parameters for the ALB stock assessments are evaluated then suggested for both base case and sensitivity. As a result, the same stock structure and seven parameters used in the 2019 ALB stock assessments are suggested again as a base case to apply for the 2022 ALB stock assessments. We need to confirm this and also discuss options of sensitivities during this data preparatory meeting. Some future works to improve biological parameters are suggested.

Contents

1. Introduction

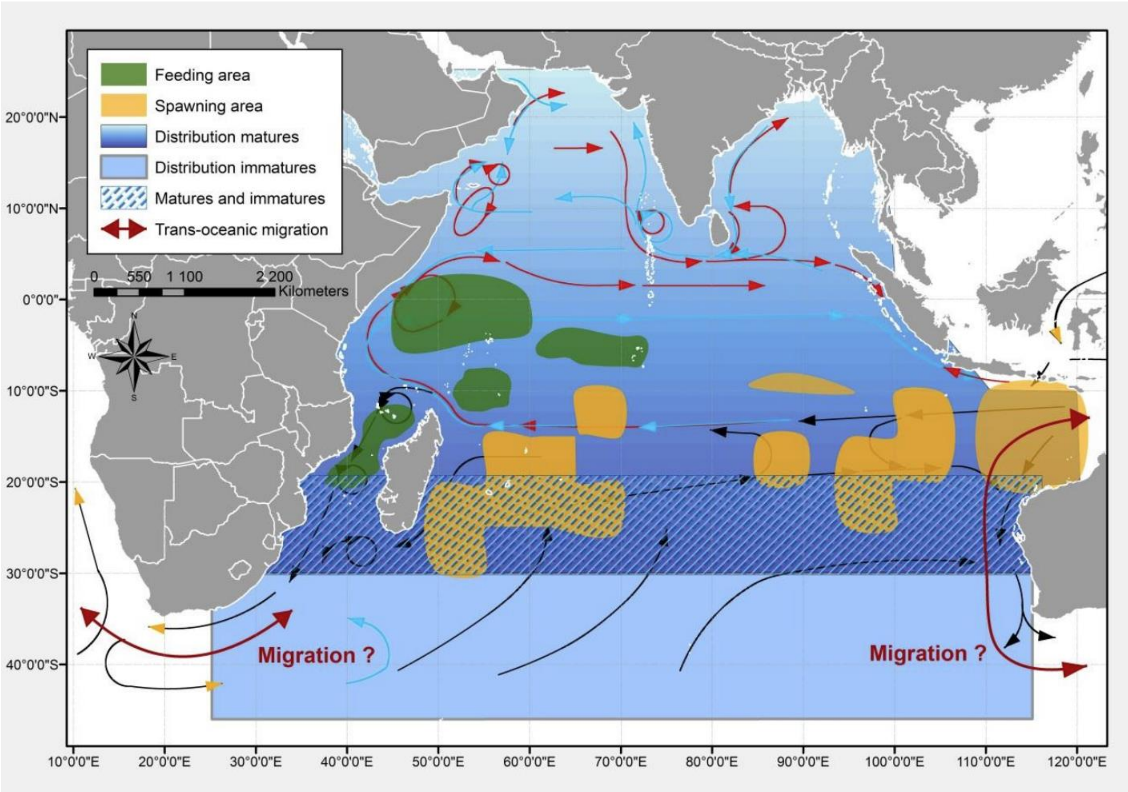
IOTC will conduct stock assessments for ALB (albacore) in the WPTmP08 (July 25-29, 2022). Before the July assessment meeting, IOTC will take place the on-line "data preparatory meeting (April 13-15, 2022)" and will discuss input data for stock assessments. In this regard, I reviewed the updated information on the stock structure and seven biological parameters of ALB to be used for the stock assessments. Seven types of biological parameters are (1) sex ratio, (2) LW relation, (3) growth equation, (4) life span (plus group), (5) natural mortality, (6) fecundity and (7) maturity-at-age. In this review, I referred to parameters used in ICCAT, WCPFC, ISC and IOTC. Then plausible parameters for the ALB stock assessments are evaluated then suggested for both base case and sensitivity. As a result, the same stock structure and seven parameters used in the 2019 ALB stock assessments are suggested again as a base case to apply for the 2022 ALB stock assessments. We need to confirm this and also discuss options of sensitivities during this data preparatory meeting. Some future works to improve biological parameters are suggested.

(*) ISC: International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean. ISC is an intergovernmental body dedicated to advancing fishery science of the North Pacific tuna and tuna-like fishes through cooperation and collaboration. Its advices are utilized in WCPFC.

2. Review for the updated information

2.1 Stock structure

In the Pacific and the Atlantic Ocean, two (north and south) stocks hypothesis has been used and stock assessments have been conducted for each stock. As for the Indian Ocean, it has a very small northern part and the synthetic map indicates the distribution of adult & immature albacore, potential migration, spawning and feeding areas taking place within the Indian Ocean (Nikolic et al, 2014) (Map 1). These facts suggest a single stock, although there is some knowledge on intermingling areas with Pacific and Atlantic stock in its eastern and western end respectively.

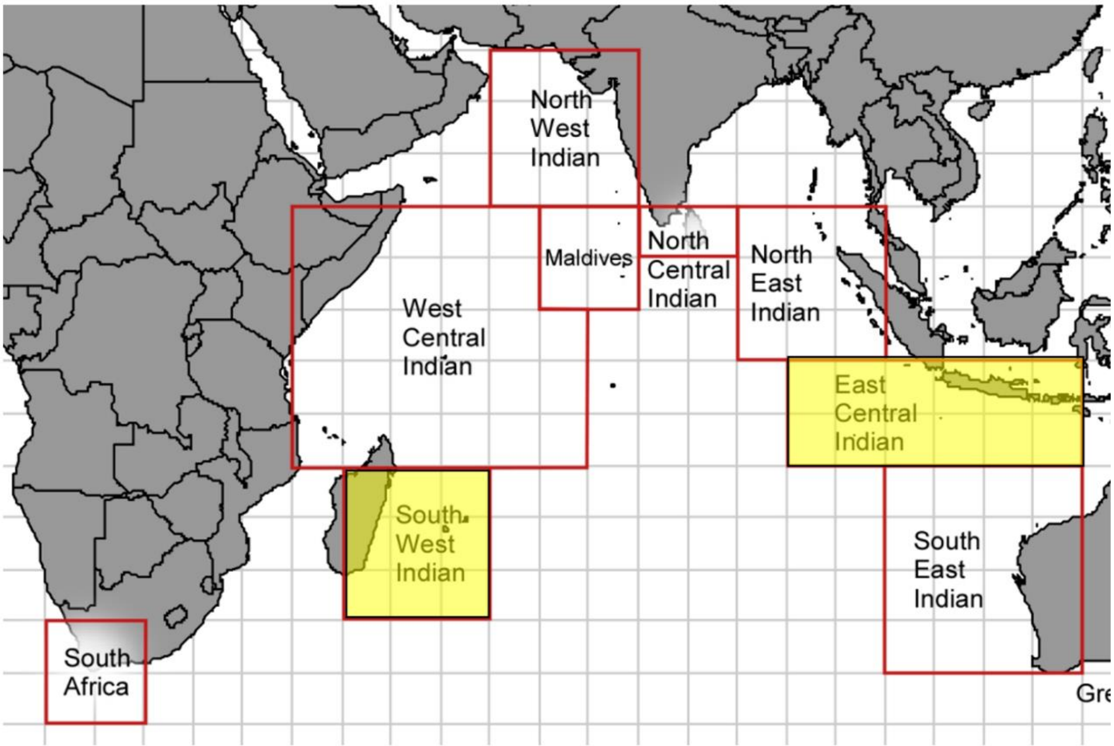


Map 1. Synthetic map of the distribution of adult and immature albacore in the Indian Ocean and potential migration (red arrow), spawning and feeding areas (Nikolic et al, 2014). Schematic representation of main currents in the Indian Ocean from Schott et al (2009).

During 2017-2019, the Population Structure and connectivity of priority Tuna and tuna-like (Billfish and others) Species within the Indian Ocean (PSTBS-IO) project was conducted by the EU fund. In the IOTC SC23 (2020), the summary of the project results was presented by Davies et al (2020). Regarding the albacore stock, it was described as follows:

Albacore Genetic analysis of out-locations indicated that there was genetic differentiation between the Indian Ocean and the Atlantic and Pacific Oceans. Samples in the Indian Ocean were available from only two locations (south-west and central-east) (yellow marker parts in Map 2) and there was no evidence of genetic structure between them. Availability of samples from sufficient locations (and narrow range of size/age classes) for otolith microchemistry also limited our ability to make strong inferences about population structure within the Indian Ocean. In future, development of structured sampling programs with key distant water fishing fleets targeting albacore, to obtain samples from the central-southern and south-eastern Indian Ocean, and Indonesia, for samples from the spawning grounds south of Java, will be important to improve the understanding of population structure of albacore within the Indian Ocean.

Because of this result (i.e., no robust conclusions on stock structure in the IO ALB due to limited samples from only two small sub-areas in the whole IO) and the above-mentioned situation, it is again suggested to assume the single stock hypothesis for the 2022 IOT ALB stock assessments.



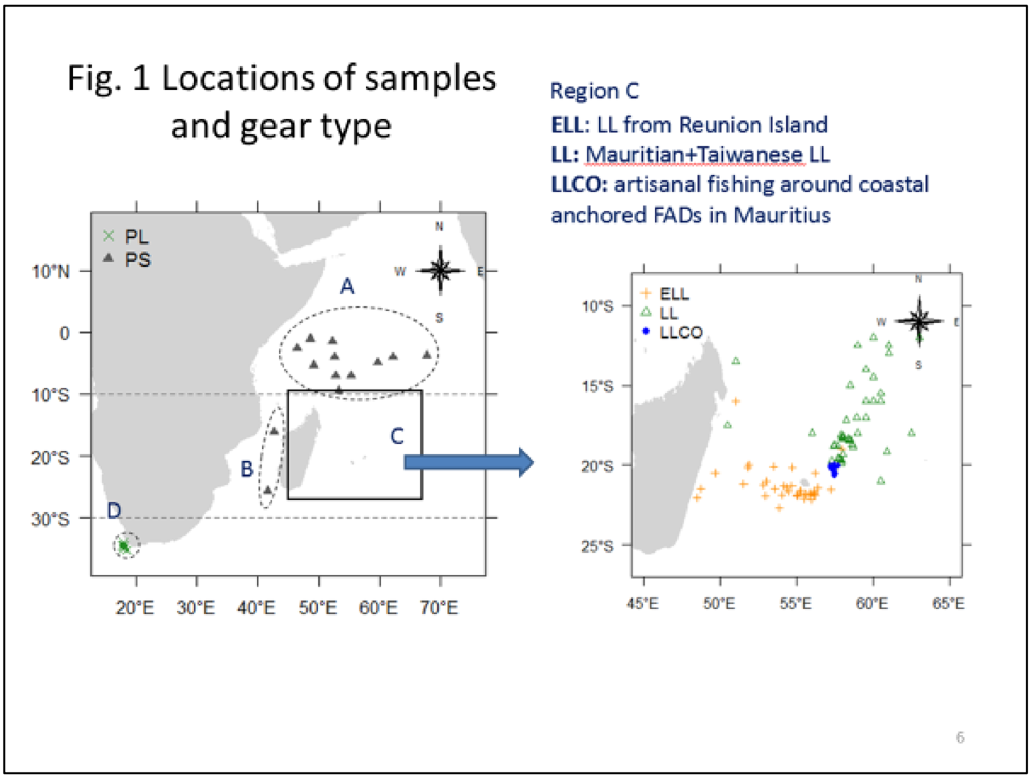
Map 2 Two locations (yellow marker parts) showing the sampling locations of genetic and otolith microchemistry in the Population Structure and connectivity of priority Tuna and tuna-like Species within the Indian Ocean (PSTBS-IO) project funded by the EU (2017-2019) (Davies et al, 2020).

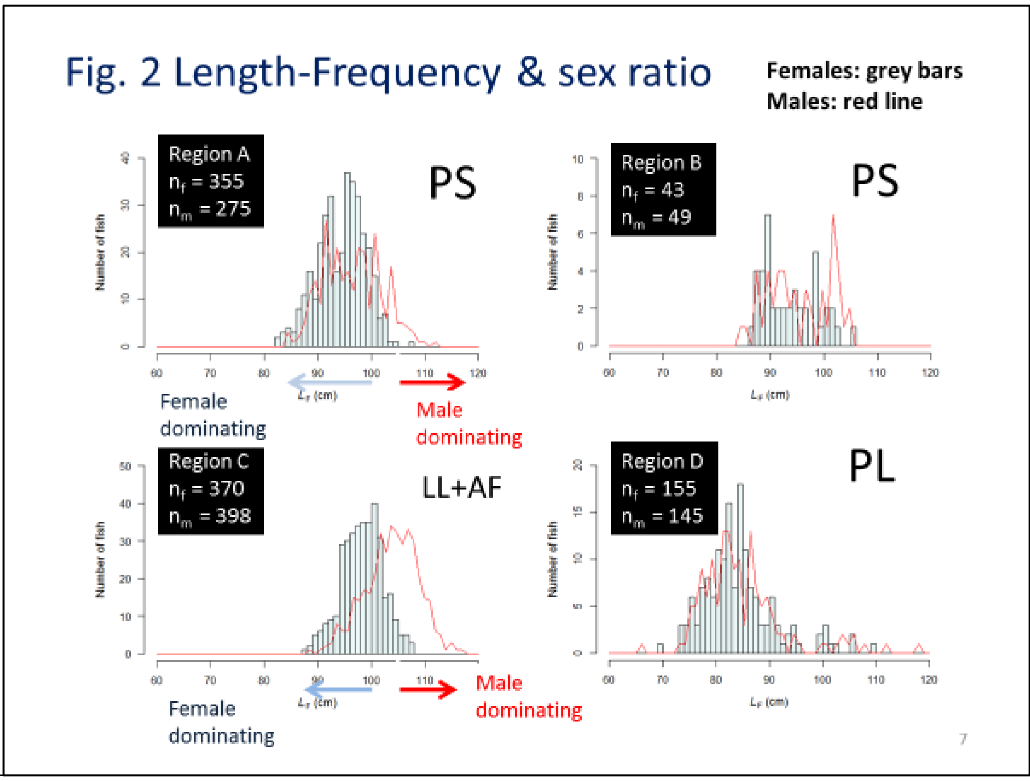
2.2 Biological parameters

(1) Sex ratio

It has been reported that sex ratio of immature ALB is approximately 1:1, while for mature, the male ratio is higher than female by ISC (2017), ICCAT (2014), WCPFC (2018) and Dhurmeea *et al* (2016) (western Indian Ocean) (Figs. 1 and 2). In ISC, WCPFC and ICCAT, due to sampling problems, 1:1 sex ratio had been used for stock assessments.

IOTC also used 1:1 in the past. In the ISC, the sex structured stock assessment was conducted using the heterogenous sex ratio (ISC, 2020). We have the information from Dhurmeea et al (2016) and we need to discuss if we can conduct the two-sex stock assessments as a sensitivity, while we conduct the sex combined stock assessment as a base case as in the past.





(2) LW relation

Table 1 shows the summary of the LW relations by Ocean (tuna RFMO). In the Indian Ocean there are four LW relations. Among them, the ones by Hsu (1999) and Setyadi et al (2012) were based on gillnet and longline. Thus the size ranges are limited hence the LW relations are likely biased. By that the reason, they were not used in the past IOTC ALB stock assessments. The LW relation by Penny (1994) from the south Atlantic Ocean adjacent to the Indian Ocean was used in the past IOTC ALB stock assessments in 2016 or before. This is because there are possible intermingling in the bordering waters likely reflecting the LW relations in the western Indian Ocean to some extent and there are the wider range of size samples (46-118cm) with a large sample size (n=1,008).

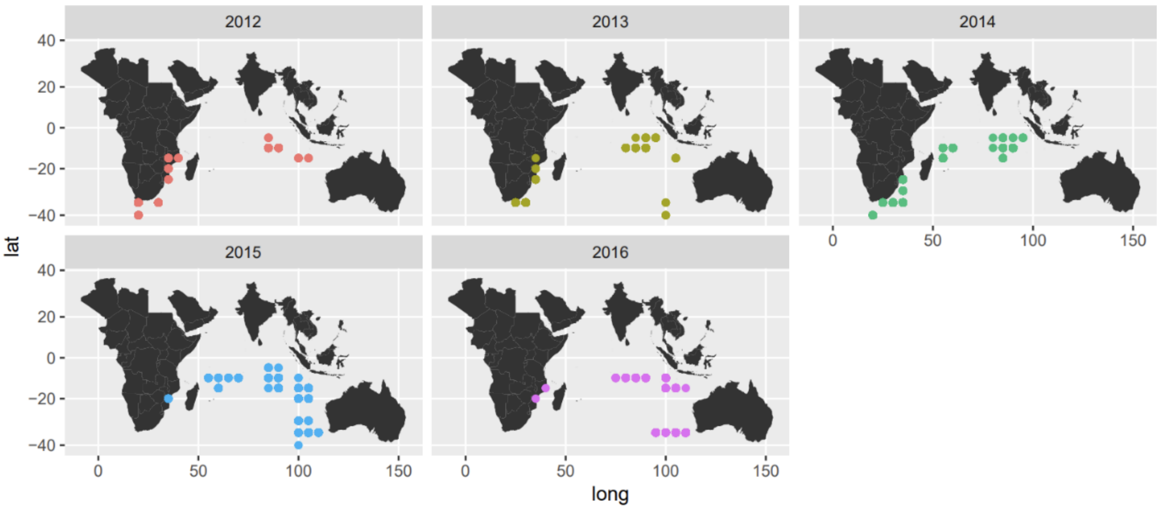
Table 1 Summary of LW relation by Ocean (tuna RFMO) and fisheries

Ocean	Equations W: Round weight (kg) L: Fork length (cm)	Authors (year)	Type of gear, ranges and n (sample size)	Assessment year (RFMO) and models
Indian	$W = (0.69 \times 10^{-5}) * L^{3.2263}$	Kitakado et al. (2019)	Whole Indian Ocean (2012-2016) (all gears?) (50-130 cm)	2019 (IOTC) SS3+ASPM
	$W = (5.6907 \times 10^{-5}) * L^{2.75140}$	Hsu (1999)	Gillnet (n=2,499) (46-112 cm)	2012 (IOTC) SS3+ASPM
	$W = (8.0000 \times 10^{-5}) * L^{2.27271}$	Setyadi et al (2012)	Eastern LL (n=497) (83-106cm)	
	[♂] $W = (4.3378 \times 10^{-6}) * L^{3.3551}$	Dhurmeea et al (2016) (Western IO)	All (n= 702) (67-118cm)	
	[♀] $W = (1.7551 \times 10^{-6}) * L^{3.5625}$		All (n= 814) (70-110cm)	
	[♂+♀] $W = (3.2537 \times 10^{-6}) * L^{3.4240}$		All (1,516) (67-118cm)	
N. Atlantic	$W = (1.3390 \times 10^{-5}) * L^{3.1066}$	Santiago (1993)	All (n=714) (42-117cm)	2013・2016 (ICCAT) SS3 MFCL and VPA+2BOX
S. Atlantic	$W = (1.3718 \times 10^{-5}) * L^{3.0973}$	Penney (1994)	All (n=1,008) (46-118cm)	2016 (IOTC) SS3＋SCAA
N. Pacific	$W = (8.7000 \times 10^{-5}) * L^{2.6700}$	Watanabe *et al.* (2006)	All (Japan + USA + Taiwan) (1989-2004)	2011・2017 (ISC) SS3 + VPA-2BOX
S. Pacific	$W = (0.69587 \times 10^{-5}) * L^{3.2351}$	Hampton (2002)	All	2012 ・2018 (WCPFC) MFCL

In 2016, Dhurmeea et al (2016) estimated the LW relation by sex, based on samples from the western Indian Ocean. However, there are no samples from the smaller fish (size less than 70cm) thus the LW relation is biased to some extent. By that reason, they were not used in the 2016 IOTC ALB stock assessment, and the one by Penny (1994) was used again.

In 2019, the new LW relation was estimated by Kitakado et al (2019) using samples covering the wider size ranges (50-130cm) by major gears in the whole Indian Ocean (Map 3). Thus this LW relation is considered to reflect the real situation. By that reason, it was used in the 2019 stock assessment.

Fig. 3 shows the comparisons among three LW relations by Penny (1994), Dhurmeea et al (2016) (sex combined) and Kitakado et al (2019). As samples from the smaller fish size less than 70cm are not available in the LW relation by Dhurmeea et al (2016), it is likely over estimated. The LW relations between Penny (1994) and Kitakado et al (2019) are similar, but Penny (1994) did not cover larger fish > 118 cm, while Kitakado et al (2019) cover the full ranges (50-130cm). Thus, it is suggested again to use the LW relation by Kitakado et al (2019) based on samples from the whole Indian Ocean for the 2022 IOTC ALB stock assessments



Map 3 Annual sampling locations (2012-2016) used to estimate the LW relation estimated by Kitakado et al (2019).

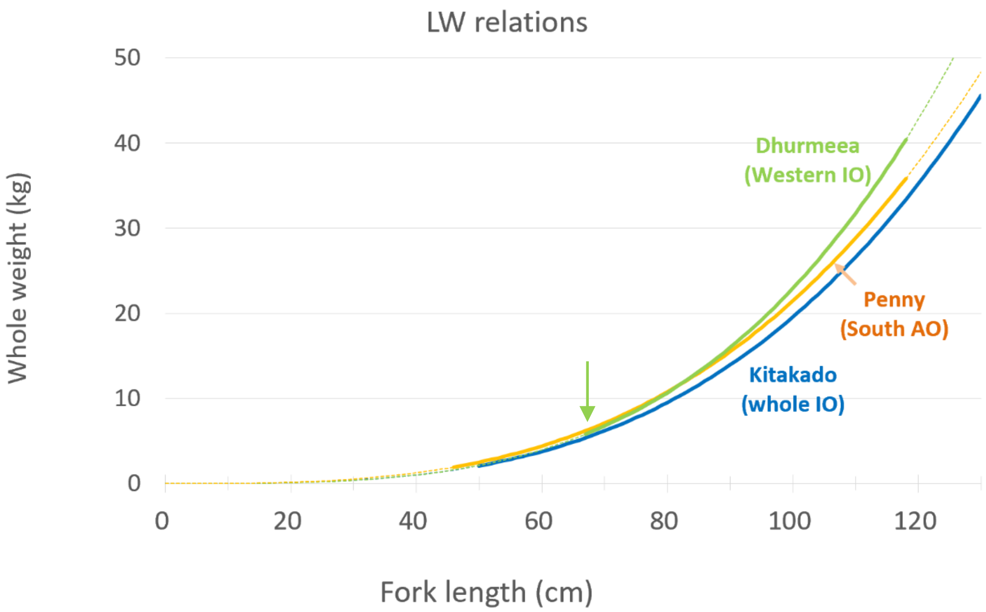


Fig. 3 Comparisons among three LW relations by Penny (1994), Dhurmeea et al (2016) and Kitakado et al (2019) (Solid lines represent the size range).

(3) Growth equations

Table 2 lists growth equations by Ocean (tuna RFMOs). In the Indian Ocean, there are six equations. Among them, five equations by Huang et al (1990), Lee and Liu (1992), Chang et al (1993), and Lee and Yeh (2007), are based on scale patterns, vertebrate rings, size frequency, and spine & Vertebra respectively. The WPTmT in the past, prefers to use those based on otolith, thus these five equations were not used for stock assessments. There are three growth equations in North Pacific Ocean, i.e., Chen et al (2012), Well et al (2013) and Xu et al (2014). Among them, the size range (frequency) by Chen et al (2012) is similar to those in the Indian Ocean. By that reason, its growth equation have been used in the IOTC ALB stock assessment in 2016 or before

The last (sixth) growth equation by sex is estimated by Farley et al (2019) using otoliths collected in the western Indian Ocean (Seychelles, South Africa, Reunion and Mauritius) (Map 4). It was suggested that sample of smaller size (< 75cm) are needed to provide more plausible growth equations. Figs. 4 and 5 are comparisons between two growth curves by Farley et al (2019) and Chen et al (2012) by male and female respectively. Although there may be potential biases in the Farley's equation due to no smaller size data (< 70 cm), the Farley's equation was used for the 2019 IOTC ALB stock assessments because the two equations are similar and the Farley's equation are based on otoliths from the western Indian Ocean.

Table 2 Summary of growth equations by Ocean (tuna RFMO), range, sample size and SA methods.

Ocean	Equations L: fork length(cm) t: year	Range(cm) Sample size (n)	Authors (year)	Estimation method	Assessment year (RFMO) SA models
Indian	$L(t)=128.13\,[1-e^{-0.1620\,(t+0.8970)}]$	65-106 (n=227)	Huang *et al* (1990)	Scale patterns	
	$L(t)=163.70\,[1-e^{-0.1019\,(t+2.0668)}]$		Lee + Liu (1992)	Vertebrate rings	
	$L(t)=136.00\,[1-e^{-0.1590\,(t+1.6849)}]$		Chang et al (1993)	Size frequency	
	$L(t)=147.50\,[1-e^{-0.1260\,(t+1.8900)}]$	51-131 (n=469)	Lee and Yeh (2007)	Spine and Vertebra	2012 (IOTC) SS3+ASPM
	[♂] $L(t)=110.6\,[1-e^{-0.34\,(t+0.87)}]$	67-115 (n=251)	Farley et al (2019)	Otolith	2019 (IOTC) SS3+SCAA
	[♀] $L(t)=103.8\,[1-e^{-0.38\,(t+0.86)}]$	74-108 (n=251)			
N Pacific	[♂] $L(t)=114.0\,[1-e^{-0.253\,(t+1.01)}]$	44-118 (n=148)	Chen *et al* (2012)	Otolith	2013(IOTC) SS2+ASPM 2016(IOTC) SS3+SCAS
	[♀] $L(t)=103.5\,[1-e^{-0.340\,(t+0.53)}]$	46-100 (n=125)			
	$L(t)=124.10\,[1-e^{-0.164\,(t+2.2390)}]$	52-128	Well *et al* (2013)	Otolith	2014 (ISC) SS3 2016 (IOTC) SCAA
	[♂] $Lt = 119.15 + (47.563 - 119.15)\, e^{(-0.20769*(t-1))}$ [♀] $L(t) = 106.57 + (43.504 - 106.57)\, e^{(-0.29763*(t-1))}$ [♂+♀] $L(t) = 112.379 + (45.628 - 112.38)\, e^{(-0.2483*(t-1))}$		Xu *et al* (2014) (base on Chen- Wells equations)	Otolith	Equation by sex 2017 (WCPFC) N Pacific: SS3 2018 (WCPFC) S Pacific: MFCL
S Pacific	$L(t)=121.00\,[1-e^{-0.1340\,(t+1.9220)}]$	44-110	Labelle *et al* (1993)	Vertebrate rings	2011 (WCPFC)MFCL
	Growth equation estimated by MFCL with L1 parameter (length at which individuals first enter the fishery) of 34.2 cm and sex-combined growth equation by Williams et al. (2012)				2018 (WCPFC) MFCL
N Atlantic	$L(t)=124.74\,[1-e^{-0.2300\,(t+0.9892)}]$	46-113	Bard (1981)	Spine (n=352)	2016 (ICCAT) SS3+ MFCL
	$L(t)=127.10\,[1-e^{-0.2300\,(t+0.9892)}]$	40-119	Santiago *et al* (2005)	Spine	
S Atlantic	$L(t)=147.50\,[1-e^{-0.1260\,(t+1.8900)}]$	51-131 (n=469)	Lee and Yeh (2007)	Spine and Vertebra	*not used as production models were applied*

Map 4
Locations of otoliths collected in the age and growth study by Farley et al (2019) in the western Indian Ocean

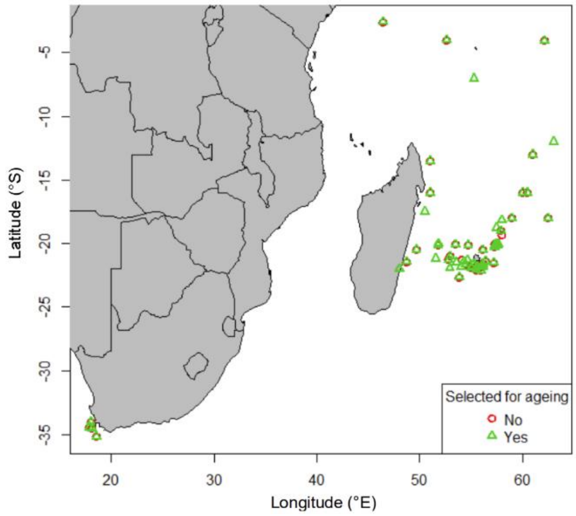


Fig. 4 Comparisons of growth curves (males)
W. Indian (Farley, 2019) vs. N. Pacific (Chen, 2012)

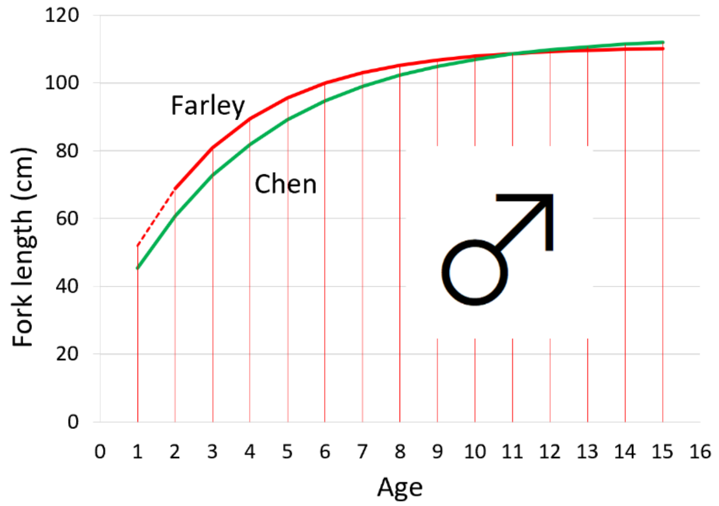
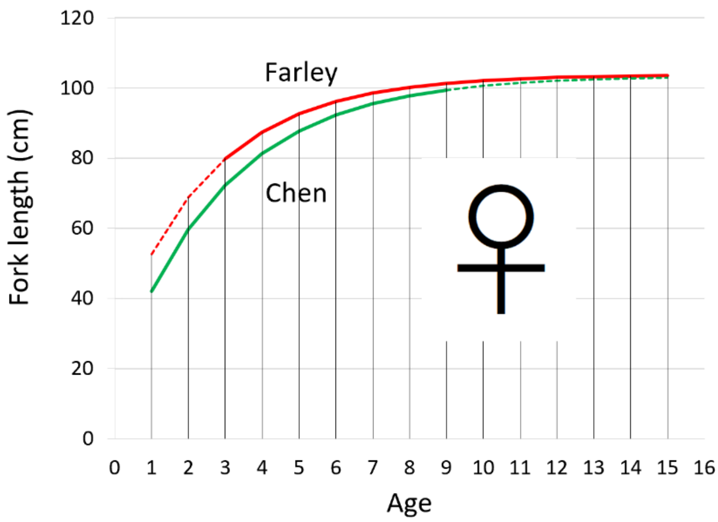


Fig. 5 Comparisons of growth curves (females)
W. Indian (Farley, 2019) vs. N. Pacific (Chen, 2012)



(4) Life span

Table 3 shows the life span and + group and Fig. 6 shows the life span by Ocean (tuna RFMO), indicating large variations among them. According to the tag recovery information (N. Pacific), Age 16 is recorded as maximum. In addition, based on the age estimation by otolith, the maximum age is 14 (S. Pacific). Therefore, Age 14-16 are likely plausible life span. Thus, it is suggested to use age 14 (life span) and the age 14+ as the plus group for the 2022 IOTC ALB stock assessments as in the past (2016 and 2019).

Table 3 Summary of life spans and + group age by Ocean (tuna RFMO)

Ocean	Life span (years old)	Authors/RFMO (year)	Method	Assessment year (RFMO) Stock assessment models
Indian	8	Huang *et al.* (1990)	Scale	Not used in assessment
	10	IOTC (2012)		2012 (IOTC) SS3+ASPM
	14	IOTC (2016 & 2019)	Refereed to N Pacific, i.e., age 14 (otolith)	2016 (IOTC) SS3 + ASPM 2019 (IOTC) SS3 + SCAA
N. Atlantic	8	ICCAT (2013)		2013+2016 (ICCAT) MFCL, VPA+2BOX and SS3
S. Atlantic				Not used in assessment
N. Pacific	16	Anon (2013)	Tagging (based on the long-term recovery)	Not used in assessment
	14			2011 +2017 (ISC) SS3 + VPA-2BOX
S. Pacific	11		Tagging (based recovery data)	Not used in assessment
	12			2012+2018 (WCPFC) MFCL
	14		Otolith	Not used in assessment

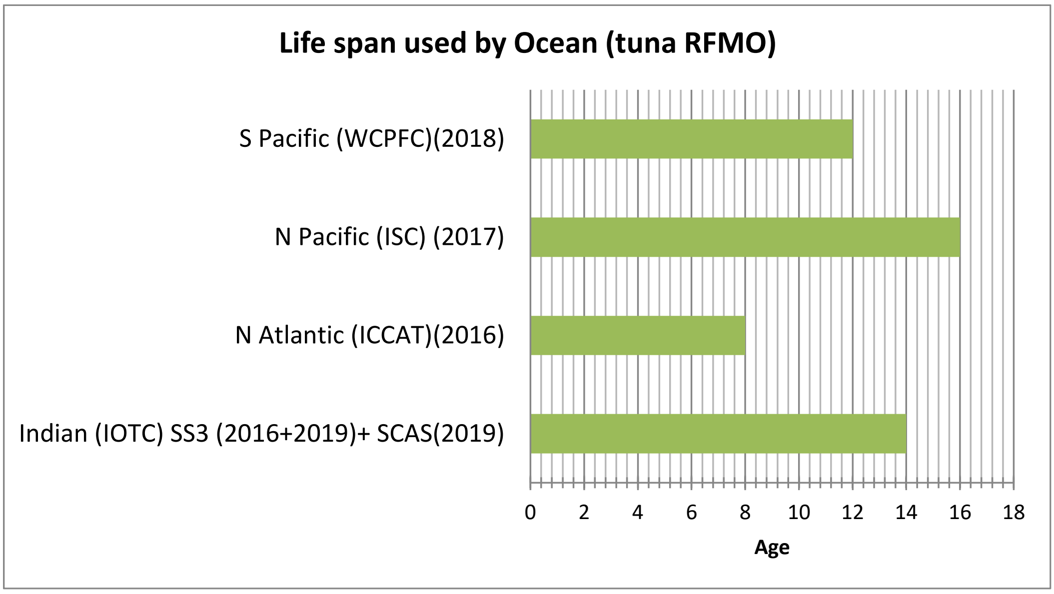


Fig. 6 Life span by Ocean (tuna RFMO) used for their stock assessments

(5) Natural mortality

Table 4 and Fig. 7 show natural mortality (M) by age, sex and Ocean (tuna RFMO) used in the past stock assessments indicating both base case and sensitivities. Fig. 8 shows M used in IOTC stock assessments (2016 and 2019). Bases on Table 5 and Fig. 7, M in the Indian Ocean is much lower (< 0.22) than those in other RFMOs. As M=0.3 are common among RFMOs, it is again suggested to use M=0.3 as the base case and the hybrid one (M=0.2207 and M=0.4) as the sensitivity to reflect the plausible situation in the Indian Ocean for the 2022 IOTC ALB stock assessments.

Table 4 M by age, sex and Ocean (tuna RFMO) used in past stock assessments.

Ocean	Parameters: base case (sensitivities)	Authors (year)	Estimation method	Assessment year (RFMO) Stock assessment models
Indian (IOTC)	0.2207 (0.4)	Lee and Liu (1992)	Estimated by Z=q*F+M using LL data	2012(IOTC) SS3 and ASPM
	0.2060	Lee *et al.* (1990)	Pauly (1980) method (using temperature)	
	0.3 (0.2207 and hybrid, see Fig. 7)	(N Atlantic and N Pacific)		2016 & 2019 (IOTC) SS3+SCAA
N. Atlantic (ICCAT)	0.3 (age 0-14) (0.63; 0.46; 0.38; 0.34; 0.31; 0.29; 0.31; 0.34; 0.38; 0.44; 0.55; 0.55; 0.55; 0.55; 0.55)	Santiago (2004)	M is from SPC (2003) and M by age is estimated by Chen and Watanabe (1988) using the Bard's method	2013 + 2017 (ICCAT) SS3, MFCL, SS3 and VPA+2BOX
	Age 0-2 Male age 3+; 0.39 Female 3+: 0.48			
N. Pacific (ISC)	0.3	Watanabe et al (2006)		2011 (ISC) SS3 + VPA-2BOX 2014 (ISC) SS3
	Female Male Age 0: 1.36 1.36 Age 1: 0.56 0.56 Age 2: 0.45 0.45 Age-3+: 0.48 0.39	Teo (2017a)		2017(ISC) (SS3)
S. Pacific (WCPFC)	0.4 (0.3 and 0.5)	Hoyle et al (2012)		2012 (WCPFC) MFCL
	0.3 (0.2, 0.4 and 0.5)	Tremblay-Boyer et al (2018)		2018 (WCPFC) MFCL

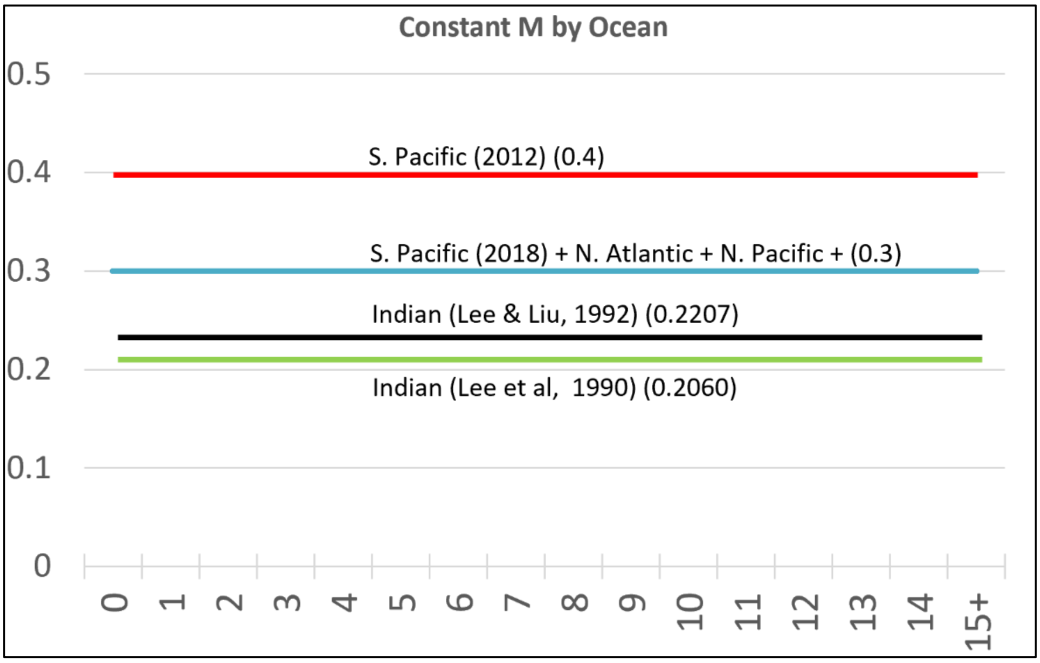


Fig. 7 Constant M by Ocean

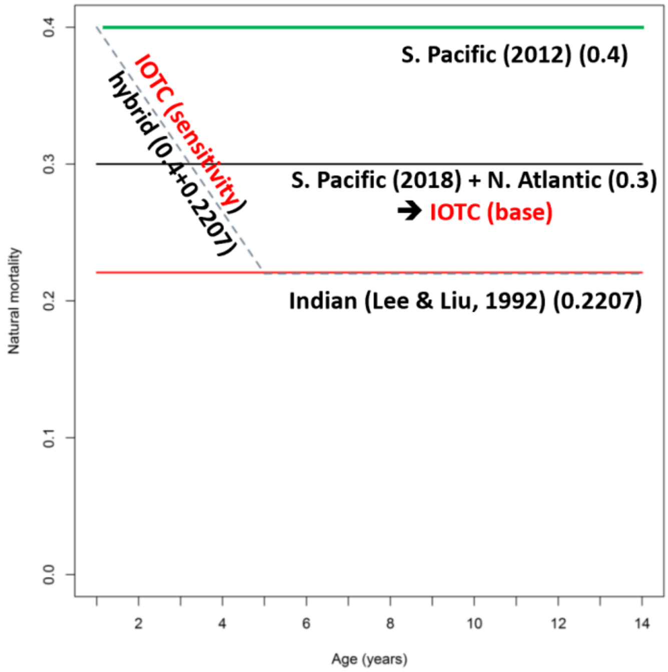


Fig. 8 M=0.3 (based case) used in the last 2 stock assessments in IOTC (2016 and 2019) (black solid line), while for sensitivity, the hybrid with 0.2207 and 0.4 (dotted line).

Discussion (age specific M)

M=0.3 or 0.4 are commonly used as base cases for stock assessments in all Oceans (t-RFMOs). These two values are likely empirical basis as no concrete explanations are found in references. There are age specific M used in N. Pacific (based on the Lorenzen theory) and N. Atlantic (based on the Bard method) (Fig. 9). However, these were used for the sensitivities as M=0.3 or M=0.4 likely provided the plausible stock assessment results.

As the biological point of view (the Lorenzen theory), it is clear that the immature M should be higher than in matures. In our case in the Indian Ocean, we use such scenario in the sensitivity as shown in Fig. 8, thus it may be more plausible. However, there are no theoretical background about this scenario. Thus, we need to explore the science-based age specific M as the future work.

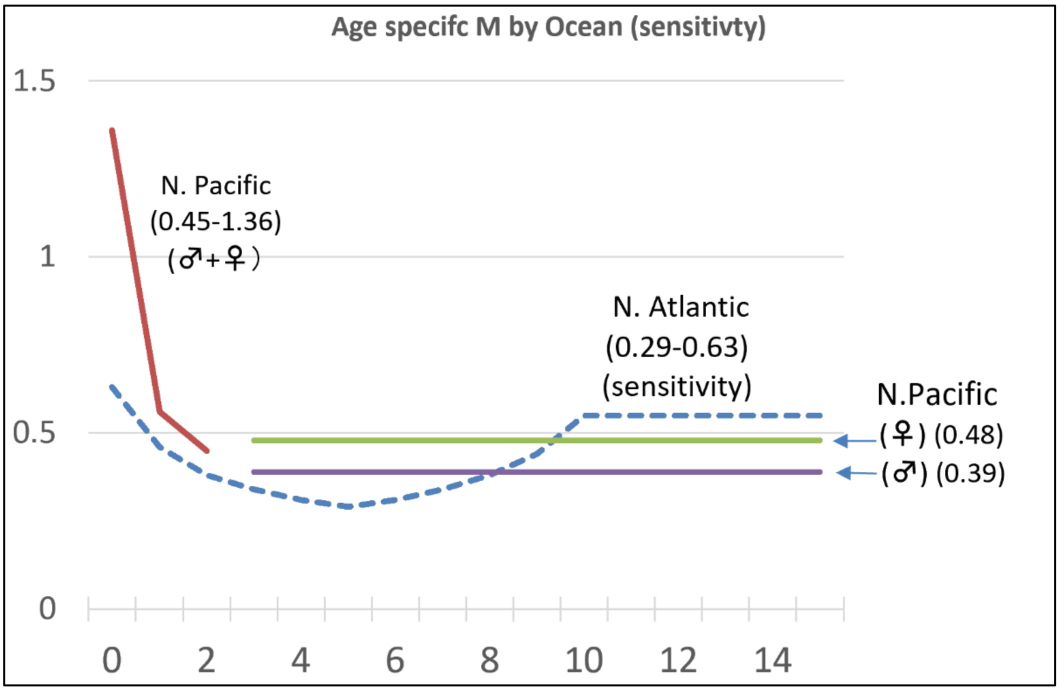


Fig. 9 Age specific M used as sensitivities in the stock assessments
(N. Pacific and N. Atlantic)

(6) Fecundity-at-age

Fecundity is directly related to female biomass (Wt) i.e. eggs=Wt*(a+b*Wt) with a=0 and b=1 (Langley, 2019), which can be substituted by proportion to female weight at age (Nishida and Dhurmeea, 2016).

(7) Maturity-At-Age

Table 5 and Fig. 10 show the summary of Maturity-At-Age information by Ocean (tuna RFMO). In the past, two types of maturity-at-age were used in the IOTC ALB stock assessment, i.e., (a) 0 (age <=4), 0.5 (age=5) and 1.0 (age =>6) by Bard (1981) (N. Atlantic) in MFCL and SS3 (ICCAT) and (b) Age specific maturity-at-age developed by Farley et al (2014) (S. Pacific). The larger number of samples were used in S. Pacific thus the maturity-at-age is likely more robust than the one in N. Atlantic based on crude knife edge type M. By that reason, the Farley's maturity-at-age were applied for the IOTC ALB stock assessment in 2016 or before.

The first maturity-at-size in the Indian Ocean was estimated by Dhurmeea et al (2016) (Fig. 10) and presented in the WPTmT06(2016) meeting. The meeting noted that the length at maturity (L50) (85cm or 3.2 years old), appears to be much younger than those in other Oceans due to samples being from only limited areas and time. Thus, the meeting suggested that additional samples covering more area and time in the whole Indian Ocean to confirm the findings of the study. Hence, it is again suggested to use the Farley's maturity-at-age in S. Pacific for the 2022 IOTC ALB stock assessments.

Table 5 Summary on Maturity-at-age by Ocean (tuna RFMO)

Ocean	Parameters	Authors (year)	Assessment year (RFMO) and models
Indian	0 (age <=3), 0.25 (age=4), 0,5 (age=5), 0.75 (age 6) and 1 (age =>7)	Anon (2012)	2012 (IOTC) SS3+ASPM
	0.5 (85cm) or age 3.2 bases on the growth eq. by Farley et al (2019)	Dhurmeea et al (2016) Western Indian Ocean	
N. Atlantic	0 (age <=4), 0.5 (age=5) and 1.0 (age =>6)	Bard (1981 and 1982)	2013 and 2016 (ICCAT) MFCL and SS3
N. Pacific			2011and 2017 (ISC) SS3
S. Pacific	0, 0, 0, 0, 0.089, 0.466, 0.746, 0.881, 0.944, 0.973, 0.987, 0.994, 0.997 and 1 for older ages	Biological data by Farley et al (2014) and derived by the method by Hoyle (2008)	2012 and 2018 (WCPFC) MFCL 2019 or before (IOTC) SS3+SCAA
	0 (age<=4), 0.23 (age 5), 0.57 (age=6), 0.88 (age=7) and 1 (age=> 8)	Anon (2011)	2011 (ISC) SS3

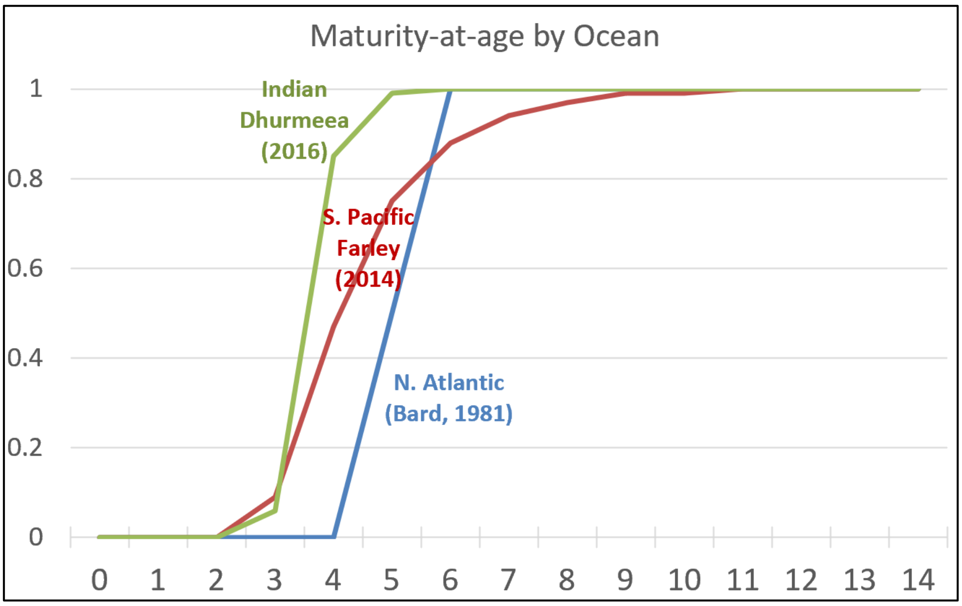


Fig. 10 Maturity-at-age by Ocean (tuna RFMO)

3. Future works

We need the sex-based stock assessments in the future (e.g. ISC, 2020), which reduce biases and uncertainties caused by the mature male dominant sex ratio. To do this, we need to investigate following information in the future:

Priority works

- Sex ratio by area and season;
- LW relations by sex;
- Growth equations (W IO) by sex by Farley et al (2019) need to be improved using more otolith samples from all gear types in the whole Indian Ocean;
- M by age and sex; and
- Maturity-At-Age (W IO) by Dhurmeea et al (2016) need to be improved using more samples from all gear types in the whole Indian Ocean.

Less priority works:

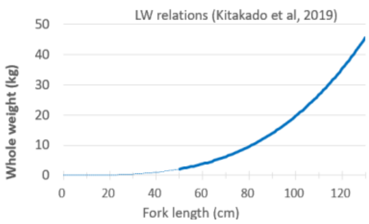
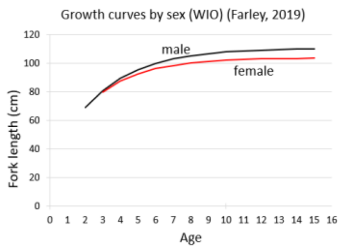
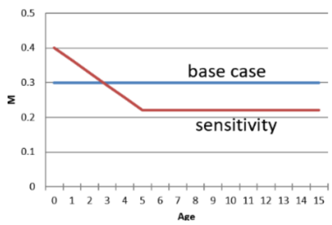
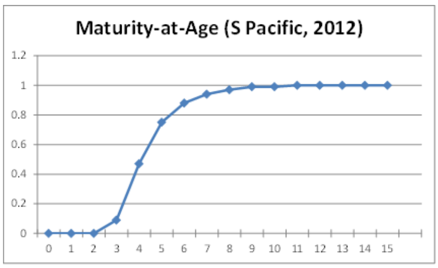
- Stock structure using samples (tissues and otoliths) from the whole IO; and
- Life span by sex using age estimation by otoliths.

To do these future works, we need to seek funds. For example, refer to IOTC-2022-WPTmT08(DP)-INF01, i.e., Review the Improving biological knowledge of albacore tuna in the Indian Ocean: a scoping study prepared for FAO by Moore et al (2020).

4. Summary

Table 6 shows suggestions of biological and ecological parameters (base case and sensitivities) for the 2022 IOTC ALB stock assessment. The base case is resulted as identical as in the 2019 IOTC ALB stock assessments. We need to discuss if it is acceptable. In addition, we need to consider the sensitivity.

Table 6 Summary on the suggested parameters for 2022 ALB stock assessments in the Indian Ocean.

Parameters	Base case	Sensitivity
Stock structure	Single	(No)
Biological parameters		
(1) Sex ratio	1:1	Heterogenous rates
(2) LW relation	$W = (0.69 \times 10^{-5}) * L^{3.2263}$ Kitakado et al (2019) 	
(3) Growth equation	♂ L(t)=110.6 [1-e-0.34 (t+0.87)] ♀ L(t)=103.8 [1-e-0.38 (t+0.86)] Farley et al (2019) SS3 incorporates the sex based growth equations. 	
(4) Life span	Age 14+	
(5) M by age	0.3 (N. Atlantic and N & S Pacific) 	hybrid 0.2207 (Indian) & 0.4 (S. Pacific)
(6) Fecundity	Fecundity is directly related to female biomass (Wt) i.e. eggs=Wt*(a+b*Wt) with a=0 and b=1 (Langley, 2019), which can be substituted by proportion to female weight at age (Nishida and Dhurmeea, 2016).	
(7) Maturity-at-age	Farley et al (2012) (S. Pacific) Age (0-15): 0, 0, 0, 0.09, 0.47,0.75, 0.88, 0.94, 0.97, 0.99, 0.99, 1, 1, 1 	

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