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APPLICABILITY OF HISTORICALLY BASED LIMIT REFERENCE POINTS TO THE NORTHERN TUNA STOCKS IN THE PACIFIC

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Applicability of historically-based limit reference points to North Pacific tuna stocks

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Abstract

Temperate tunas in the North Pacific including Pacific bluefin tuna and the northern stock of albacore tuna have been observed to experience considerable fluctuations in stock abundance over a long period of time, whereas the abundance of tropical tunas in the western and central Pacific (i.e. the southern stocks) has consistently decreased during relatively short exploitation histories. In consideration of these characteristics, we examined, theoretically as well as empirically, the applicability of historically-based limit reference points (LRPs) such as F_{loss} to North Pacific stocks and contrasted these with maximum sustainable yield (MSY)-based LRPs such as F_{MSY} proposed for Western and Central Pacific southern stocks. Numerical simulations indicated that historically-based LRPs are appropriate for northern stocks when recruitment compensation is high (i.e. when "steepness" in the stock recruitment relationship is high). In contrast, MSY-based LRPs often have a high risk of allowing recruitment overfishing of northern stocks when process errors are large. Based on these results, we suggest that LRPs set with reference to historical stock sizes are worthy of consideration for temperate tunas in the North Pacific.

Introduction

The Western and Central Pacific Fisheries Commission (WCPFC) established a hierarchical approach to identifying limit reference points (LRPs) based on the extent of biological knowledge available for each stock (Table 1; Harley et al. 2012). The applicability of such LRPs to tropical tunas in the southern Western and Central Pacific, including yellowfin tuna (YFT, *Thunnus albacares*), bigeye tuna (BET, *Thunnus obesus*), and the southern stock of albacore tuna (ALB-S, *Thunnus alalunga*), has been considered. However, estimation of demographic parameters related to these LRPs would be problematic for temperate tunas in the North Pacific, including Pacific bluefin tuna (PBF, *Thunnus orientalis*), and the North Pacific stock of albacore tuna (ALB-N), because there is a large degree of uncertainty in the estimates of unfished biomass (B_0) and natural mortality (M) (Aires-da-Silva et al. 2009, Anon. 2011).

The historical population dynamics of tropical tunas in the southern Western and Central Pacific is different from that of temperate tunas in the North Pacific (Kurota and Kai 2012). In this paper, tropical tunas in the Western and Central Pacific are referred to as "southern stocks" and the temperate tunas in the North Pacific are referred to as "northern stocks". Southern stocks are characterized by one-way decreasing trends of spawning stock size (S) over relatively short exploitation histories. This means that S in the earliest years of the fishery was at or near virgin spawning stock size (S_0) (**Fig. 1**). In addition, for the southern stocks, while the trends in S during the time period covered by stock assessments tend to gradually decrease, S is still maintained near or above S_{MSY}, the stock size at maximum sustainable yield (MSY) (Aires-da-Silva and Maunder 2010, 2011; Davies et al. 2011; Langley et al. 2011; Hoyle et al. 2012). In contrast, northern stocks have experienced long-term temporal fluctuations in S over the centuries due to climate change (e.g. regime shift) as well as fishing pressure. The initial value S for the northern stocks during the period examined in the stock assessments is considered to have already declined from S_0 (Anon. 2010, 2011). S for northern stocks during the assessment period was maintained below S_{MSY} for PBF and above S_{MSY} for ALB-N, and reached historical minima for S (S_{loss}) of 15,223 t (2.67% of S_0) in 1988 for PBF and 263,935 t (30.8% of S_0) in 1985 for ALB-N (Anon. 2010, 2011). However, because recruitment (R) in the northern stocks (PBF) did not substantially decrease even at very low levels of S, it is considered that recruitment overfishing, which occurs when a population has been fished down to a point where recruitment is substantially reduced or fails (Sissenwine and Shepherd 1987), did not occur. In the 1990s, S of the northern stocks recovered and was subsequently maintained near the historical median levels (**Fig. 1,** Anon. 2010, 2011). Therefore, we assume that the population dynamics scenario for the southern stocks is a "one way trip" over a relatively short history of exploitation (**Fig. 2**), whereas the population dynamics scenario for the northern stocks is a "V-shaped turnaround" over a relatively long history of exploitation (**Fig. 2**).

In developing appropriate fisheries management measures, demographic features such as life history strategies and exploitation histories of target species to be managed should be taken into account. Hilborn and Stokes (2010) discussed the definition of “overfished” and warned that biological reference points (RPs) based on stock biomass corresponding to MSY (B_{MSY}) and virgin stock biomass (B_0) are arbitrarily used for fisheries management despite difficulties of interpretation and estimation of these quantities. For example, it is known that in the case of fishes with high productivity, yields that are close to MSY (for example "Pretty Good Yield") can be obtained over a broad range of stock sizes (i.e. even when stock size is lower than B_{MSY}; Hilborn 2010). As an alternative, they recommended using historical stock sizes as target or limit RPs, because these RPs have the advantages of being based on species-specific experience, are easily understood, and are not subject to uncertainties in model assumptions. Such RPs based on historical stock sizes are commonly applied in fisheries management (ICES 2008, Kanaiwa 2012). Therefore, it is considered valuable to examine the performance of historically-based RPs such as F_{loss} (**Table 2**, Cook 1998) both theoretically and empirically when determining management strategies. The objectives of this paper are (1) to propose alternative historically-based limit reference points (LRPs) such as F_{loss} for northern stocks; (2) to compare the performance of historically-based and MSY-based LRPs (F_{loss} and F_{MSY}) using numerical simulations for northern and southern stocks; and (3) to discuss the applicability and advantages of historically-based LRPs for particular northern stocks (**Table 2**).

A series of documents submitted by Japan to the WCPFC Management Objectives Workshop are not intended to re-open the valuable discussions held at WCPFC Scientific Committee meetings regarding reference points for WCPFC stocks. However, we believe that it is valuable and constructive to present additional ideas on other candidate RPs potentially applicable to the northern stocks of the WCPFC which have not yet been discussed at the SC meetings.

Methods

We present a basic simulation model which can be used to evaluate the differential performance of two LRPs defined in terms of fishing mortality (F) for southern and northern stocks in the Western and Central Pacific Ocean. This model is used to contrast the historically-based LRP F_{loss} with the MSY-based LRP, F_{MSY} (**Table 2)**. In addition, in order to create a set of indicators of varying sensitivity to the risk of recruitment overfishing, we estimated fishing mortality rates (F) at various fractions of S_{MSY} (i.e. 100%, 50%, 20% and 10%, and S=0), each of which represents varying degrees of depletion of stock biomass. We then evaluated the performance of F_{loss} and F_{MSY} in terms of the probability that either of these candidate LRPs would exceed the value of F at the various depletion levels, and would therefore represent a risk of recruitment overfishing.

Simulation model

A basic population dynamics model ("operating model") was used to define the "true state" of the system for the purpose of the simulation. The details of the model in terms of its equations and derivations are given in the **Appendix.** We assume that the population (in number) is increased by recruitment and decreased by fishing and natural mortalities in annual increments. The recruitment is given by the Beverton-Holt (BH) stock recruitment (SR) model or Ricker (RI) SR model. The former is characterized by an asymptotic recruitment plateau and the latter is characterized by a recruitment decline at high stock sizes. Steepness (h), which is the fraction of recruitment (R) from an unfished population (R_0) when S is 20% of its unfished level (Mace and Doonan 1988), is intrinsically related to the resilience of a species to harvesting and effectively determines the average productivity of fishery resources within a stationary environmental regime (Mangel et al. 2010). Steepness is determined by the parameters of the SR relationship as well as the population size at its unfished level. The population dynamics scenarios for southern and northern stocks were produced by the operating model and its parameterization which set steepness and initial population size as leading parameters. Age-structure after recruitment and individual weight are ignored for simplicity. The annual catch is expressed by the exploited population number. LRPs defined in terms of fishing mortality, such as F_{loss} and F_{MSY}, can be derived from the deterministic process model numerically. In order to evaluate the estimation error associated with F_{loss} and F_{MSY} under stochastic conditions, we 1) examined the effect of process error, which arises from the natural variability associated with fish production systems (Caddy and Mahon 1995), using sensitivity analysis for two levels of process error; and 2) examined observation error by generating a number of pseudo-datasets from the survey indices with observation error.

Simulation analysis

Simulated data were generated based on the operating model and used to evaluate the performance of F_{loss} and F_{MSY} for southern and northern stocks while accounting for uncertainties arising from population dynamics. The procedure consisted of the following five steps (**Fig. 3**).

1. Create the "true state" of the population dynamics for a 50–year time period using a process model (i.e. assume that all parameters are known exactly). The parameters used in the model are listed in **Table 3**. The initial, mid-term and recent states of S are parameterized to reproduce the population dynamics scenario in the northern and southern stocks (**Table 4, Fig. 2**) based on the results of actual stock assessments (**Fig. 1**). For the southern stocks, S_0 is given as initial stock size and it is assumed that S gradually declines to S_{MSY} (i.e. a "one-way trip"). In contrast, the northern stocks in the initial year are assumed to be below S_0 because northern stocks have been exploited for many years prior to the stock assessment period (Ito 1961, Au and Cayan 1998, Muto et al. 2008). It is also assumed that S reaches S_{loss} in the mid-term period and gradually recovers by the end of the period through reduction of F (i.e. a " V-shaped turnaround "). Since the stock levels of the northern stocks relative to unfished levels are different between PBF and ALB-N (Anon. 2010, 2011), we conducted separate analyses for these two stocks.

2. Define various thresholds for recruitment overfishing and calculate fishing mortality rates (Fs) corresponding to these thresholds (**Table 5**) from the process model.

3. Generate 100 pseudo-datasets (time series of S, R, and the survey indices) from the operating model using numerical simulation. Two cases were conducted as a sensitivity test: "small variance" (process errors = 0.2) and "large variance" (process errors = 0.6). The magnitude of large variance corresponded to the commonly used value in the stock assessment models for the northern stocks (Anon. 2010, 2011) and small variance was set arbitrarily to provide a contrast.

4. Estimate the parameters (e.g. steepness) for the 100 datasets using the grid method and then compute the statistical estimators (i.e. F_{MSY} and F_{loss}) (see **Appendix**).

5. Compare the statistical estimators with the fishing mortality rates associated with the thresholds of recruitment overfishing in Step 2. The probability that the statistical estimators exceed the F thresholds is used as a performance statistic. Higher probabilities for a given statistical estimator indicate a higher risk of recruitment overfishing associated with its use as a LRP.

Simulation scenarios

Three simulation scenarios (**Table 6**) in addition to the base case were conducted to examine the effect of uncertainty arising from 1) the relationship between S and R; 2) productivity shifts caused by climate change such as regime shifts (Kurota and Kai 2012); and 3) difficulties in accurately estimating natural mortality (M), a frequent source of uncertainty in fish stock assessments (Vetter 1987). The following scenarios were conducted:

Scenario (I): Intentional mis-specification of the SR model by assuming that the RI model is the "true" SR relationship but using the BH model to estimate the parameters.

Scenario (II): The effect of a regime shift is simulated as a change in the SR relationships due to environmental forcing, i.e. the parameter a of the SR relationship for the first half of the simulation period (first 25 years) is set to 1.5 times the value of a for the second half. This results in an increase in steepness for the first half of the simulation.

Scenario (III): Intentional mis-specification of M, i.e. M is assumed to be 1.5 times larger than the default value.

All analyses were conducted using the R statistical software (http://www.r-project.org/).

Results

Table 7 shows the probabilities that the estimates of F_{loss} and F_{MSY} exceed the thresholds representing recruitment overfishing (e.g. F_{SMSY}, $F_{50\%\mathrm{SMSY}}$, $F_{20\%\mathrm{SMSY}}$, $F_{10\%\mathrm{SMSY}}$ and $F_{S=0}$). **Table 7a** shows the results of the base case. For the southern stocks, the performance of both candidate LRPs is fairly good when steepness is high ($h \geq 0.6$). However, the performance of both F_{loss} and F_{MSY} is poor when steepness is low ($h = 0.3$).

For northern stocks (PBF), the performance of F_{loss} is superior to that of F_{MSY} when steepness is high ($h = 0.9$) and process errors ("variance") are large ($\sigma = 0.6$). The performance of both F_{MSY} and F_{loss} is fairly good with high steepness ($h \geq 0.6$) and small process errors ("variance") ($\sigma = 0.2$). In contrast, the performance of both F_{loss} and F_{MSY} is poor when steepness is low (h=0.3) and process errors are large ($\sigma = 0.6$). However, the performance of F_{loss} is much worse than that of F_{MSY} when steepness is low ($h = 0.3$) and process errors are small ($\sigma = 0.2$). For northern stocks (ALB-N), the performance of F_{MSY} is poor when process errors are small ($\sigma = 0.2$) regardless of the steepness value. Similar results for northern stocks (PBF) are obtained when process errors are large ($\sigma = 0.6$).

Table 7b shows the results for the scenario exploring uncertainty in the SR model (Scenario I). The performance of F_{loss} for all stocks with low steepness ($h = 0.3$) is worse than when steepness is high. When steepness is high ($h \geq 0.6$), for southern stocks, the performance of F_{MSY} is worse than that of F_{loss} irrespective of the magnitude of process errors. For northern stocks (PBF), the performance of F_{MSY} is better than that of F_{loss} when process errors are small ($\sigma = 0.2$), but worse when process errors are large ($\sigma = 0.6$). For northern stocks (ALB-N), the performance of F_{MSY} is worse than that of F_{loss} regardless of the process errors.

Table 7c shows the effect of a regime shift simulation (Scenario II). The performance of F_{loss} and F_{MSY} for all stocks is fairly good even when process errors are large ($\sigma = 0.6$).

Table 7d shows the uncertainty arising from mis-specification of natural mortality (Scenario III). For southern stocks, the performance of both F_{loss} and F_{MSY} is poor when steepness is low (h=0.3), whereas both perform well when steepness is high ($h \geq 0.6$). For northern stocks, when steepness is low ($h = 0.3$), the performance of F_{loss} and F_{MSY} is poor. When steepness is high ($h \geq 0.6$), both candidate LRPs are better when process errors are small ($\sigma = 0.2$). With large process errors ($\sigma = 0.6$)

and high steepness ($h \geq 0.6$), the performance of F_{loss} is better than that of F_{MSY} for the northern stocks.

These results can be summarized as follows:

(1) For southern stocks, the performance of both F_{loss} and F_{MSY} is good when steepness is high, regardless of the magnitude of process errors.

(2) For northern stocks, the performance of F_{loss} is better than F_{MSY} if the steepness and process errors are high.

(3) F_{loss} is more robust than F_{MSY} to the mis-specification of the SR relationship and the value of natural mortality, and to changes in productivity due to regime shifts, as long as the steepness is high.

Discussion

The applicability of F_{loss} to temperate tunas in the North Pacific as a LRP was examined through comparing the performance of F_{loss} and F_{MSY}. When large process errors ($\sigma = 0.6$) were specified in simulations, F_{MSY} had a higher risk than F_{loss} of causing recruitment overfishing of northern stocks, even if recruitment compensation was high (i.e. "steepness" in the stock recruitment relationship is high) (**Table 7a**). Therefore, it is considered that F_{loss} is more appropriate than F_{MSY} as a LRP for northern stocks which are expected to have high process errors.

Harley et al (2011) estimated a range of values of steepness using meta-analysis (Myers et al. 1999) for the world's ten tuna stocks and selected the value of 0.8 (range of 0.65-0.95) as the reference case value for WCPFC assessments of southern stocks. In contrast, the steepness of northern stocks was estimated at around 1.0 (0.999 with a range of 0.8-1.0 for PBF and 0.955 with a range 0.7-1.0 for ALB-N) from life history parameters (Mangel et al. 2011, Iwata et al. 2011, 2012). However, it was noted that there remains considerable uncertainty about plausible values of steepness. Estimates of steepness strongly depend on mortality rates at early life stages, which are known to exhibit high year-to-year variations (Simon et al. 2012), and hence the estimate of steepness has a high uncertainty due to uncertainties associated with early life history parameters. These uncertainties about the plausible values of steepness make the use of MSY-based reference points problematic because the MSY estimate is strongly related to the value of steepness.

In this study, the estimate of steepness was allowed to vary and was shown to produce large biases, particularly when process errors are large. These uncertainties in the estimate of steepness are mainly caused by a lack of contrast in the data (e.g. one-way trip) and the magnitude of process errors. The most serious problem in estimating SR relationships for most datasets is a lack of contrast in spawning stock level (S) (Hilborn and Walters 1992). In other words, to understand how recruitment will respond over a range of S, the stock must have been observed over a broad range of S. We assumed that southern stocks had a one-way decreasing trend from S_0 (15,000) to the MSY level (6,844 for h = 0.3; 5,314 for h = 0.6; and 3,440 for h = 0.9), while both northern stocks have no history of being at their MSY level during the stock assessment period (516-3,000 for PBF; 4,816-12,000 for ALB-N, when h = 0.9), i.e. PBF was below S_{MSY} at the beginning of the simulation period and has remained below it, whereas ALB-N has remained above S_{MSY} throughout the simulation period. This means that the ranges of S for northern stocks are narrower than the ranges for southern stocks. As a result, it is difficult to accurately estimate steepness for northern stocks, especially for PBF, even if the process errors are small. In addition, short-term, large variations in S combined with large process errors further complicates accurate estimation of steepness because the relationships between S and R become unclear. The poor performance of F_{MSY} for the northern stocks is strongly attributable to the lack of data contrast as well as the magnitude of process errors (**Table 7a**). On the other hand, the performance of F_{loss} was fairly good even for northern stocks (**Table 7a**). This is because large process errors caused overestimation of the steepness (e.g. 0.999) that resulted in overestimation of F_{MSY}, but F_{loss} is less affected than F_{MSY} by uncertainties in the estimation when steepness is high (**Fig. 4**)

In Scenario (I), when stock size is low relative to initial levels (S/S_0), as with the northern stocks (e.g. PBF), relative R (R/R_0) under the RI model is lower than that of the BH model (**Fig. 5**). Accordingly, the accuracy of the steepness estimation is fairly high due to the tight SR relationship. As a result, the performance of F_{MSY} was better than F_{loss}, and its performance for northern stocks (e.g. PBF) was better than for southern stocks. In contrast, when relative S is large as for the southern stocks, the relative R of the RI model is larger than that of the BH model (**Fig. 5**). Hence, the accuracy of steepness estimation is lower due to the scattering of the SR relationships. Consequently, under these circumstances the performance of F_{MSY} is poor.

In Scenario (II), the steepness was intentionally underestimated by specifying a clear contrast in S and R between first-half and second-half simulation periods (**Fig. 6**). If the period of regime shift were reversed, the performance of both F_{MSY} and F_{loss} for southern and northern stocks would be worse because of unclear SR relationships.

In Scenario (III), the increase of M from 0.25 to 0.375 with fixed steepness resulted in an increase in the parameter a of the SR relationship (**Fig. 7**). Since there is a positive correlation between parameter a and steepness, the steepness estimate increases with the increase of M. Consequently, higher values of steepness have a large impact on the estimate of F_{MSY} for northern stocks. This means that F_{MSY} is inappropriate as a LRP for northern stocks.

MSY-based LRPs such as F_{MSY} are commonly used to avoid recruitment overfishing (Caddy and Mahon 1995). However, it can be difficult to estimate MSY when there is high uncertainty in the models and in the data (Punt and Smith 2002, Hilborn 2002, Hilborn and Stokes 2010, Mesnil 2012). In this situation, a proxy for F_{MSY} such as $F_{X\%SPR}$ or $F_{X\%S0}$ is often proposed as an alternative RP. **Fig. 8** shows the relationships between %SPR and $F_{\%SPR}$ at different natural mortality coefficients, and the relationships between the ratio of S_0 and $F_{\%S0}$ at different values of steepness. These relationships were derived from the mathmatical model used in this study (see **Appendix**). If 20%SPR and 20%S_0 are used as LRPs, the values of $F_{\%SPR}$ and $F_{\%S0}$ change significantly when there is mis-specification of the values of the natural mortality coefficient and steepness. For PBF, high uncertainty in the estimate of S_0, which has a negative relationship with steepness, and also high uncertainty in the value of the natural mortality coefficient, were identified in the stock assessment (Anon. 2010). Therefore, we consider that the application of %SPR and %S_0 as LRPs could be inappropriate for northern stocks such as PBF.

$F_{SSB\text{-}ATHL}$ is a LRP currently used for ALB-N (Conser et al 2005, Anon. 2008). This RP corresponds to the value of F that attains a future desirable level of S with a certain probability or above. In the case of ALB-N, the threshold of recruitment overfishing is defined as the average of the ten historically lowest (ATHL) values of S and the probability is set at 50%. Ichinokawa et al. (2010) interpret the simulation based reference point of $F_{SSB\text{-}ATHL}$ as a precautionary reference point. Although both RPs (i.e. F_{loss} and $F_{SSB\text{-}ATHL}$) originate from a similar concept of avoiding future values of S falling below S_{loss}, $F_{SSB\text{-}ATHL}$ is more risk-averse than F_{loss} because it takes account of several uncertainties. In particular, $F_{SSB\text{-}ATHL}$ is determined by stochastic future simulations incorporating uncertainty arising from non-equilibrium dynamics of recruitment as well as uncertainty in parameter estimation in the stock assessment model. In future work, it is considered important to examine the usefulness of $F_{SSB\text{-}ATHL}$, or other formulations of F_{SSB}, as LRPs.

Conclusions

Accurate estimation of steepness using basic simulation techniques is more difficult for temperate tunas in the north Pacific than for southern stocks because of the differences of a lack of data contrast. Poor estimation of steepness leads to overestimation of F_{MSY} which in turn is associated with a high risk of recruitment overfishing and stock depletion. For these reasons, MSY-based LRPs such as F_{MSY} are considered inappropriate for northern stocks. On the other hand, the F_{loss} LRP was robust to the overestimation of steepness. We suggest that historically-based LRPs such as F_{loss} can be used to achieve risk-averse and conservative fisheries management and would be appropriate for northern stocks such as PBF and ALB-N.

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Tables

Table 1. The hierarchical table used by the WCPFC to identify limit reference points (LRPs) for target species in the Western and Central Pacific Ocean. This table has been modified to reflect the outcomes of discussions held at WCPFC SC8.

Level	LRPs	Application
Level 1	F_{MSY} and B_{MSY}	
Level 2	$F_{X\%SPR0}$ and either $X\%SB_0$ or $X\%SB_{current,\ F=0}$	Bigeye and yellowfin tuna
Level 3	$X\%SB_0$ or $X\%SB_{current,\ F=0}$	Albacore (South)

Table 2. F-based limit reference points used as statistical estimators and their definitions.

F-based RP	Definition
F_{msy}	The rate of fishing mortality that maximizes catch over the long term. This is determined by the upper limit on the allowable rate of fishing when the stock size is at S_{MSY}.
F_{loss}	The rate of fishing mortality that produces a spawning biomass per recruit associated with the historically lowest spawning stock biomass (S_{loss}) given the expected level of recruitment (R_{loss}) at S_{loss} (Cook 1998). This is determined by the value of F at S_{loss}.

Table 3. Parameters used in the operating model to produce the population dynamics of the southern and northern stocks. Values in parentheses indicate the default values.

	Interpretation	**Values**
Fixed parameters		
S_0	Virgin spawning stock size	15000
	Length of time series (year)	50
q	Catchability coefficient for recruitment (R) and spawning stock size (S)	0.1
σ_O	Log scale variance of observation error for R and S	0.2
p	Penalty	10 ^ 6
Variable parameters		
h	Steepness	0.3, 0.6, 0.9
F	Fishing mortality coefficient (year^{-1})	Dependent on the h, stock, and the period
M	Natural mortality coefficient (year^{-1})	(0.25), 0.375
σ_P	Log scale variance of process error for R and S	(0.2), 0.6

Table 4. Parameters used to reproduce the population dynamics of the northern and southern stocks, where S is spawning stock size, S_0 is virgin S, and S_{MSY} is S corresponding to MSY. YFT: yellowfin tuna, BET: bigeye tuna, ALB-S: albacore-southern stock, ALB-N: albacore-northern stock, PBF: Pacific bluefin tuna.

	Southern stock	**Northern stock**	
	YFT, BET, ALB-S	ALB-N	PBF
Initial simulation period	S_0	$0.8S_0$	$0.2S_0$
Mid-term simulation period	$1.2\ S_{MSY}$	$1.2S_{MSY}$	$0.15S_{MSY}$
Recent simulation period	S_{MSY}	$1.4S_{MSY}$	$0.3S_{MSY}$

Table 5. Fishing mortality rates calculated for various thresholds of potential recruitment overfishing (i.e. various levels of depletion of the spawning stock biomass).

SR model	h	S_0	S_{MSY}	F_{MSY}	$F_{50\%SMSY}$	$F_{20\%SMSY}$	$F_{10\%SMSY}$	$F_{S=0}$
Beverton-Holt	0.3	15,000	6,844	0.05	0.08	0.10	0.10	0.11
	0.6	15,000	5,314	0.20	0.31	0.40	0.44	0.47
	0.9	15,000	3,440	0.47	0.73	0.97	1.07	1.17
Ricker	0.3	15,000	7,383	0.05	0.08	0.09	0.10	0.10
	0.6	15,000	7,289	0.18	0.26	0.31	0.32	0.34
	0.9	15,000	7,342	0.28	0.40	0.46	0.48	0.50

Table 6. Base case and three simulation scenarios to examine the effects of uncertainty.

Scenarios	"True" SR relationship (Beverton-Holt model is used to estimate the parameters)	Regime shift (parameter a of SR relationship for first half of the simulation period is 1.5 times for the second half)	Mis-specification of the natural mortality (1.5 times larger than default value)
Base case	Beverton-Holt	No	No
Scenario (I):	Ricker	No	No
Scenario (II):	Beverton-Holt	Yes	No
Scenario (III):	Beverton-Holt	No	Yes

Table 7. Probabilities that F_{MSY} and F_{loss} exceed the thresholds representing recruitment overfishing. Green cells indicate probabilities less than 5% of exceeding the thresholds, with darker shading for lower values. Red cells indicate probabilities greater than 10%, with darker shading for higher values. Small variance ($\sigma = 0.2$) and large variance ($\sigma = 0.6$) indicate the magnitude of the process errors for spawning stock size and recruitment. The magnitude of observation error is set at a default value of $\sigma = 0.2$.

(a) Base case

Thresholds	Southern stocks				Northern stocks (PBF)				Northern stocks (ALB-N)			
	Small variance		Large variance		Small variance		Large variance		Small variance		Large variance	
	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}
***h* = 0.3**												
Pr (> F_{Smsy})	0.48	0.49	0.4	0.23	0.74	0.94	0.65	0.47	0.72	0.5	0.54	0.19
Pr (> $F_{50\%\mathrm{Smsy}}$)	0.29	0.25	0.29	0.17	0.43	0.72	0.52	0.39	0.54	0.25	0.42	0.12
Pr (> $F_{20\%\mathrm{Smsy}}$)	0.19	0.18	0.24	0.15	0.22	0.49	0.48	0.33	0.43	0.21	0.4	0.11
Pr (> $F_{10\%\mathrm{Smsy}}$)	0.19	0.13	0.23	0.11	0.15	0.43	0.46	0.33	0.4	0.14	0.38	0.1
Pr (> $F_{\mathrm{S=0}}$)	0.13	0.11	0.21	0.09	0.11	0.39	0.41	0.31	0.38	0.12	0.36	0.08
***h* = 0.6**												
Pr (> F_{Smsy})	0.24	0.21	0.07	0.02	0.13	0.47	0.33	0.11	0.47	0.05	0.3	0.03
Pr (> $F_{50\%\mathrm{Smsy}}$)	0.06	0.02	0.05	0.01	0.01	0.13	0.29	0.05	0.2	0	0.25	0.02
Pr (> $F_{20\%\mathrm{Smsy}}$)	0	0.01	0.05	0	0	0.05	0.29	0.04	0.11	0	0.24	0.01
Pr (> $F_{10\%\mathrm{Smsy}}$)	0	0.01	0.05	0	0	0.01	0.29	0.02	0.11	0	0.24	0.01
Pr (> $F_{\mathrm{S=0}}$)	0	0	0.04	0	0	0.01	0.29	0	0.09	0	0.23	0
***h* = 0.9**												
Pr (> F_{Smsy})	0.07	0.02	0.03	0	0.11	0.03	0.45	0	0.38	0	0.33	0.01
Pr (> $F_{50\%\mathrm{Smsy}}$)	0	0	0.03	0	0.11	0.01	0.45	0	0.33	0	0.33	0
Pr (> $F_{20\%\mathrm{Smsy}}$)	0	0	0.03	0	0.11	0	0.45	0	0.33	0	0.33	0
Pr (> $F_{10\%\mathrm{Smsy}}$)	0	0	0.03	0	0.11	0	0.45	0	0.33	0	0.33	0
Pr (> $F_{\mathrm{S=0}}$)	0	0	0.03	0	0.11	0	0.45	0	0.33	0	0.33	0

(b) Scenario (I): Uncertainty in the SR model. The “true” SR relationship is assumed to follow the Ricker model but the Beverton-Holt model is used to estimate the parameters.

Thresholds	Southern stocks				Northern stocks (PBF)				Northern stocks (ALB-N)			
	Small variance		Large variance		Small variance		Large variance		Small variance		Large variance	
	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}
h = 0.3												
Pr (> F_{Smsy})	0.5	0.43	0.45	0.21	0.79	0.96	0.63	0.35	0.67	0.35	0.67	0.29
Pr (> $F_{50\%Smsy}$)	0.32	0.24	0.31	0.17	0.46	0.74	0.55	0.26	0.51	0.21	0.64	0.24
Pr (> $F_{20\%Smsy}$)	0.27	0.16	0.27	0.14	0.29	0.67	0.5	0.2	0.46	0.13	0.6	0.2
Pr (> $F_{10\%Smsy}$)	0.24	0.13	0.24	0.11	0.22	0.58	0.49	0.19	0.44	0.12	0.59	0.2
Pr (> $F_{S=0}$)	0.2	0.1	0.24	0.11	0.21	0.52	0.48	0.19	0.43	0.11	0.57	0.19
h = 0.6												
Pr (> F_{Smsy})	0.29	0.05	0.15	0.01	0.18	0.37	0.24	0.1	0.76	0.02	0.59	0
Pr (> $F_{50\%Smsy}$)	0.12	0.01	0.11	0	0.07	0.14	0.24	0.04	0.67	0	0.56	0
Pr (> $F_{20\%Smsy}$)	0.11	0.01	0.11	0	0.04	0.08	0.24	0.01	0.62	0	0.53	0
Pr (> $F_{10\%Smsy}$)	0.1	0.01	0.11	0	0.04	0.07	0.24	0	0.61	0	0.53	0
Pr (> $F_{S=0}$)	0.1	0.01	0.11	0	0.04	0.07	0.24	0	0.6	0	0.53	0
h = 0.9												
Pr (> F_{Smsy})	0.35	0	0.17	0	0.09	0.11	0.45	0	0.8	0	0.47	0.01
Pr (> $F_{50\%Smsy}$)	0.25	0	0.15	0	0.06	0.03	0.45	0	0.73	0	0.47	0
Pr (> $F_{20\%Smsy}$)	0.23	0	0.14	0	0.06	0.02	0.45	0	0.72	0	0.47	0
Pr (> $F_{10\%Smsy}$)	0.22	0	0.14	0	0.06	0.02	0.45	0	0.72	0	0.47	0
Pr (> $F_{S=0}$)	0.21	0	0.14	0	0.06	0.01	0.45	0	0.72	0	0.47	0

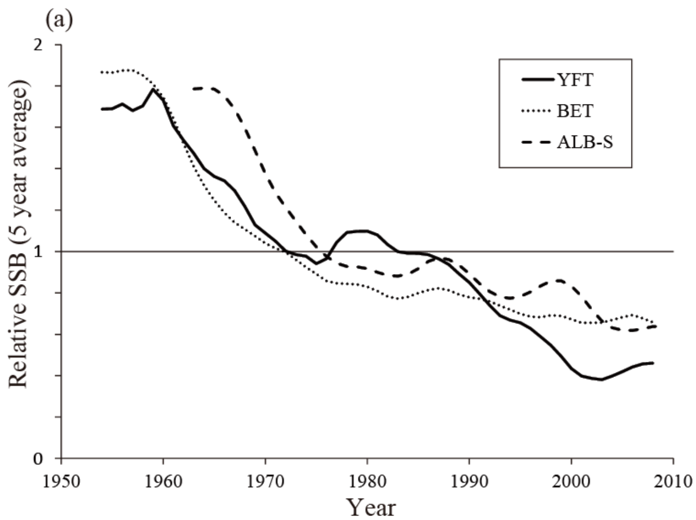
(c) Scenario (II): Uncertainty due to the effect of regime shifts. The parameter a of the SR relationship for the first half of the simulation period is set at 1.5 times that of the second half.

Thresholds	Southern stocks				Northern stocks (PBF)				Northern stocks (ALB-N)			
	Small variance		Large variance		Small variance		Large variance		Small variance		Large variance	
	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}
h = 0.3												
Pr (> F_{Smsy})	0	0	0.18	0.26	0.08	0.69	0.34	0.6	0	0	0.21	0.28
Pr (> $F_{50\%Smsy}$)	0	0	0.07	0.21	0	0.16	0.21	0.39	0	0	0.17	0.15
Pr (> $F_{20\%Smsy}$)	0	0	0.05	0.11	0	0.1	0.15	0.28	0	0	0.14	0.06
Pr (> $F_{10\%Smsy}$)	0	0	0.05	0.09	0	0.07	0.15	0.26	0	0	0.14	0.06
Pr (> $F_{S=0}$)	0	0	0.05	0.05	0	0.04	0.14	0.25	0	0	0.14	0.06
h = 0.6												
Pr (> F_{Smsy})	0	0	0.01	0.04	0	0.14	0.07	0.22	0.01	0	0.22	0.06
Pr (> $F_{50\%Smsy}$)	0	0	0	0.01	0	0	0.03	0.09	0	0	0.19	0
Pr (> $F_{20\%Smsy}$)	0	0	0	0	0	0	0.03	0.03	0	0	0.18	0
Pr (> $F_{10\%Smsy}$)	0	0	0	0	0	0	0.03	0.01	0	0	0.18	0
Pr (> $F_{S=0}$)	0	0	0	0	0	0	0.03	0.01	0	0	0.18	0
h = 0.9												
Pr (> F_{Smsy})	0	0	0	0	0	0.08	0.1	0	0.1	0	0.16	0
Pr (> $F_{50\%Smsy}$)	0	0	0	0	0	0	0.1	0	0.1	0	0.16	0
Pr (> $F_{20\%Smsy}$)	0	0	0	0	0	0	0.1	0	0.1	0	0.16	0
Pr (> $F_{10\%Smsy}$)	0	0	0	0	0	0	0.1	0	0.1	0	0.16	0
Pr (> $F_{S=0}$)	0	0	0	0	0	0	0.1	0	0.1	0	0.16	0

(d)Scenario (III): Uncertainty due to mis-specification of natural mortality (M). M is set at 1.5 times the default value.

Thresholds	Southern stocks				Northern stocks (PBF)				Northern stocks (ALB-N)			
	Small variance		Large variance		Small variance		Large variance		Small variance		Large variance	
	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}	F_{MSY}	F_{loss}
***h* = 0.3**												
Pr (> F_{Smsy})	0.5	0.47	0.46	0.27	0.78	0.92	0.71	0.49	0.59	0.45	0.55	0.16
Pr (> $F_{50\%Smsy}$)	0.32	0.25	0.27	0.16	0.51	0.74	0.61	0.4	0.48	0.34	0.49	0.14
Pr (> $F_{20\%Smsy}$)	0.16	0.17	0.19	0.14	0.17	0.55	0.47	0.39	0.35	0.25	0.4	0.12
Pr (> $F_{10\%Smsy}$)	0.12	0.14	0.18	0.12	0.13	0.54	0.43	0.37	0.32	0.24	0.39	0.1
Pr (> $F_{S=0}$)	0.1	0.12	0.17	0.11	0.11	0.48	0.41	0.34	0.31	0.22	0.37	0.08
***h* = 0.6**												
Pr (> F_{Smsy})	0.21	0.27	0.07	0.04	0.14	0.52	0.25	0.15	0.36	0.13	0.35	0.05
Pr (> $F_{50\%Smsy}$)	0	0.07	0.06	0.01	0	0.11	0.23	0.02	0.11	0.04	0.32	0.01
Pr (> $F_{20\%Smsy}$)	0	0.02	0.06	0	0	0.06	0.23	0.01	0.04	0.02	0.32	0
Pr (> $F_{10\%Smsy}$)	0	0	0.06	0	0	0.03	0.23	0	0.03	0.01	0.32	0
Pr (> $F_{S=0}$)	0	0	0.06	0	0	0.02	0.23	0	0.02	0.01	0.31	0
***h* = 0.9**												
Pr (> F_{Smsy})	0.01	0.08	0.04	0	0.15	0.02	0.37	0	0.17	0.06	0.13	0
Pr (> $F_{50\%Smsy}$)	0	0	0.04	0	0.15	0	0.37	0	0.06	0.01	0.13	0
Pr (> $F_{20\%Smsy}$)	0	0	0.04	0	0.15	0	0.37	0	0.05	0.01	0.13	0
Pr (> $F_{10\%Smsy}$)	0	0	0.04	0	0.15	0	0.37	0	0.05	0.01	0.13	0
Pr (> $F_{S=0}$)	0	0	0.04	0	0.15	0	0.37	0	0.05	0.01	0.13	0

Figures



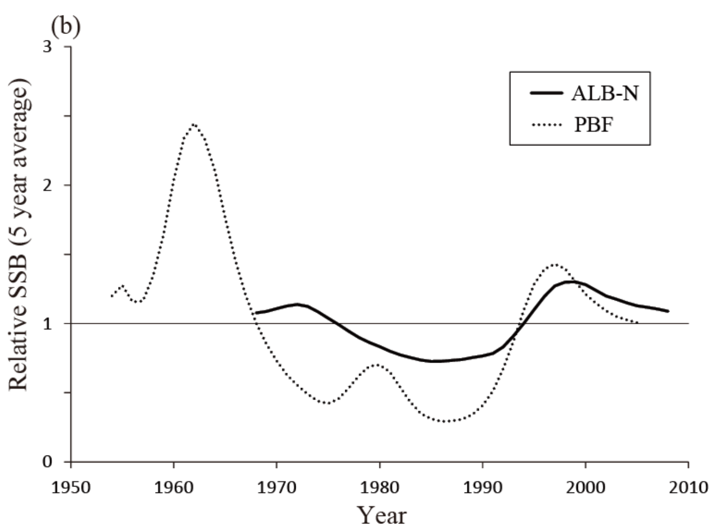


Fig.1. Historical time series of spawning stock biomass (SSB, five-year average) relative to the average of each stock of (a) three tropical tunas in the Western and Central Pacific and (b) two temperate tunas in the North Pacific. YFT: yellowfin tuna, BET: bigeye tuna, ALB-S: albacore tuna-southern stock, ALB-N: albacore tuna-northern stock, PBF: Pacific bluefin tuna.

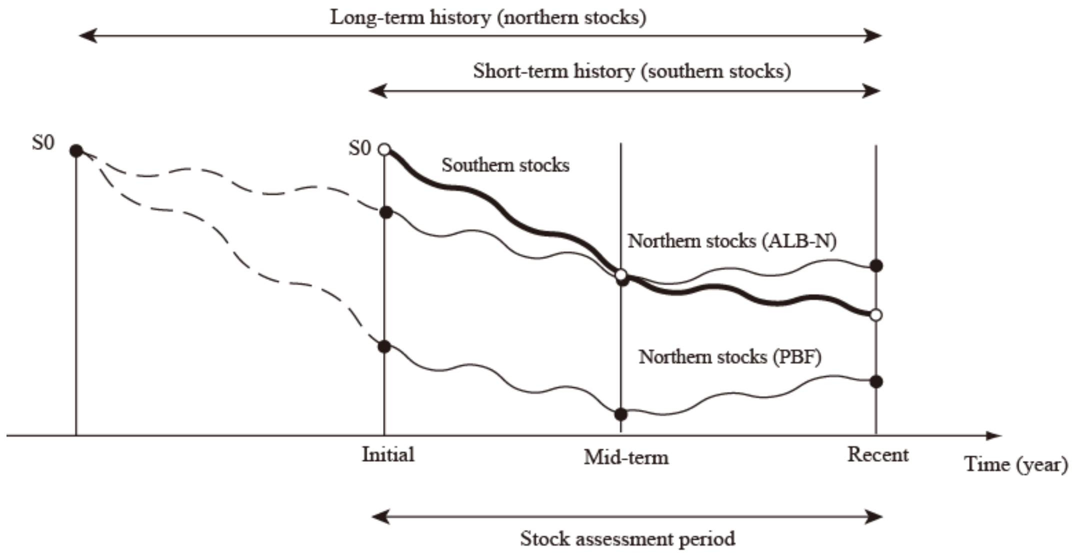


Fig.2. Schematic diagram of historical population dynamics scenarios for southern (thick line with open circle) and northern (thin lines with filled circles) tuna stocks in the Pacific. Dashed lines indicate depletions from virgin spawning stock size (S_0) to initial S. Note that the average S over the time series for PBF is substantially lower than that for ALB-N.

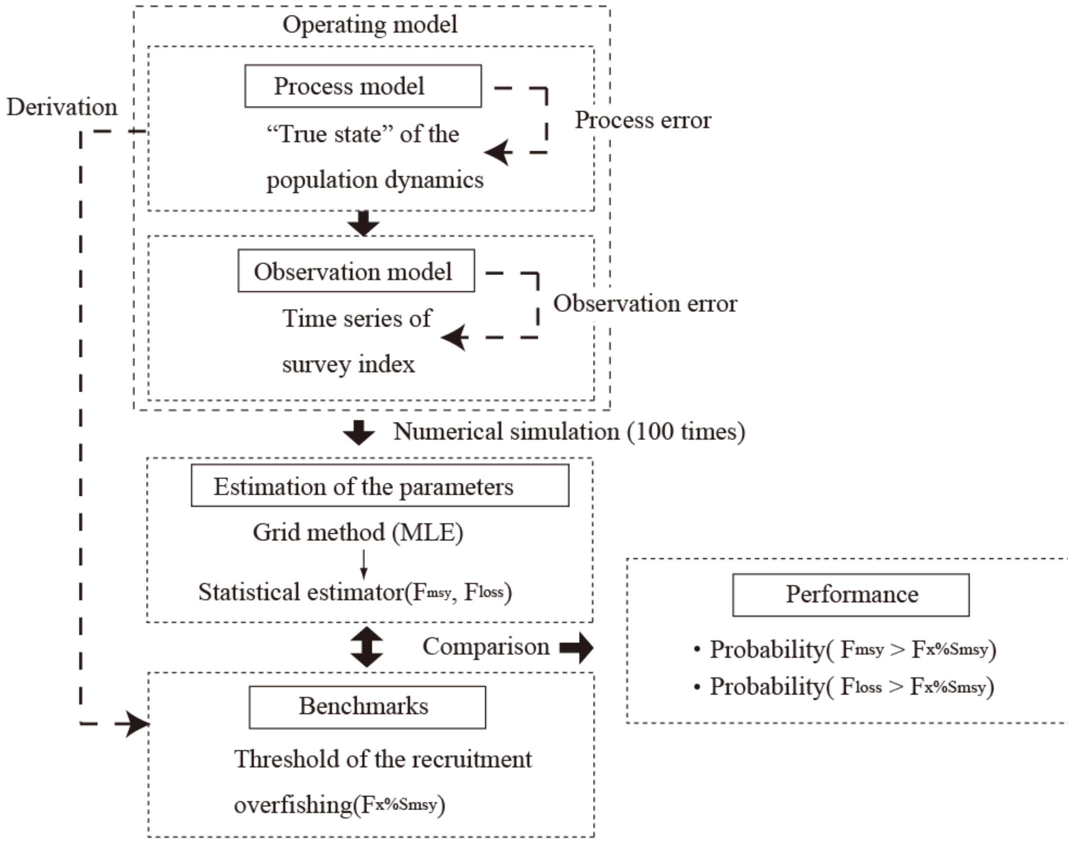


Fig.3. Schematic of the simulation analysis. First, the operating model reproduces the "true state" of the population dynamics. Second, thresholds for recruitment overfishing are set and corresponding values of *F* are calculated. Third, a time series of population dynamics and survey indices are generated using numerical simulation. Fourth, parameters and statistical estimators are estimated using maximum likelihood estimates and the grid method. Finally, the probability that each statistical estimator exceeds the threshold of recruitment overfishing is compared.

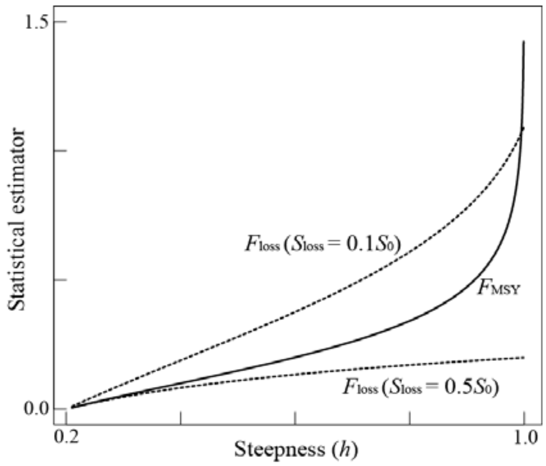


Fig.4. The relationship between steepness (h) and statistical estimators (F_{MSY} (solid line) and F_{loss} (dotted lines)). The estimate of F_{loss} is dependent on the size of S_{loss}.

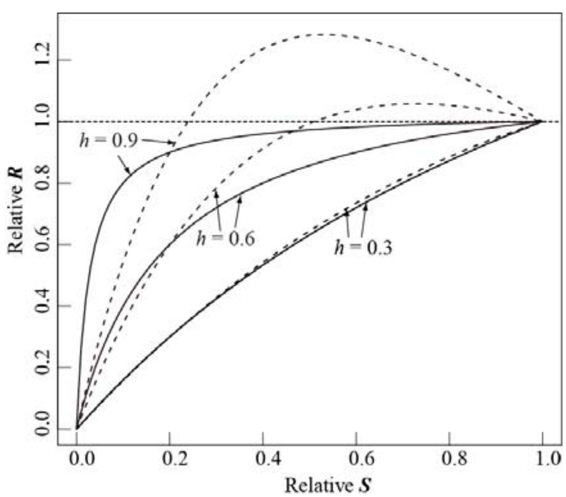


Fig.5. Relationship between relative spawning stock size (S/S_0) and relative recruitment (R/R_0) under different values of steepness (h) and different *SR* models. Solid lines indicate the Beverton-Holt SR model and dashed lines indicate the Ricker SR model.

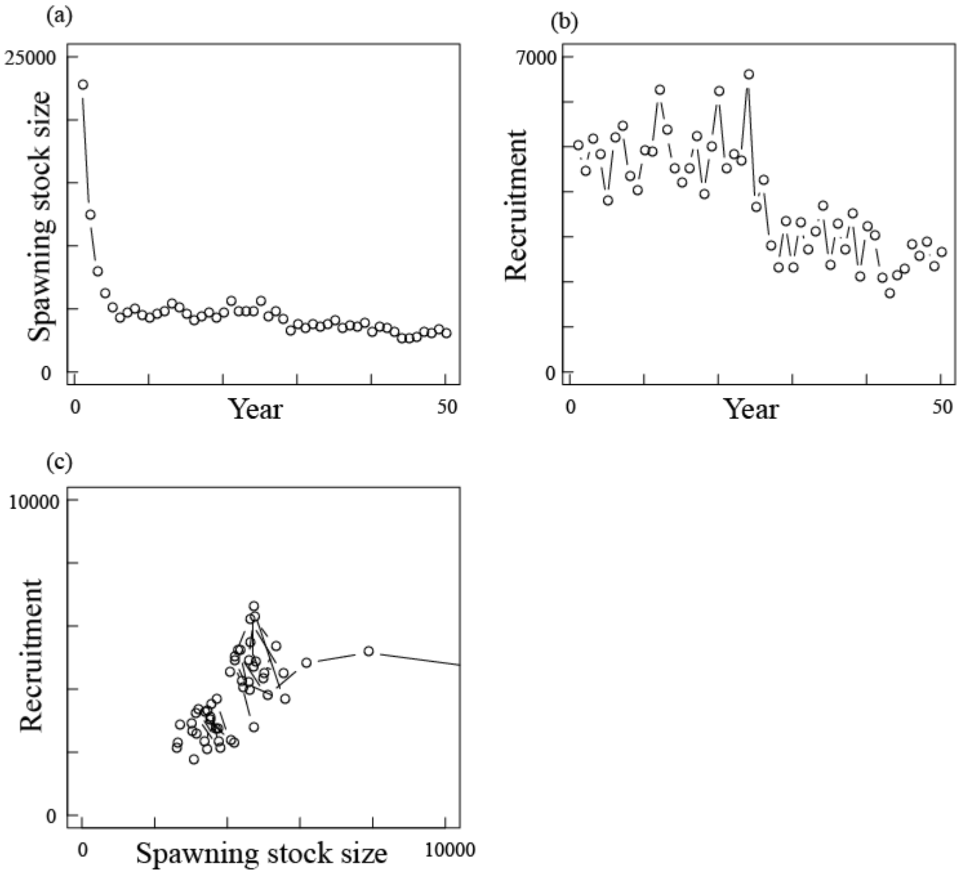


Fig.6. (a) Time series of spawning stock size; (b) time series of recruitment; and (c) the relationships between them when a regime shift occurs in the first half of the simulation period.

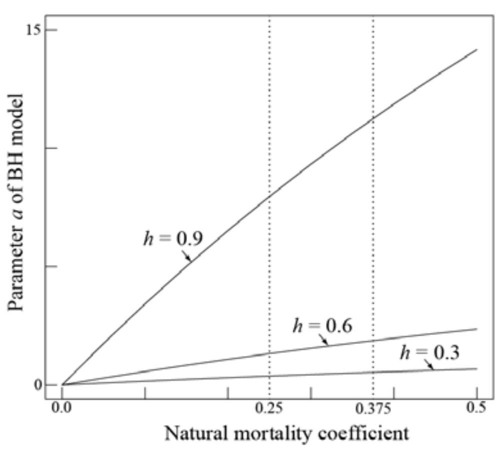


Fig.7. Relationships between the natural mortality coefficient (*M*) and parameter *a* of the Beverton-Holt (BH) SR model with different values of steepness. The default value of *M* is 0.25.

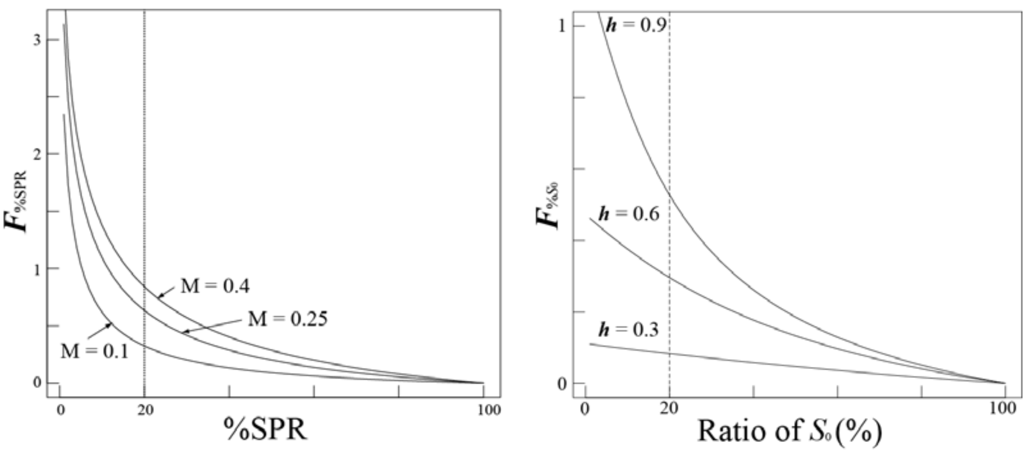


Fig.8. The effect of natural mortality and steepness on proxy MSY-based reference points: (a) relationships between %SPR and $F_{\%SPR}$ with different natural mortality coefficients; and (b) relationships between the ratio of S_0 and $F_{\% S0}$ with different values of steepness.

Appendix

Simulation model

The basic population dynamics are given as:

$$S_{t+1} = S_t e^{-F_t - Me^{\zeta_t}} + R_t e^{-wF_t} \qquad \zeta_t \sim \mathrm{N}\,(0, \sigma_{SP}{}^2) \qquad (1)$$

$$R_{t+1} = f(S_t, F_t) e^{\xi_t} \qquad \xi_t \sim \mathrm{N}\,(0, \sigma_{RP}{}^2) \qquad (2)$$

where S_t is the spawning stock size at the start of the year t; F is fishing mortality; M is natural mortality which is assumed to be constant; R is the number of recruits; w is the fraction of the F for the recruitment; f is the function of the stock-recruitment relationship; ζ and ξ the normally distributed errors associated with the spawning stock size and the stock-recruitment relationships; and σ is the log-scale variance of the process errors.

The function f is replaced by the following two basic stock recruitment (SR) models.
Beverton-Holt (BH) SR model:

$$f(S_t, F_t) = \frac{aS_t e^{-F_t}}{1 + bS_t e^{-F_t}} \qquad (2\text{-a})$$

Ricker (RI) SR model:

$$f(S_t, F_t) = a(S_t e^{-F_t}) e^{-bS_t e^{-F_t}} \qquad (2\text{-b})$$

where a and b are constants. The BH model uses density-dependent compensation, while the RI model uses over-compensation. The observation model is described as:

$$\tilde{S}_t = qS_t e^{\varepsilon_t} \qquad \varepsilon_t \sim \mathrm{N}(0, \sigma_{SO}{}^2) \qquad (3)$$

$$\tilde{R}_t = vR_t e^{\tau_t} \qquad \tau_t \sim \mathrm{N}(0, \sigma_{RO}{}^2) \qquad (4)$$

where $\tilde{S}$ and $\tilde{R}$ are survey indices of the observed number of fish; q and v are proportionality constants; and ε and τ are the observation errors. The catch is given by the equation:

$$C_t = S_t(1 - e^{-F_t}) + R_t(1 - e^{-wF_t}) \qquad (5)$$

where C is the number of exploited fish (i.e. catch). The value of w is set to one for simplicity.

Derivation of statistical estimators

From the three equations (1), (2), and (5) we can calculate statistical estimators such as F_{MSY} and F_{loss} analytically and numerically. F-based LRPs are calculated under the steady state assumption as follows:

(I) The following equation can be derived from equation (5) at the steady state (*):

$$\frac{dC^*}{dF^*} = \frac{dS^*}{dF^*}(1 - e^{-F_{\mathrm{MSY}^*}}) + \frac{dR^*}{dF^*}(1 - e^{-wF_{\mathrm{MSY}^*}}) + S^* e^{-F_{\mathrm{MSY}^*}} + R^* w e^{-wF_{\mathrm{MSY}^*}} = 0$$

(II) F_{loss} can be derived from equations (1) and (2) for the BH and RI SR models as follows:

BH:

$$S_{\mathrm{loss}} = S_{\mathrm{loss}} e^{-F\mathrm{loss}-M} + \frac{aS_{\mathrm{loss}} e^{-F\mathrm{loss}}}{1 + bS_{\mathrm{loss}} e^{-F\mathrm{loss}}} e^{-wF\mathrm{loss}}$$

$$1 = e^{-F\mathrm{loss}-M} + \frac{a e^{-F\mathrm{loss}}}{1 + bS_{\mathrm{loss}} e^{-F\mathrm{loss}}} e^{-wF\mathrm{loss}}$$

$$1 + bS_{\mathrm{loss}} e^{-F\mathrm{loss}} = \left(1 + bS_{\mathrm{loss}} e^{-F\mathrm{loss}}\right) e^{-F\mathrm{loss}-M} + a e^{-(1+w)F\mathrm{loss}}$$

$$1 + bS_{loss}U = (1 + bS_{loss}U)UH + aUH_w$$

where $e^{-Floss} = U$、$e^{-M} = H$、$e^{-wFloss} = H_w$

RI:

$$S_{loss} = S_{loss} e^{-F\mathrm{loss}-M} + aS_{loss} e^{-F\mathrm{loss}-bS_{loss}e^{-F\mathrm{loss}}} e^{-wF\mathrm{loss}^*}$$

$$1 = e^{-F\mathrm{loss}-M} + a e^{-F\mathrm{loss}-bS_{loss}e^{-F\mathrm{loss}}} e^{-wF\mathrm{loss}^*}$$

$$1 = UH + aUe^{-bS_{loss}U} H_w$$

F_{MSY} and F_{loss} can be obtained numerically from these equations.

Estimation method of parameters

Point estimates of two parameters (S_0, h) are simultaneously obtained using a two dimensional grid method which selects a maximum likelihood estimate (MLE) for the combination of the parameters in the grid. The parameter S_0 ranges from 1,000 to 100,000 with 500 intervals and the parameter h ranges from 0.2 to 1.0 with intervals of 0.01. The following objective function is maximized to find the point estimates:

$$\ln(L) = -\sum_t \{\ln(qS_t) - \ln(\widehat{qS_t})\}^2 - \sum_t \{\ln(vR_t) - \ln(\widehat{vR_t})\}^2 + \sum_t p\delta_t \quad (6)$$

where $\begin{cases} \delta = 1, \text{ if } S < 0.0001 \text{ or } R < 0.0001 \\ \delta = 0, \text{ otherwise} \end{cases}$,

and

$\ln(L)$ is a penalized objective function, and p is a constant imposed for violation of the constraint. The first and second terms indicate a difference between observed and estimated survey indices and the third term indicates a penalty.

Others

In the steady state ($\sigma_{SP} = \sigma_{RP} = 0$), SPR at $t = 0$ is expressed from equations (1) and (2) as follows:

$$SPR_0 = \frac{1}{1-e^{-M}} \quad (7)$$

The equations (2-a) and (2-b), re-written using the steepness (h) of the stock recruitment relationship and the parameters a and b, are expressed as follows:

BH SR model:

$$hR_0 = \frac{a0.2S_0}{1+b0.2S_0}$$

$$a = \frac{4h}{SPR_0(1-h)} \quad (8)$$

$$b = \frac{5h-1}{S_0(1-h)} \quad (9)$$

RI SR model:

$$hR_0 = a0.2S_0e^{-0.2bS_0}$$

$$a = \frac{5h^{(5/4)}}{SPR_0} \quad (10)$$

$$b = \frac{5\log(5h)}{4S_0} \quad (11)$$

The relationships between M and parameter a of the BH model with different values of steepness can be derived from equations (7) and (8) as follows:

$$\frac{1}{1-e^{-M}} = \frac{4h}{a(1-h)}$$

$$a = \frac{4h}{(1-h)}(1-e^{-M}) \quad (12)$$

$F_{\%\mathrm{SPR}}$ can be derived from equations (1) and (7) as follows:

$$\mathrm{X}\%SPR = \mathrm{X}\%SPRe^{-F_{X\%SPR}-M} + e^{-F_{X\%SPR}}$$

$$F_{X\%SPR} = -\log\left\{\frac{X}{1+(X-1)e^{-M}}\right\}, \tag{13}$$

where X is the fraction of SPR and we assume that $w = 1$ and $\sigma = 0$.

$F_{\mathrm{X}\%\mathrm{S0}}$ can be derived from the equations (1) and (2-a) for the BH SR model as follows:

$$S_{\mathrm{X}\%\mathrm{S0}} = S_{\mathrm{X}\%\mathrm{S0}}e^{-F\mathrm{X}\%\mathrm{S0}-M} + \frac{aS_{\mathrm{X}\%\mathrm{S0}}e^{-F\mathrm{X}\%\mathrm{S0}}}{1+bS_{\mathrm{X}\%\mathrm{S0}}e^{-F\mathrm{X}\%\mathrm{S0}}}e^{-F\mathrm{X}\%\mathrm{S0}}$$

$$F_{\mathrm{X}\%\mathrm{S0}} = g(a, b, S_{\mathrm{X}\%\mathrm{S0}}, M),$$

where g is a function and the solution is obtained numerically.