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Evaluating harvest control rules for bigeye tuna (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*) fisheries in the Indian Ocean

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ABSTRACT

Bigeye tuna (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*) support two of the most important fisheries in the Indian Ocean. However, there is little research evaluating harvest control rules (HCRs) for their management. In this study we evaluated four HCRs, 'knife-edged', 'linear', 'convex', and 'concave', for these two species. These four HCRs defined management rules for how annual fishing mortality should be adjusted based on perceived stock status. Fishing mortality was adjusted linearly, convexly and concavely for the 'linear', 'convex', and 'concave' HCRs, respectively when the current spawning stock biomass (SSB) was between the limit and target SSB-based biological reference points (BRPs). Two age-structured operating models were developed to simulate fisheries managed under these HCRs for a 25-year management period. Implementation and process errors, and uncertainties in key fisheries parameters were considered as sources of uncertainty in this study. All four HCRs were found to be effective in driving both stocks to the status defined by maximum sustainable yield-based BRPs. The 'knife-edged' HCR, which has constant fishing mortality but switches fishing mortality to 0 when stock biomass is below the limit SSB-based BRP, led to relatively poor performance. Our results indicate that a simulation study is needed to evaluate the performance of BRPs and HCRs in managing bigeye tuna and yellowfin tuna fisheries in the Indian Ocean.

1. Introduction

A harvest control rule (HCR), with its ability to translate predetermined biological reference points (BRPs) and fish stock status into fishery management actions, is one of the essential components in management strategy evaluation (Breen et al., 2003; Smith and Smith, 2005; Apostolaki and Hillary, 2009). Traditional HCRs used in fisheries management include the "constant catch", "constant effort" and "constant escapement" HCRs, which, respectively, keep landings, fishing mortality (F) and survivors constant (Steinshamn, 1998; Deroba and Bence, 2008; Siddeek et al., 2009; Zhang et al., 2011). Recent studies evaluating management strategies have considered HCRs which adjust management regulations depending on the status of stocks relative to BRPs, including F-based BRPs and biomass/abundance-based BRPs, such as the "F linear", "proportional threshold harvesting", and "catch linear" HCRs (Deroba and Bence, 2008; Irwin et al., 2008; Smith et al., 2008; Breen, 2009). The F-based HCR is one of the most commonly-used fishery status-dependent HCRs because it tends to be more robust to uncertainty in recruitment dynamics (Deroba and Bence, 2008; Needle, 2008; Siddeek et al., 2009).

Bigeye tuna (*T. obesus*) and yellowfin tuna (*T. albacares*) are two of the top predator species in the Indian Ocean ecosystem (Potier et al., 2007; Nootmorn et al., 2008). They support two of the most valuable tuna fisheries in the world. According to the Food and Agriculture Organization (FAO), the average annual landing during 2000–2008 was 125,159 mt for bigeye tuna and 377,129 mt for yellowfin tuna, which constituted nearly 10% of the total production of tuna and tuna-like fisheries worldwide. The landings in these fisheries have increased substantially over the last two decades (Nishida and Shono, 2007; Kolody et al., 2010), and current landings are more than three times the average during the early 1980s, raising concerns that the stocks are being depleted (Safina, 2001; Polacheck, 2006). In response to these concerns, current management regulations should be reviewed and, if necessary, alternative management actions providing for long-term sustainability should be identified.

The bigeye and yellowtail tuna fisheries in the Indian Ocean are managed by the Indian Ocean Tuna Commission (IOTC). The IOTC has identified optimal stock use while ensuring long-term sustainability as their primary management objective (Allen, 2010; IOTC, 2011a). The IOTC has used several stock assessments to set

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harvest rules. The bigeye tuna stock assessment was conducted using Stock Synthesis (SS; Shono et al., 2006, 2009) and an age-structured production model (ASPM; Nishida and Rademeyer, 2010), while the yellowfin tuna stock was assessed using ASPM (Nishida and Shono, 2007) and MULTIFAN-CL (Langley et al., 2011). The spawning stock biomass (SSB) and *F* that yield maximum sustainable yield (MSY), i.e. SSB_{MSY} and F_{MSY}, were suggested to be BRPs (Shono et al., 2004; Nishida and Shono, 2007; Nishida and Rademeyer, 2010; Langley et al., 2011). According to most recent stock assessment reports, both bigeye and yellowfin were considered subjected to overfishing, but not overfished (Nishida and Shono, 2007; Shono et al., 2009), because their current SSB and *F* are higher respectively than SSB_{MSY} and F_{MSY}. In recent years, the *F*s for the tuna fisheries in the Indian Ocean have dropped (Nishida and Rademeyer, 2010; Langley et al., 2011), possibly because of piracy threats near Somalia (Marsac et al., 2009).

Only a few studies have evaluated HCRs for these two tuna fisheries. The "Kobe II Strategy Matrix" was proposed to measure the performance of several HCRs including "constant catch", "constant *F*" and "closed area" during the global summit of Tuna Regional Fishery Management Organizations (IOTC, 2011b). However, the effectiveness of the HCRs given uncertainty in stock assessment and management was not fully evaluated.

In this study, we propose four alternative *F*-based HCRs and evaluate the effectiveness of these HCRs given pre-specified BRPs for the bigeye and yellowfin tuna fisheries in the Indian Ocean. These four hypothetical HCRs were proposed to address the question: how should we adjust the harvest level? The approach developed in this study provides a framework for a systematic evaluation of HCRs for the Indian Ocean tuna fisheries.

2. Methods

2.1. Designs of harvest control rules

Four HCRs were considered (Fig. 1). In each HCR, two *F* curves, the *F* limit curve (F_l) and the *F* target curve (F_t), were defined as functions of SSB. Four BRPs, target *F*-based BRP (F_{tar}), limit *F*-based BRP (F_{lim}), target SSB-based BRP (SSB_{tar}), and limit SSB-based BRP (SSB_{lim}), were used to define each HCR. We set F_{tar} to 0.13 yr^{-1} for bigeye tuna and 0.0515 $season^{-1}$ (1 season = 0.25 year) for yellowfin tuna. SSB_{tar} was set to 331,365 mt for bigeye tuna and 1,278,227 mt for yellowfin tuna. These four BRPs were derived using the approach of Sissenwine and Shepherd (1987), and differed from the BRPs estimated in the actual assessments (Shono et al., 2004; Langley et al., 2011) due to differences in model assumptions. Limit BRPs were assumed to be proportional to the target BRPs: F_{lim} was set to 1.5 F_{tar} and SSB_{lim} to 0.5 SSB_{tar}. The BRPs mentioned above, together with the HCRs, divided the fishery status into seven control areas (Fig. 1) with each control area having a unique management action for the next time-step (Table 1).

The first HCR, 'knife-edged' (Fig. 1a), sets the *F*, on which management is based, to 0 when the current SSB is lower than SSB_{lim}. However, when the current SSB is higher than SSB_{lim}, two levels of *F*, F_{tar} and F_{lim}, are used to set the *F*. Thus, the two *F* curves can be expressed as:

$$F_{l1} = \begin{cases} 0 & \text{if} \quad SSB \le SSB_{\text{lim}} \\ F_{\text{lim}} & \text{if} \quad SSB > SSB_{\text{lim}} \end{cases} \tag{1}$$

and

$$F_{t1} = \begin{cases} 0 & \text{if} \quad SSB \le SSB_{\text{lim}} \\ F_{tar} & \text{if} \quad SSB > SSB_{\text{lim}} \end{cases} \tag{2}$$

The second HCR, 'linear' (Fig. 1b) adjusts *F* in proportion to the change in SSB when the SSB is higher than SSB_{lim} but lower than SSB_{tar}:

$$F_{l2} = \begin{cases} 0 & \text{if} \quad SSB \le SSB_{\text{lim}} \\ a_1 \; SSB + b_1 & \text{if} \quad SSB_{\text{lim}} < SSB \le SSB_{tar} \\ F_{\text{lim}} & \text{if} \quad SSB > SSB_{tar} \end{cases} \tag{3}$$

and

$$F_{t2} = \begin{cases} 0 & \text{if} \quad SSB \le SSB_{\text{lim}} \\ a_2 SSB + b_2 & \text{if} \quad SSB_{\text{lim}} < SSB \le SSB_{tar} \\ F_{tar} & \text{if} \quad SSB > SSB_{tar} \end{cases} \tag{4}$$

where $a_1 = F_{\text{lim}}/(SSB_{tar} - SSB_{\text{lim}})$, $b_1 = -F_{\text{lim}} SSB_{\text{lim}}/(SSB_{tar} - SSB_{\text{lim}})$, $a_2 = F_{tar}/(SSB_{tar} - SSB_{\text{lim}})$, $b_2 = -F_{tar} SSB_{\text{lim}}/(SSB_{tar} - SSB_{\text{lim}})$.

The third HCR, 'convex' (Fig. 1c), involves a nonlinear relationship between *F* curves and SSB when SSB is between SSB_{lim} and SSB_{tar}. The two *F* curves can be described as:

$$F_{l3} = \begin{cases} 0 & \text{if} \quad SSB \le SSB_{\text{lim}} \\ a_3(SSB - b_3)/(SSB - 0.8b_3) & \text{if} \quad SSB_{\text{lim}} < SSB \le SSB_{tar} \\ F_{\text{lim}} & \text{if} \quad SSB > SSB_{tar} \end{cases} \tag{5}$$

and

$$F_{t3} = \begin{cases} 0 & \text{if} \quad SSB \le SSB_{\text{lim}} \\ a_4(SSB - b_4)/(SSB - 0.8b_4) & \text{if} \quad SSB_{\text{lim}} < SSB \le SSB_{tar} \\ F_{tar} & \text{if} \quad SSB > SSB_{tar} \end{cases} \tag{6}$$

where $a_3 = F_{\text{lim}}(SSB_{tar} - 0.8SSB_{\text{lim}})/(SSB_{tar} - SSB_{\text{lim}})$, $b_3 = SSB_{\text{lim}}$, $a_4 = F_{tar}(SSB_{tar} - 0.8SSB_{\text{lim}})/(SSB_{tar} - SSB_{\text{lim}})$

$b_4 = SSB_{\text{lim}}$

The fourth HCR, 'concave' HCR (Fig. 1d), involves a quadratic function between *F* curves and SSB, implying a higher rate of increase in *F* when the SSB approaches SSB_{tar}, but a lower rate of decrease when the SSB approaches SSB_{lim}:

$$F_{l4} = \begin{cases} 0 & \text{if} \quad SSB \le SSB_{\text{lim}} \\ a_5(SSB - b_5)^2 & \text{if} \quad SSB_{\text{lim}} < SSB \le SSB_{tar} \\ F_{\text{lim}} & \text{if} \quad SSB > SSB_{tar} \end{cases} \tag{7}$$

and

$$F_{t4} = \begin{cases} 0 & \text{if} \quad SSB \le SSB_{\text{lim}} \\ a_6(SSB - b_6)^2 & \text{if} \quad SSB_{\text{lim}} < SSB \le SSB_{tar} \\ F_{tar} & \text{if} \quad SSB > SSB_{tar} \end{cases} \tag{8}$$

where $a_5 = F_{\text{lim}}/SSB_{\text{lim}}^2$, $b_5 = SSB_{\text{lim}}$, $a_6 = F_{tar}/SSB_{\text{lim}}^2$, $b_6 = SSB_{\text{lim}}$.

Management actions were defined by *F* for most of the control areas in Fig. 1. However, management actions were defined by SSB for areas 1 and 4 (Table 1). For example, when a fishery falls into Area 4 (Fig. 1), we increase the SSB for the next year half of the difference between SSB_{tar} and current SSB. By doing this, we implicitly assume that the fishery with the status in Area 4 will get rebuilt after a 5-year recovery plan (i.e., be very close to SSB_{tar}). We adopted the 5-year plan because the generation time for tropical tuna may be less than 10 years (Shono et al., 2009; Langley et al., 2011). We found this approach could result in unrealistically large changes in *F* from one time-step to the next. The following constrains are implemented to avoid these changes: the *F* estimated cannot exceed F_{tar} in control area 1 and cannot be higher than the target curve in control area 4.

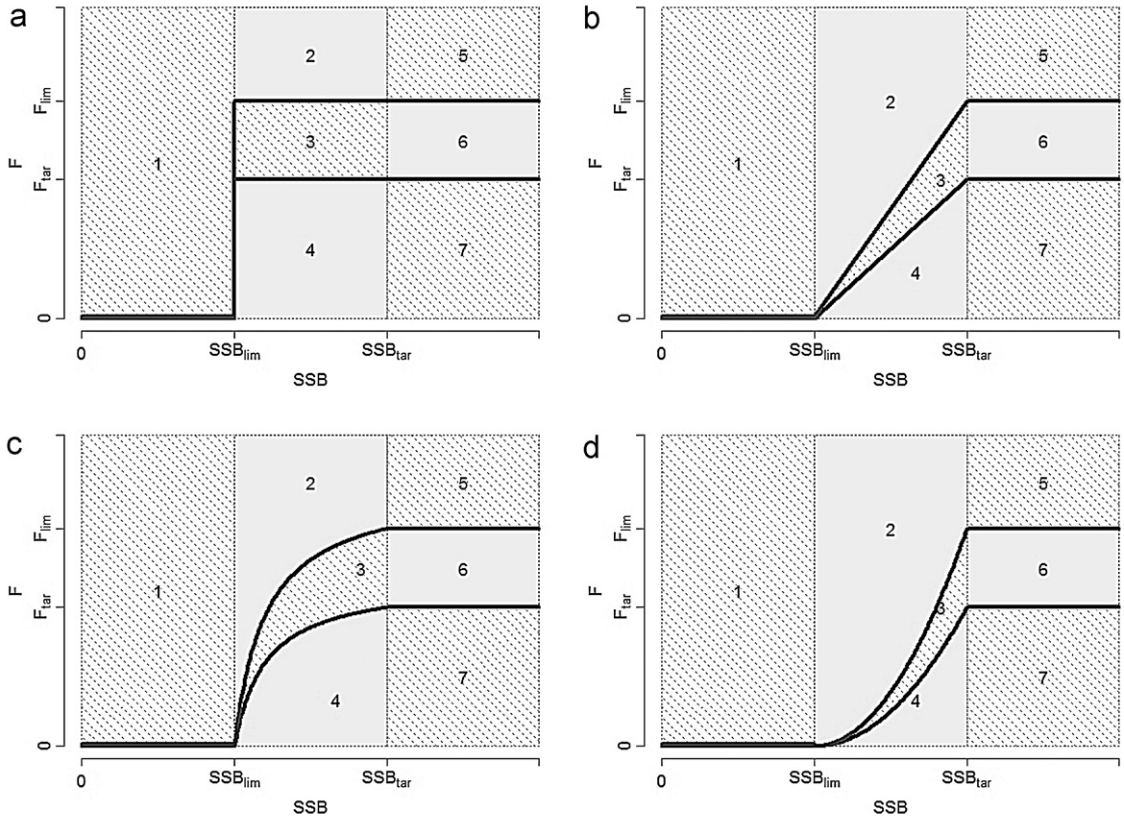

Fig. 1. The harvest control rules: (a) 'knife-edged', (b) 'linear', (c) 'convex', and (d) 'concave'.

2.2. Operating models and uncertainties

An operating model (OM) is required to simulate fishery dynamics (A'mar et al., 2010; Murua et al., 2010; Milner-Gulland et al., 2011). We developed two age-structured OMs, one for each of bigeye and yellowfin. The OM included a growth sub-model, a catch-at-age sub-model, a stock-recruitment sub-model and the exponential survival equation. Life history parameters and fisheries data were taken from IOTC stock assessment reports and relevant references (Shono et al., 2004; Nishida and Shono, 2007). We parameterized the bigeye tuna OM based on the output from the Stock Synthesis model, and the yellowfin tuna OM on the output from MULTIFAN-CL. The time-steps used in the OMs were year for bigeye and season (0.25 year) for yellowfin, to be consistent with the time-steps used in IOTC stock assessments. Relevant equations and parameter values for the OM are provided in Appendix. The management period simulated was 25 years.

The OMs can incorporate various forms of uncertainty that might affect management performance (Jones et al., 2009). We considered uncertainties associated with initial stock abundance, age-composition data, and fishing mortality (Table 2). In addition, we considered process errors associated with recruitment and age-specific natural mortality, as well as errors in implementing HCRs (Table 2). One-hundred Monte Carlo simulation runs were conducted for each HCR. Implementation and process errors and uncertainty for the parameters followed log-normal distribution (except for the initial age-composition which was multinomially distributed; Chen and Wilson, 2002), as is common when simulating the performance of HCRs (Hilborn and Walters, 1992; Shelton, 1992; Quinn and Deriso, 1999). The parameters estimated from stock assessment models or the management actions defined based on BRPs and the HCRs were considered as "true" values and multiplied by log-normally distributed random errors $exp(\varepsilon)$, i.e., $\varepsilon \sim N(-\sigma^2/2, \sigma^2)$ in each of the Monte Carlo simulation. The lower and upper boundary values for the log-normal distributed errors were set as 50% and 200% of the means to avoid biologically unrealistic values being randomly drawn in a given simulation run.

A set of pre-defined performance measures (see below) were recorded at the end of each simulation, and the summary statistics

Table 1
Summary of the seven control areas.

Area	Descriptions	Next time-step rules
1	Overfished	$SSB'_y = SSB_{lim}$ & $F'_y \le F_{tar}$
2	Overfishing with low SSB	$F'_y = F_l$
3	F is higher than F_{tar}, SSB is lower than SSB_{tar}	$F'_y = F_t$
4	Low F, low SSB	$SSB'_y = SSB_{y-1} + (SSB_{tar} - SSB_{y-1})/2$ (for an annual time-step) $SSB'_y = SSB_{y-1} + (SSB_{tar} - SSB_{y-1})/18$ (for a seasonal time-step) & $F'_y \le F_t$
5	Overfishing but SSB is high	$F'_y = F_{lim}$
6	F is between F_{tar} and F_{lim}, SSB is higher than SSB_{tar}	$F'_y = F_{y-1}$
7	Low F, high SSB	$F'_y = F_{tar}$

Table 2
Uncertainty incorporated in the operating model.

Parameters	Error type	Distribution	'Base case'
Management actions in the next time-step	Implementation error	Log-normal	$\sigma = 0.2$
Initial abundance[a]	Parameter uncertainty	Log-normal	$\sigma = 0.25$
Initial fishing mortality[a]	Parameter uncertainty	Log-normal	$\sigma = 0.25$
Recruitment	Process error	Log-normal	$\sigma = 0.6$
Natural mortality for each age class	Process error	Log-normal	$\sigma = 0.2$
Accumulative initial age frequency distribution[a]	Parameter uncertainty	Probabilistic-proportional	ESS = 1000

σ: standard deviation of error term after logarithm; ESS: effective sample size.

[a] The initial abundance, initial age frequency distribution and initial fishing mortality were used to derive initial stock status, and to determine the management action in the first year of the simulated fishery.

for the 100 runs were used to evaluate the effectiveness of HCRs in managing the tuna fisheries.

2.3. Performance measures

The following measures were used to quantify the performance: (1) total catch landed during the management period; (2) CV of the annual catch during the management period (inter-annual catch variation); (3) SSB at the end of the management period (terminal SSB); and (4) the minimum SSB during the simulated management period (minimum SSB). The first two performance measures are related to outputs (i.e., catch) of the fishery, and the other two measures are related to the conservation (i.e., level of SSB). An effective HCR should result in high total landings, low inter-annual variation in catch, high SSB at the end of management period, and high minimum SSB during the management period, although there might be trade-offs among these measures (A'mar et al., 2010; Zhang et al., 2011). The four HCRs were also ranked in terms of the median values of the performance measures from the 100 Monte Carlo simulations, with lower ranks indicating better performance.

3. Results

The four HCRs resulted in different stock status, and involved different management actions when the SSB was between SSB_{lim} and SSB_{tar}.

3.1. Bigeye tuna

The dynamics of the simulated bigeye tuna fishery in the Indian Ocean from 2004 to 2029 are illustrated using trajectory plots (Fig. 2). Stock status stabilized within 10 years and converged at the point (SSB_{tar} and F_{tar}) for all the four HCRs (Fig. 2). This indicates that the four HCRs were all effective in driving the bigeye tuna fishery to a desirable status.

The summary statistics, especially the median values, can be used to quantify the effectiveness of HCRs. The 'linear' HCR achieved the highest total catch, the lowest inter-annual catch variation and the second highest terminal SSB. However, it also resulted in the second lowest value for the minimum SSB during the simulated management period. The 'concave' HCR resulted in the poorest catch-related performance measures, but the best SSB-related performance measures, which shows a typical trade-off between exploitation and conservation measures. The 'convex' HCR had the second highest total catch, a relatively higher minimum SSB, but the lowest terminal SSB. The 'knife-edge' HCR tended to have the worst performance for all the four measures (Table 3).

3.2. Yellowfin tuna

The simulation results for yellowfin tuna managed under each HCR are summarized in Fig. 3. The stock stabilized at an SSB that was close to SSB_{tar} in median terms, but at a relative lower F in mean terms. The differences in ranks among the four HCRs were small (Table 3). However, the 'concave' HCR tended to perform relatively better and the 'knife-edged' HCR had relatively poor performance (Table 3).

4. Discussion

We developed two age-structured OMs to evaluate the effectiveness of the four HCRs for managing the bigeye and yellowfin tuna fisheries in the Indian Ocean. The trajectory plots indicated that all the four HCRs were effective in managing these fisheries for the simulation scenarios considered in this study. The relatively poor performance of the 'knife-edged' HCR, compared with those of the other three HCRs, for both tuna fisheries indicates that it is necessary to adjust F when SSB is between SSB_{lim} and SSB_{tar}. This is consistent with the results reported in previous studies (e.g., Needle, 2008; Siddeek et al., 2009). The 'linear' and 'concave' HCRs performed relatively better than the 'convex' and 'knife-edge' HCRs as they led to higher SSBs. This result is consistent with precautionary management practice (Garcia, 1996).

An HCR is usually defined by a set of BRPs, which can greatly influence its performance. In this study, both target and limit BRPs were incorporated into the HCRs as boundaries. However, one set of BRPs was considered for each tuna species. The choice of a limit BRP is critical in helping fish stocks recover before collapse (Caddy and Mahon, 1995). Therefore, limit BRPs should be considered as important as target BRPs in fisheries management. The limit BRPs were fixed to be proportional to the target BRPs in this study to reduce complexity. In future, different BRPs should be evaluated, and inconsistencies among BRPs derived from different models should also be carefully examined for a given HCR.

Table 3
Comparison of the median values of the performance measures for the bigeye and yellowfin tuna fisheries in the Indian Ocean for the 'knife-edged', 'linear', 'convex' and 'concave' HCRs. Lower ranks are better.

Rank		Bigeye tuna	Yellowfin tuna
Total catch	'knife-edged'	3	4
	'linear'	1	2
	'convex'	2	1
	'concave'	4	3
Inter-annual catch variation	'knife-edged'	2	4
	'linear'	1	2
	'convex'	3	3
	'concave'	4	1
Terminal SSB	'knife-edged'	3	2
	'linear'	2	3
	'convex'	4	4
	'concave'	1	1
Minimum SSB	'knife-edged'	4	1
	'linear'	3	4
	'convex'	2	3
	'concave'	1	2

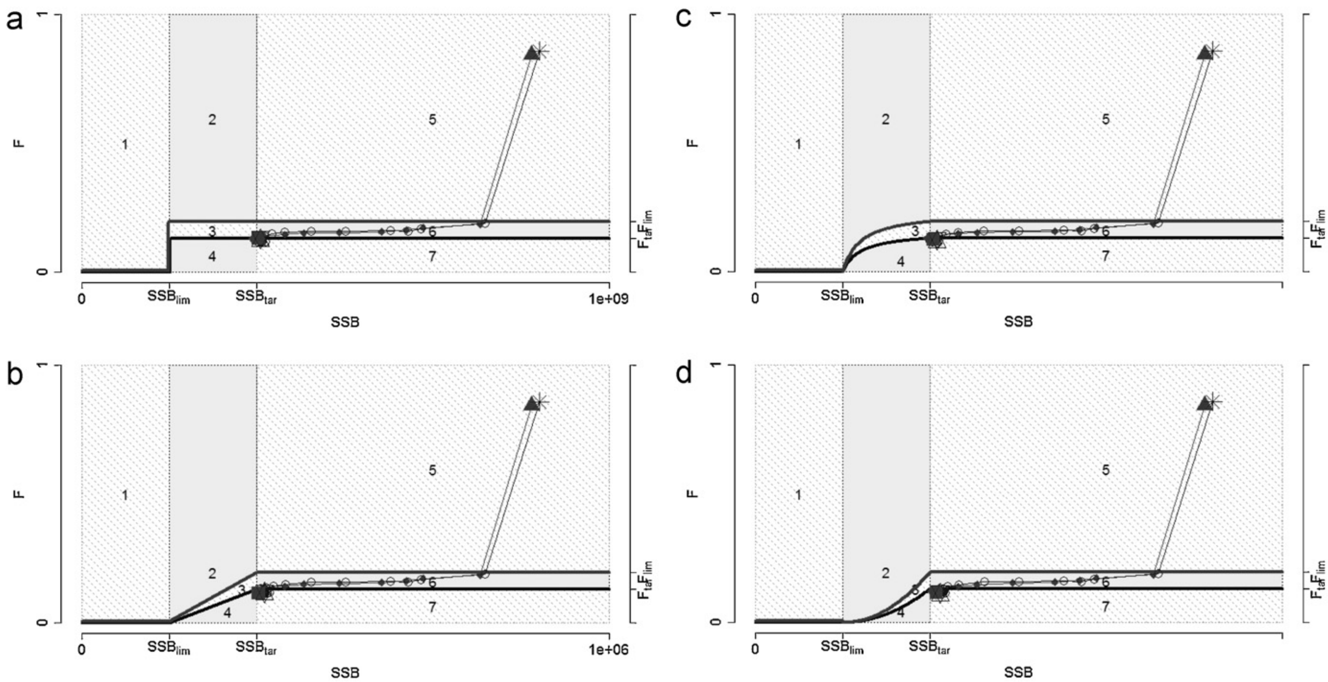

Fig. 2. Predicted dynamics of the bigeye tuna fishery in the Indian Ocean at the end of each year during the management period over the 100 simulation runs: (a) 'knife-edged' harvest control rule, (b) 'linear' harvest control rule, (c) 'convex' harvest control rule, and (d) 'concave' harvest control rule. The diamond projection line is the median annual fishing mortality versus the median spawning stock biomass at the end of each year and the circle projection line is the average fishing mortality versus the average spawning stock biomass over the 100 simulation runs. The distance between the median and mean projection lines indicates the variation of fisheries status. The closed triangle and closed square respectively indicate the median fishery status at the start and end of management period. The eight pointed asterisk and the open hexagram respectively indicate the mean fishery status at the start and end of the management period.

It is important to consider uncertainty in fisheries management (Cadrin and Pastoors, 2008). Monte Carlo simulation is often used to evaluate the impact of uncertainty associated with life history and fishery processes on HCRs in achieving management objectives. Uncertainty was defined somewhat arbitrarily in this study. For example, we considered that recruitment followed a log-normal distribution with a standard deviation of 0.6 (Aires-da-Silva and Maunder, 2012a, 2012b) because the IOTC stock assessment reports did not include process error for recruitment. On the other hand, we excluded the process error resulting from uncertainty in stock structure. Future studies should be focused on improving understanding of

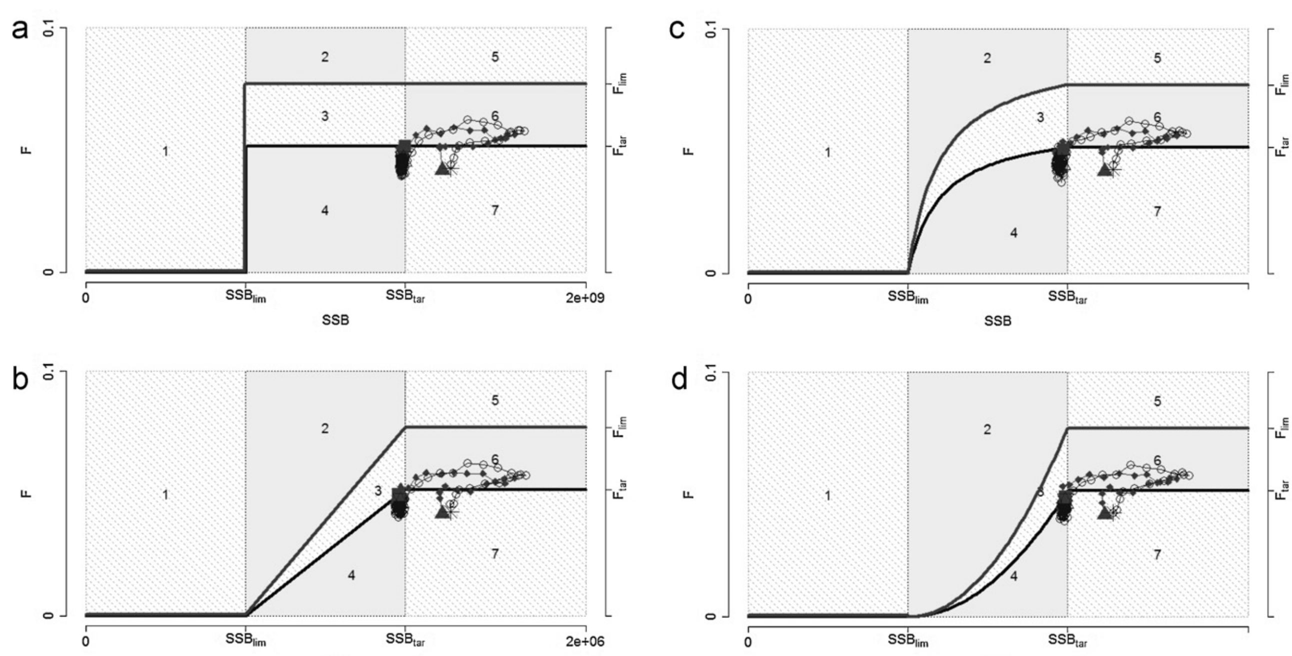

Fig. 3. Predicted dynamics of the yellowfin tuna fishery status in the Indian Ocean at the end of each year during the management period over the 100 simulation runs: (a) 'knife-edged' harvest control rule, (b) 'linear' harvest control rule, (c) 'convex' harvest control rule, and (d) 'concave' harvest control rule. The symbols are the same as in Fig. 2.

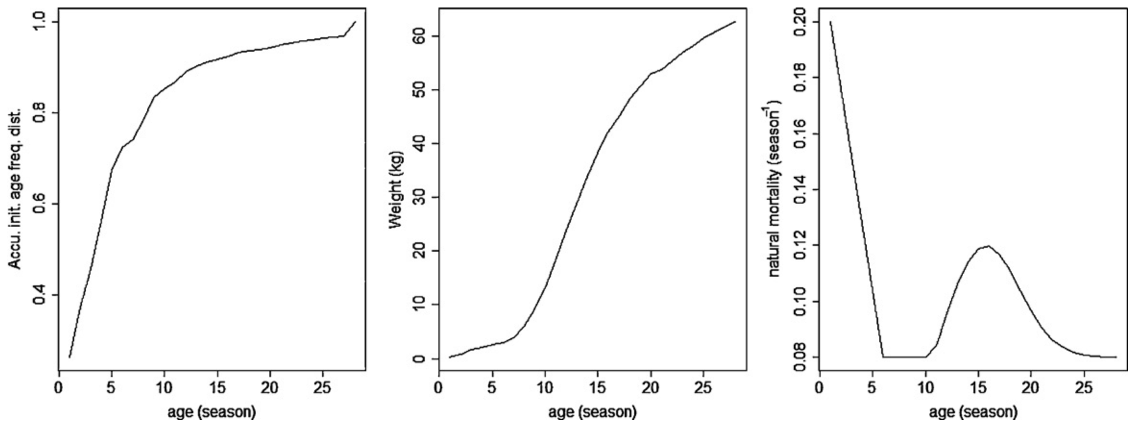

Fig. A1. Parameters used in the operating model for yellowfin tuna, (a) initial age frequency distribution, (b) weight, and (c) natural mortality.

uncertainty associated with the tuna biological and fishery processes.

F-based and SSB-based BRPs were used to determine the status of tuna fisheries in this study. HCRs were designed to control stock status via taking F-based management actions directly or indirectly. However, effort and catch limits and time-area closures are used in the management of the actual tuna fisheries in the Indian Ocean (IOTC, 2011a). Given this, we included log-normally distributed implementation error with a standard deviation of 0.2 in the OM to simulate the imperfect implementation of a defined management action. However, the impact of proposed errors on the management of tuna fisheries in the Indian Ocean needs to be further evaluated.

Assessment errors, which include estimation errors in stock assessments, might be another major source of uncertainty (Bruyn et al., 2010), but were not included in the current OM. Only the projection component was included, with the assumption that managers can estimate stock size perfectly. This is not consistent with the reality, as the IOTC conducts a benchmark stock assessment on a routine basis to incorporate improved biological and fishery knowledge. Our next step is to add an assessment component to the OM and compare the results with and without assessment errors.

In summary, this study provides a framework that can be used to evaluate the performance of alternative HCRs in achieving fisheries objectives. Although the framework was parameterized using information obtained from relevant stock assessment reports, more studies are needed to refine the parameter estimates to improve the simulation of the bigeye and yellowtail tuna fisheries. The framework developed in this study for a systematic evaluation of HCRs may also be useful to other fisheries.

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Appendix A.

Key equations and parameters used in the operating models (Fig. A1).

The operating model consists of two components. The first component determines a management action for the next time-step based on the current stock status and the defined HCR. Log-normal implementation error is added to the management action (Act_{for}) when it is determined for the next time-step (Table A1):

$$Act_{real} = Act_{for} \exp\left(\frac{\varepsilon_{yA} - \sigma_{y_A}^2}{2}\right), \ \varepsilon_{yA} \sim N(0, \sigma_{y_A}^2) \quad \text{(A1)}$$

The second component simulates the fish stock dynamics (i.e., recruitment, growth, and natural and fishing mortality). The basic population dynamics are quantified as follows:

$$N_{y,a} = \begin{cases} R_y & \text{if} \quad a = 0 \\ N_{y-1,a-1} e^{-(M_{y-1,a-1}+F^{total}_{y-1,a-1})} & \text{if} \quad 1 \le a < n \\ N_{y-1,a-1} e^{-(M_{y-1,a-1}+F^{total}_{y-1,a-1})} + N_{y-1,a} e^{-(M_{y-1,a}+F^{total}_{y-1,a})} & \text{if} \quad a = n \end{cases} \quad \text{(A2)}$$

where $N_{y,a}$ is the abundance of fish of age a at the start of time-step y; n is the maximum age class (a plus age class); R_y is the recruitment during time-step y (recruitment is assumed to occur at the start of each time-step); $F^{total}_{y,a}$ is the total fishing mortality for age a during time-step y; $M_{y,a}$ is the natural mortality for fish of age a during time-step y, assumed to be log-normally distributed:

$$M_{y,a} = M_a \exp\left(\frac{\varepsilon_{y_M} - \sigma_{y_M}^2}{2}\right), \ \varepsilon_{y_M} \sim N(0, \sigma_{y_M}^2) \quad \text{(A3)}$$

where M_a is the average natural mortality for fish of age a and σ_{yM} is the standard deviation of logarithmic natural mortality.

The stock-recruitment relationship for both tuna species follows the Beverton-Holt model, with a log-normally distributed process error:

$$R_y = \frac{\alpha SSB_y}{(\beta + SSB_y)} \exp\left(\frac{\varepsilon_{y_R} - \sigma_{y_R}^2}{2}\right), \ \varepsilon_{y_R} \sim N(0, \sigma_{y_R}^2) \quad \text{(A4)}$$

where α and β are the parameters of the stock-recruitment relationship; σ_{yR} is the standard deviation of logarithmic recruitment; and SSB_y is the spawning stock biomass at the start of time-step y, i.e.:

$$SSB_y = \sum_{a=0}^{n} N_{y,a} Mat_a W_a \quad \text{(A5)}$$

Table A1
Parameters used in the operating models and their sources, (a) bigeye tuna and (b) yellowfin tuna.

(a)

Parameters	Values									References
Start year	2004									
Initial abundance (million)	107.15									Personal communication from Dr. Y. Tong
Initial fishing mortality (year^{-1})	0.87									Personal communication from Dr. Y. Tong
Stock-recruit function (000 mt ∼ million)	α = 88.472727				β = 156.36364					Personal communication from Dr. Y. Tong
Age classes	0	1	2	3	4	5	6	7	8+	(Shono et al., 2004)
Accumulative initial age Frequency distribution	0.597	0.736	0.799	0.873	0.939	0.975	0.990	0.996	1	Personal communication from Dr. Y. Tong
Proportion mature	0	0	0	0.5	1	1	1	1	1	(Shono et al., 2004)
Weight (kg)	0	5	17	31	46	60	71	80	86	(Shono et al., 2006)
Natural mortality (year^{-1})	0.8	0.8	0.4	0.4	0.4	0.4	0.4	0.4	0.4	(Shono et al., 2004)

(b)

Parameters	Values					References
Start year	2010					
Initial abundance (million)	218.31159					Personal communication from Dr. A. Langley
Initial fishing mortality (season^{-1})	0.0432					Personal communication from Dr. A. Langley
Stock-recruit function (mt ∼ #)	α = 30465986.2781783				β = 194497.228532585	Personal communication from Dr. A. Langley
Age classes	0∼27+					(Langley et al., 2011)
Accumulative initial age frequency distribution	See Fig. A1					(Langley et al., 2011)
Proportion mature	0–8: 0	9: 0.25	10: 0.5	11:0.75	12–27+: 1	(Langley et al., 2011)
Weight (kg)	See Fig. A1					(Langley et al., 2011)
Natural mortality (season^{-1})	See Fig. A1					(Langley et al., 2011)

where Mat_a is the proportion of fish which are mature at age a and W_a is the average weight of a fish of age a.$F_{y,a}^{total}$ is obtained from the stock assessment report for both bigeye and yellowfin tuna. The total catch (in weight) during time-step y is:

$$C_y = \sum_{a=0}^{n} \left(\frac{F_{y,a}^{total}}{(M_{y,a} + F_{y,a}^{total}) N_{y,a} (1 - e^{-(M_{y,a}+F_{y,a}^{total})}) W_a} \right) \quad \text{(A6)}$$

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