DRAFT

INTER-AMERICAN TROPICAL TUNA COMMISSION

EXTERNAL REVIEW OF IATTC YELLOWFIN TUNA ASSESSMENT

La Jolla, California (USA)
15-19 October 2012

DOCUMENT YFT-01-05 (DRAFT)

A REVIEW AND EVALUATION OF RECRUITMENT AND THE STOCK-RECRUITMENT RELATIONSHIP FOR THE ASSESSMENT AND MANAGEMENT OF YELLOWFIN TUNA IN THE EASTERN PACIFIC OCEAN

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1. ABSTRACT

In general, it is difficult to estimate the stock recruitment relationship and results are either imprecise or biased, often towards recruitment being independent of stock size. In contrast, parameter estimates of the Beverton-Holt stock-recruitment relationship are biased low for EPO yellowfin tuna because of a regime shift in recruitment. Recruitment drives spawning biomass, but this gives the impression that spawning biomass is driving recruitment through the stock-recruitment relationship. Simulation analysis for EPO yellowfin tuna to test the estimability of steepness of the Beverton-Holt stock recruitment relationship were problematic with convergence problems, but did confirm that regime shifts could cause substantial negative bias in the estimates of steepness. It is unlikely that reliable estimates of steepness will be available for EPO yellowfin tuna in the near future. Management quantities that are used for managing EPO yellowfin tuna (e.g. $F_{multiplyer}$ and $S_{current}/S_{MSY}$) are highly sensitive to the assumed value of steepness. However, it less risky in terms of lost equilibrium yield to under-estimate rather than over-estimate steepness. These analyses suggest that a lower, more conservative, value for steepness might be appropriate. However, if fishing mortality has to be reduced from current levels based on the new pre-specified value of steepness, there will be short term loss in yield. Regime shifts in recruitment have a large impact on management quantities such as MSY and S_{MSY}. However, they do not impact F_{MSY}, which is used for managing EPO yellowfin tuna.

2. INTRODUCTION

Recruitment is the natural process that is most influential in driving yields from fish populations. Recruitment generally has the highest temporal variation and the strongest density dependence of all the natural processes (recruitment, natural mortality, growth) perhaps with the exception of movement and spatial distribution. Therefore, understanding recruitment is vital in determining appropriate management actions. Recruitment is particularly influential for short lived species like yellowfin tuna since the population is comprised of only a few age classes.

The stock-recruitment relationship is one of the most uncertain components of stock assessment models and it impacts many management quantities including some commonly used reference points. Uncertainty about the stock-recruitment relationship is a consequence of several factors including the lack of data from low population sizes, temporal correlation in variation around the stock-recruitment relationship, lack of contrast in the stock size, nonstationarity, process variability, and errors in estimating stock size and recruitment (Hilborn and Walters 1992; Quinn and Direso 1999). Attempts to estimate the parameters of the stock-recruitment relationship inside the stock assessment model have shown that the parameter estimates are imprecise or are biased towards recruitment being independent of stock size (Magnusson and Hilborn 2007, Conn et al. 2010; Lee et al. 2012). Meta-analyses have been conducted in an attempt to improve estimates of the parameters of the stock-recruitment relationship (Myers et al. 1999; Dorn 2002), but these studies are questionable because the authors lack knowledge of the individual data sets that have been used (e.g. they ignore the influence of regime-shifts), are fellable to the same issues mentioned above, or make biased assumptions (Maunder 2012). Life history theory has also been used to infer the parameters of the stock-recruitment relationship (He et al. 2006; Mangel et al. 2010), but these approaches do not provide useful estimates (Maunder 2012).

We provide a comprehensive review of recruitment and the stock-recruitment relationship relevant to yellowfin tuna in the eastern Pacific Ocean (EPO). First we describe how recruitment has been treated historically. Next we describe the different components of recruitment, the important issues, and methods to estimate the stock-recruitment relationship. We also evaluate the sensitivity of management quantities to the steepness of the Beverton-Holt stock-recruitment relationship used in the EPO yellowfin tuna stock assessment and to regime shifts. We use simulation analysis to test if steepness can be estimated from the data available for EPO yellowfin tuna. Finally, we evaluate the loss in yield caused by mispecifying steepness.

History

Early stock assessments of yellowfin tuna in the EPO were based on surplus production models (Schaefer 1954; Pella and Tomlinson 1969) which combine recruitment with the other population processes into a single production function. The production function encapsulates the rates of recruitment and other population and fishery processes (e.g. natural mortality, growth, selectivity) as well as any density dependence. The Pella-Tomlinson model is generally more appropriate than the Schaefer model because the shape parameter of the production function can be set to represent the appropriate dynamics including the stock-recruitment relationship (Maunder 2003). However, it is generally difficult to reliably estimate the shape parameter from typical data used to fit surplus production models (e.g. an index of relative abundance). These traditional surplus production models do not allow for temporal variation in recruitment. The Pella-Tomlinson model was replaced by cohort analysis because the Pella-Tomlinson model could no longer describe the yellowfin population dynamics due to changes in selectivity (different method of fishing) and productivity (recruitment).

Cohort analysis directly integrates each of the population processes (recruitment, natural mortality, and growth/aging) into an age-structured model and allows for estimates of annual recruitment. Recruitment is simply back calculated from the catch of the corresponding cohort adjusted for natural mortality. Yellowfin tuna generally spawn year around as long as the water temperature is above 24°C (Margulies et al. 2007) so a single annual recruitment as assumed for temperate species in not appropriate. The cohort analysis was conducted assuming two cohorts a year corresponding to the northern and southern hemisphere summers based on Hennemuth (1961) who reported that there are two peaks of spawning of yellowfin in the EPO. Cohort analysis requires tuning to estimate the size of cohorts not fully represented in the catch-at-age data and the general approach used for the EPO yellowfin assessment was to keep the recruitment constant in recent years.

The cohort analysis was replaced with more contemporary integrated statistical age-based approaches (Maunder and Punt in press). First using ASCALA (Maunder and Watters 2003) and later using Stock Synthesis (Methot and Wetzel in press). These two approaches make similar assumptions about recruitment. Recruitment is quarterly and varies lognormally around the Beverton-Holt stock-recruitment relationship. The standard deviation of the lognormal deviate is fixed at 0.6. The basecase assessment assumed that recruitment was independent of stock size (the steepness of the stock-recruitment relationship, the recruitment realized when the population is at 20% of its unexploited level as a ratio of the recruitment from an unexploited level, is fixed equal to one). Sensitivity analyses are conducted by fixing steepness at 0.75 and also by estimating steepness. Steepness is generally estimated at a low value (approximately 0.7), but this is thought to be a consequence of a regime shift in recruitment rather than the presence of a stock-recruitment relationship.

The functional form of the stock-recruitment relationship

There are a range of models available to represent the relationship between stock and recruitment. The two parameter Beverton-Holt (Beverton and Holt 1957) and the Ricker (Ricker 1954) models are the most commonly used. There are also three parameter models that have the Beverton-Holt and Ricker models as special cases. The Ricker model is most often used for salmonids and for species where cannibalism is considered to be an important factor and for species whose prey can be depleted by them (Quinn and Deriso 1999). The Beverton-Holt model is most commonly used for marine teleost species. The three parameter models are not commonly used because there is usually insufficient information in the data to reliably estimate all three parameters.

The EPO yellowfin tuna assessment uses the Beverton-Holt stock recruitment relationship, which is available in the Stock Synthesis software (Methot and Wetzel in press). The model is parameterized in terms of the average recruitment at the unexploited equilibrium or virgin recruitment (R0), and steepness (h). Steepness measures the level of compensatory density dependence and is defined as the fraction of R0 when the spawner biomass is 20% of the virgin level (S0) (Mace and Doonan, 1988; Francis, 1992). The higher h, the more resilient the population is to exploitation.

Definition of spawning biomass

Development of a stock-recruitment relationship requires a definition of the effective spawning biomass. If the spawning biomass is defined incorrectly, then the relationship will be biased and may be difficult to estimate from the available data. It is common to assume that effective spawning biomass is proportional to the weight of mature individuals. However, egg production is generally not a linear function of body weight and the viability of eggs may differ with age. Generally, only female spawning biomass is used and imbalances in the ratio of males and females and its effect of fertilization are ignored. In single sex models, imbalances in sex ratio will cause biased estimates of the female spawning biomass since they generally assume that spawning biomass is proportional to the combined male and female abundance

The spawning potential of EPO yellowfin tuna is estimated from the numbers of mature females adjusted for batch fecundity and spawning frequency (Schaefer 1998). Specifically using female abundance is important because the sex ratio changes with age, which is assumed to be caused by differences in female and male natural mortality. In early stock assessments conducted using ASCALA, which is a single sex model, sex ratio data at age was applied to the combined male and female abundance at age to calculate female abundance. In the current Stock Synthesis assessments, the model is sex specific so females are modeled explicitly. Margulies et al. (2007) found that spawning females increased their egg production in response to increases in food and that egg size increased with female size, although hatching success was not related to egg size.

Estimation of the stock-recruitment relationship from time series of stock and recruitment data

The most common historical approach to estimate the stock-recruitment relationship has been to fit the model to time series of stock size and recruitment. The time series have generally been outputs of virtual population analysis (VPA), cohort analysis, or related methods that fit to time series of catch-at-age data. In some cases (typically salmonids) direct estimates using surveys and counts are made of the stock size and recruitment independently. The Ricker model has commonly been used because it can be linearized eliminating the need for nonlinear estimation.

The EPO yellowfin tuna Stock Synthesis model estimates both spawning stock and recruitment on a quarterly basis (Figure 1). It has been argued that visualization of the data is better on an annual basis (Figure 2). The time series illustrate clearly that there is strong autocorrelation in both the recruitment and spawning biomass (Figures 1 and 2). The lower panels of Figures 1 and 2 show the three hypothesized regime shifts in recruitment. Figure 3 shows the fit of Ricker and Beverton-Holt models to the quarterly estimates of stock-size and recruitment. The fits are similar for both models and show a strong relationship between recruitment and stock size, although this is probably due to the autocorrelation in recruitment (regime shifts) driven by the environment.

Estimation of the stock-recruitment relationship inside the stock assessment model

Theoretically, it should be possible to estimate the stock-recruitment relationship within the stock assessment model, particularly when multiple data sets are available in an integrated stock assessment (Maunder and Punt in press). Estimating the relationship inside the stock assessment model should be superior to the two-step approach that uses previously estimated time series of stock and recruitment data because it automatically accounts for the uncertainty in the estimates of stock and recruitment. However, several studies have shown that the estimates can be imprecise or biased (Magnusson and Hilborn 2007, Conn et al. 2010; Lee et al. 2012). Particularly concerning is the tendency towards positively biased estimates of steepness. However, in some cases, typically when there is contrast in the spawning biomass at low levels, the stock-recruitment relationship can be estimated, although there still tends to be some positive bias (e.g. Maunder 2012).

The Stock-Synthesis assessment model for EPO yellowfin tuna estimates steepness of the Beverton-Holt stock-recruitment model at 0.69. However, this estimate is thought to be a consequence of the regime shift in recruitment that drives spawning biomass rather than spawning biomass driving recruitment.

Life history theory

He et al. (2006) developed priors for steepness based on the evolutionary principle that persistence of any species, given its life history and exposure to recruitment variability, requires a minimum recruitment compensation to enable the species to rebound consistently from low abundance. Unfortunately, the priors from their method are very broad and provide no advice over that which is already assumed when considering plausible values for steepness.

Mangel et al. (2010) used life history parameters to construct priors for steepness. Their method is based on the maximum per capita productivity, which is estimated from survival of eggs and larvae, and natural mortality. Survival of eggs and larvae are calculated using the equations of McGurk (1986). Unfortunately, the method is dependent on assumptions that are violated and data that is generally not available. The mortality rates of eggs and larvae are unknown for most species and even if they were available for the species of interest their reliability would be suspect. Calculation of the maximum per capita productivity needs survival rates at very low abundance levels and it is unlikely that these abundance levels would have been observed. The method also requires that the stock-recruitment model accurately describes the stock-recruitment relationship at low abundance levels so that it can be expanded to spawning biomass levels related to the steepness parameters, which occurs at 20% of the unexploited level. The use of stock-recruitment models in stock assessment only requires the stock-recruitment model to accurately represent the relationship for levels of spawning biomass observed and at unexploited levels, which are used to estimate reference points. Therefore, the value of the Mangel et al. (2010) approach for EPO yellowfin tuna and other species is probably limited.

Using estimates from other stocks and species

Several studies have analyzed stock-recruitment data for a range of species in an attempt to provide advice on steepness for stocks that lack information (e.g. Myers et al. 1999; Dorn 2002). Steepness is independent of population size and is therefore comparable across stocks. For example, Myers et al. (1999) applied meta-analysis to a large number of species and their analysis is commonly used to specify steepness for stocks that lack information to estimate steepness. However, their analysis was inherently biased toward estimating low values of steepness, which can be substantial, because they used the Ricker model rather than the Beverton–Holt model (see appendix 2 of Myers et al., 1999). In addition, these studies are questionable because the authors lacked knowledge of the individual data sets that have been used (e.g. they ignore the influence of regime-shifts), and are fellable to the same issues mentioned above.

Inherent correlation among life history characteristics has often been used to provide estimates of unknown parameters, particularly for estimating natural mortality (e.g. Jensen 1996). Myers et al. (1999) found a positive relationship between reproductive longevity (the expected number of years that an individual reproduces) and steepness, which Myers et al. (2002) used to develop a prior for use with stocks that have insufficient information to estimate steepness. Shertzer and Conn (2012) found no statistically significant relationships between steepness and natural mortality and age at maturity. Given the poor performance of these methods for natural mortality, it is unlikely that they will be useful for steepness.

Myers et al. (1999) estimated steepness for 8 stocks of Scombridae, including 5 tuna species. The median value of steepness was relatively low (0.52) and the median for the only yellowfin stock was 0.7 (Table 1). Harley (pers com) applied meta-analysis of steepness to stock size and recruitment time series for a variety of tuna species from the three oceans. However, these estimates are suspect because they do not account for factors such as regime shifts (e.g. the EPO data is included and contains the regime shift resulting in a h =0.69) or other bias (e.g. the increase in recruitment for EPO bigeye tuna as the floating object fishery expanded, which is thought to be an artifact of the assessment model).

Management proxies to account for uncertainty in the stock-recruitment relationship

Many common reference points are dependent on the stock-recruitment relationship as well as other parameters such as natural mortality, growth, and selectivity. Proxy reference points have been developed to be robust to uncertainty in the stock assessment parameters, particularly the stock-recruitment relationship, or to be precautionary (e.g. Clark 1991, 1993, 2002). Given that the appropriateness of some proxy reference points are dependent the true stock-recruitment relationship, proxy reference points have been discouraged (Maunder 2012). Williams and Shertzer (2003) suggest using proxy or precautionary values for the stock-recruitment parameters (e.g. steepness). If a precautionary prior is used for steepness, when strong information is contained in the data it will move the estimated steepness to be less precautionary. This would encourage the collection of additional data to make the assessment less precautionary. However, care needs to be taken to make sure that bias (e.g. regime shifts) does not influence the results.

Currently, assessments of yellowfin tuna in the EPO are always accompanied by a sensitivity analysis that uses steepness = 0.75 to provide managers with information about the consequences of a relationship between recruitment and spawning stock size. However, probability statements about this state of nature being true are not provided. No proxy reference points are used for yellowfin tuna in the EPO.

Recruitment variation

Recruitment is influenced by both density dependent and density independent components. Most contemporary sock assessments include both density dependence (through the stock-recruitment relationship) and density independent processes. The density independent process represents factors such as environmental variability that might influence the survival of individuals as larvae and juveniles before they recruit to the fishery. The standard approach assumes that recruitment is lognormally distributed around the Beverton–Holt stock–recruitment relationship. The lognormal distribution is commonly implemented by estimating parameters representing annual deviates constrained by a penalty added to the objective function based on the lognormal distribution assumption and application of a bias correction factor, the size of which depends on the amount of information about recruitment in the data (Methot and Taylor 2011). This is an approximation to a random effect or state-space modeling approach which appropriately integrates out the random variable (Maunder and Deriso 2003), but is too computationally intensive for many stock assessment applications. The standard deviation of the log normal distribution should be estimated, but this generally requires integrating out the random variable (Maunder and Deriso 2003), and is often pre-specified. The common assumption is that the standard deviation is 0.6, which is based on the average of several stocks (Beddington and Cooke 1983). Refinement of the process variation using environmental covariates (e.g. Maunder and Watters 2003b) will reduce the amount of random process variation requiring a lower standard deviation for the lognormal distribution. Auto-correlation can also be modeled in the process variation, which may impact the steepness estimates (Ianelli 2002). Recruitment variation in combination with parameter uncertainty can be included in future projections by treating the future as part of the estimation period using the method described by Maunder et al. (2006) or by using full Bayesian analysis (Punt and Hilborn 2007).

Generally, process variation is assumed to be density independent. However, the parameters of the stock-recruitment relationship (e.g. carrying capacity) may be influenced by the environment and change how density dependence influences recruitment. The process variation is generally added after density dependence (stock-recruitment relationship) and applying the process error prior to density dependence will change how process variation influences recruitment.

Recruitment in the EPO yellowfin tuna assessment is modeled to occur quarterly and therefore quarterly process errors are estimated. The quarterly recruitment is assumed to be lognormally distributed with a standard deviation of 0.6 (note that this is quarterly not annual). A seasonal (quarterly) model (a parameter for each season in addition to the temporal deviates) has been applied in past assessments, but it was found that phase shifts in the seasonal pattern occur invalidating a seasonal model. Recruitment of yellowfin in the EPO has tended to be greater after El Niño events (Joseph and Miller 1989). Previous stock assessments have included the assumption that oceanographic conditions might influence recruitment of yellowfin in the EPO (Maunder and Watters 2001, 2002). This assumption is supported by observations that spawning of yellowfin is temperature dependent (Schaefer 1998). Margulies et al. (2007) found that yellowfin generally spawn when the temperature is above 24° C, but also found that spawning ceased when temperatures declined even if the temperature was above 24° C. Margulies et al. (2007) also found that water temperature was inversely related to egg size, egg-stage duration, larval size at hatching, and yolksac larval duration. To compensate for the longer stage durations, yellowfin spawned earlier in the day when temperatures were colder.

To incorporate the possibility of an environmental influence on recruitment of yellowfin in the EPO, a temperature variable was incorporated into previous stock assessment models to determine whether there is a statistically-significant relationship between this temperature variable and estimates of recruitment. Previous assessments (Maunder and Watters 2001, 2002) showed that estimates of recruitment were essentially identical with or without the inclusion of the environmental data. Maunder (2002) correlated recruitment with the environmental time series outside the stock assessment model. For candidate variables, Maunder (2002) used the average sea-surface temperature (SST) in an area consisting of two rectangles from 20°N-10°S and 100°W-150°W and 10°N-10°S and 85°W-100°W, the total number of 1°x1° areas with average SST≥24°C, and the Southern Oscillation Index. The data were related to recruitment, adjusted to the period of hatching. However, no relationship with these variables was found.

Regime shifts

The environment can have a large influence on population processes including recruitment. The environment is often auto-correlated and can show substantial long term shifts that may produce similar patterns in recruitment. The recruitment estimates from the EPO yellowfin tuna stock assessment model show strong autocorrelation and indicate several possible recruitment regimes (e.g. 1975-1982, 1983-2002, and 2003-2009; see Figure 1).

These regimes have implications for calculation of reference points and forward projections. Reference points for EPO yellowfin tuna are calculated using the average recruitment over the whole stock assessment time period, which may include multiple regime shifts. The impact of regime shifts on reference points can be calculated for EPO yellowfin tuna by simply multiplying MSY, S_{MSY}, and S_0 by the ratio of the average recruitment in the regime to the average recruitment in the whole time series. These can then be used to calculate the other reference points and management quantities. F_{MSY} does not change. The ratio of average recruitment for the regimes 1975-1982, 1983-2002, and 2003-2009 compared to the average over 1975-2009 are 0.67, 1.19, and 0.84 respectively. Since the current abundance does not change in these calculations, but the unexploited spawning biomass does, the current spawning biomass ratio (SBR) would be 50% higher, 16% lower, and 19% higher for these scenarios, respectively. The Inter-American Tropical tuna Commission (IATTC), which is responsible for managing yellowfin tuna in the EPO (informally), bases management on F_{MSY} and management will not be impacted if the regime shift simply impacts the average recruitment.

Management consequences

Standard management reference points such as F_{MSY}, MSY and S_{MSY}/S_0 are dependent on the stock-recruitment relationship (Maunder 2012). The equilibrium yield curve that is used to calculate MSY is the product of YPR and the stock-recruitment relationship (Maunder 2008).

Reference points are often defined based on equilibrium (average) conditions, however temporal variation in recruitment can influence reference points. For example, a short lived species with high recruitment variation could conceivably change from being underfished to overfished and back again in the absence of fishing simply due to temporal variation in recruitment. In these cases, and for regime shifts presented above, it may be more appropriate to calculate dynamic reference points such as dynamic B0 (dB0) (Maunder and Watters 2003). Wang et al. (2009) described how to calculate dB0. They also described how to partition the impact of the fisheries into each fishery. Similar calculations can be conducted to calculate dB_{MSY} by projecting the population under F_{MSY} rather than F=0.

Dynamic B0 for EPO yellowfin tuna is shown in Figure 4 (dashed line). Even in the absence of fishing the abundance would have fluctuated substantially and more than doubled between 1975 and 2001, then declined substantially again by 2011. The dynamic spawning biomass ratio (estimated spawning biomass in a given year divided by the dynamic B0 in the same year) is presented in Figure 5 and shows some substantial differences over time compared to the standard spawning biomass ratio.

Even in the absence of a stock-recruitment relationship, the definition of spawning biomass can influence reference points based on spawning biomass (e.g. S_{MSY} and S_{MSY}/S_0, S_{cur}/S_{MSY}). The spawning potential of EPO yellowfin tuna is estimated from the numbers of mature females adjusted for batch fecundity and spawning frequency (Schaefer 1998) (see above).

Robust assumptions

In the face of uncertainty about the stock-recruitment relationship it would be beneficial if model assumptions or management strategies could be developed that are robust to the uncertainty. Zhu et al. (2012) demonstrated that it less risky in terms of lost equilibrium yield to under-estimate rather than over-estimate steepness. The yield curve is flat when the true steepness is high (e.g. recruitment is independent of spawning biomass) and is more domed-shaped for lower values of steepness. Therefore, equilibrium yield is much more sensitive to miscalculating fishing mortality when steepness is low. These results suggest that when steepness is uncertain, particularly given the tendency for positive estimation bias, a lower, more conservative, value for steepness should be pre-specified. However, if fishing mortality has to be reduced from current levels based on the pre-specified value of steepness, there could be greater short term loss of yield due to mispecifying steepness. The calculations of Zhu et al. (2012) have been conducted for EPO yellowfin tuna and they also demonstrate the lower risk of underspecifying steepness (Maunder and Aires-da-silva 2010). These values have been updated in Figure 6.

3. METHODS

Simulation analysis

Simulation analysis is used to evaluate the ability to estimate steepness within the stock assessment model. The simulation analysis is based on that in Maunder (2012) and is similar to that used by Lee et al. (2012) for other species:

(1) The model is fit to the original data based on a pre-specified value for steepness.

(2) The model parameters estimated in (1) are used to generate artificial data sets based on the characteristics of the data used when fitting the model (indices of abundance and catch-at-age data for the fisheries, surveys, and years available; catch is unchanged) and the sampling distribution assumptions (i.e. the likelihood functions and their sample sizes or standard deviations).

(3) The model is fit to the simulated data, this time treating steepness as an estimated parameter.

(4) Steps (2)–(3) are repeated 8 times.

(5) Steps (1)–(4) are repeated for a range of values of steepness.

Stock assessment model

The Stock Synthesis software (Methot and Wetzel in press) is used to assess the status of yellowfin tuna in the EPO (Aires da Silva and Maunder 2012). SS is an integrated statistical age-structured stock assessment model (Maunder and Punt in press). The EPO yellowfin tuna application is sex structured and uses quarterly time steps to describe the population dynamics with recruitment occurring every quarter. The model is fitted to indices of relative abundance based on CPUE and to size compositions by finding a set of population dynamics and fisheries parameters that maximize a penalized (for recruitment temporal deviates) likelihood, given the amount of catch taken by each fishery. Sixteen fisheries are defined on the basis of gear type (purse seine, pole and line, and longline), purse-seine set type (sets on schools associated with floating objects, unassociated schools, and dolphin-associated schools), and IATTC length-frequency sampling area or latitude. CPUE data is not used for fisheries that do not direct their effort at yellowfin or that have too much variability in the fishery. Parameters estimated include average recruitment and quarterly recruitment deviates, catchability coefficients for the five CPUE time series that are used as indices of abundance, coefficients of variation (CV) for likelihood functions for four of the CPUE indices used as indices of abundance (the CV of the southern longline fishery, which is assumed to be the most reliable index of abundance, is fixed at 0.2), selectivity curves for 11 of the 16 fisheries, and initial population size and age structure (recruitment offset, initial fishing mortality, and deviates for ages 1 to 16 quarters). Several parameters are assumed known including age and sex specific natural mortality, the mean length at age, parameters of a linear model relating the coefficient of variation of length at age to age, fecundity of females at age, and selectivity curves for the discard fisheries. Estimates of management quantities and future projections are computed based on the average of the 3 most recent years (2009-2011) fishing mortality rates by gear.

Scenarios

The simulation analysis was conducted under three scenarios to simulate the data:

1) True steepness = 1 and recruitment deviates are randomly generated
2) True steepness = 0.75 and recruitment deviates are randomly generated
3) True steepness = 1 and recruitment deviates are fixed to those estimated in the base case assessment. This is used to estimate the influence of regime shifts on the estimate of steepness.

Management consequences

The stock assessment model is run under different pre-set values for steepness and for the standard deviation variation used in the lognormal recruitment deviate penalty. In addition to management quantities, the negative log-likelihood for each data component is presented to investigate the information content of the data. The management quantities include

1. Maximum sustainable yield (MSY)
2. The biomass and spawning biomass corresponding to MSY (B_{MSY}, S_{MSY})
3. The biomass and spawning biomass corresponding to MSY as a ratio of the unexploited spawning biomass (B_{MSY}/B_0, S_{MSY}/S_0).
4. Recent catch as a proportion of MSY (C_{recent}/MSY).
5. Recent biomass and spawning biomass as a proportion of S_{MSY} (B_{recent}/B_{MSY} , S_{recent}/S_{MSY})
6. The multiplier that would make the current fishing mortality (or effort) equal to the fishing mortality corresponding to MSY ($F_{multiplier}$).

4. RESULTS

Estimating steepness from simulated data

The yellowfin tuna stock assessment has convergence problems when estimating steepness from the simulated data. In both cases where the simulated data was based on a model with randomly generated recruitment deviates, there were convergence issues with all 8 simulations. For the remaining scenario where steepness = 1 and the recruitment deviates used in the simulator were taken from the original estimates, the estimates of steepness were around 0.67 (Figure 7). These results suggest that regime shifts can produce substantial negative bias in estimates of the steepness of the Beverton-Holt stock-recruitment relationship.

Management consequences

Steepness

Steepness is estimated at 0.69. The model appears to converge well for higher values of steepness and the profile likelihood is smooth (Figure 8). However, convergence problems are encountered for lower levels of steepness. The recruitment penalty has the most influence on reducing the estimate of steepness.

S_{MSY}, S_{recent}/S_{MSY}, and $F_{multiplyer}$ are all highly sensitive to steepness (Table 2). MSY, S_{MSY}/S_0, and C_{recent}/MSY are moderately sensitive to steepness.

Recruitment variation

The data supports a value of 0.6 for the standard deviation of the lognormal penalty on recruitment deviations (Figure 9). The length frequency prefers a higher value and the recruitment penalty prefers a lower value. All the management quantities are relatively insensitive to the value of the standard deviation.

5. DISCUSSION

There is very little reliable information for steepness of the Beverton-Holt stock-recruitment relationship for EPO yellowfin tuna. Estimation inside the stock assessment produces low levels of steepness that appear to be biased due to regime shifts in recruitment. Simulation analysis by other authors have shown that estimates of steepness are generally imprecise or biased (Magnusson and Hilborn 2007, Conn et al.

2010; Lee et al. 2012). Simulation analysis for EPO yellowfin tuna were problematic with convergence problems.

It is unlikely that reliable estimates of steepness will be available for EPO yellowfin tuna in the near future. The current assessment assumes that recruitment is independent of stock size. Biologically this is unrealistic because recruitment should reduce as the spawning biomass gets very low. However, this assumption only has to be valid for the stock sizes experienced during the assessment period and valid in any projections. It is not clear if this is the case. Management quantities that are used for managing EPO yellowfin tuna (e.g. $F_{multiplyer}$ and $S_{current}/S_{MSY}$) are highly sensitive to the assumed value of steepness. However, it less risky in terms of lost equilibrium yield to under-estimate rather than over-estimate steepness (Maunder and Aires-da-silva 2010; Zhu et al. 2012). These analyses suggest that a lower, more conservative, value for steepness might be appropriates. However, if fishing mortality has to be reduced from current levels based on the new pre-specified value of steepness, there will be short term loss in yield. It is not clear what a lower value of steepness should be chosen.

Regime shifts in recruitment have a large impact on management quantities such as MSY and S_{MSY}. However, they do not impact F_{MSY}, which is used for managing EPO yellowfin tuna. The use of dynamic S_{MSY} would make the biomass reference points used in the Kobe Plot more consistent with F_{MSY} in the presence of regime shifts.

The estimation of steepness performed poorly in the simulation analysis with convergence problems. This occurred even though the model structure is known correctly and the initial parameter values were based on the true values. More analysis is needed to determine why these convergence issues occurred and the simulation analysis repeated. Although, based on previous studies it is unlikely that the results from the simulation analysis will be encouraging.

Acknowledgements

This research addresses topic X:recruitment of the good practices guide to stock assessment program of the Center for the Advancement of Population Assessment Methodology (CAPAM) and is contribution number Y. Hui-Hua Lee assisted with the simulation analysis.

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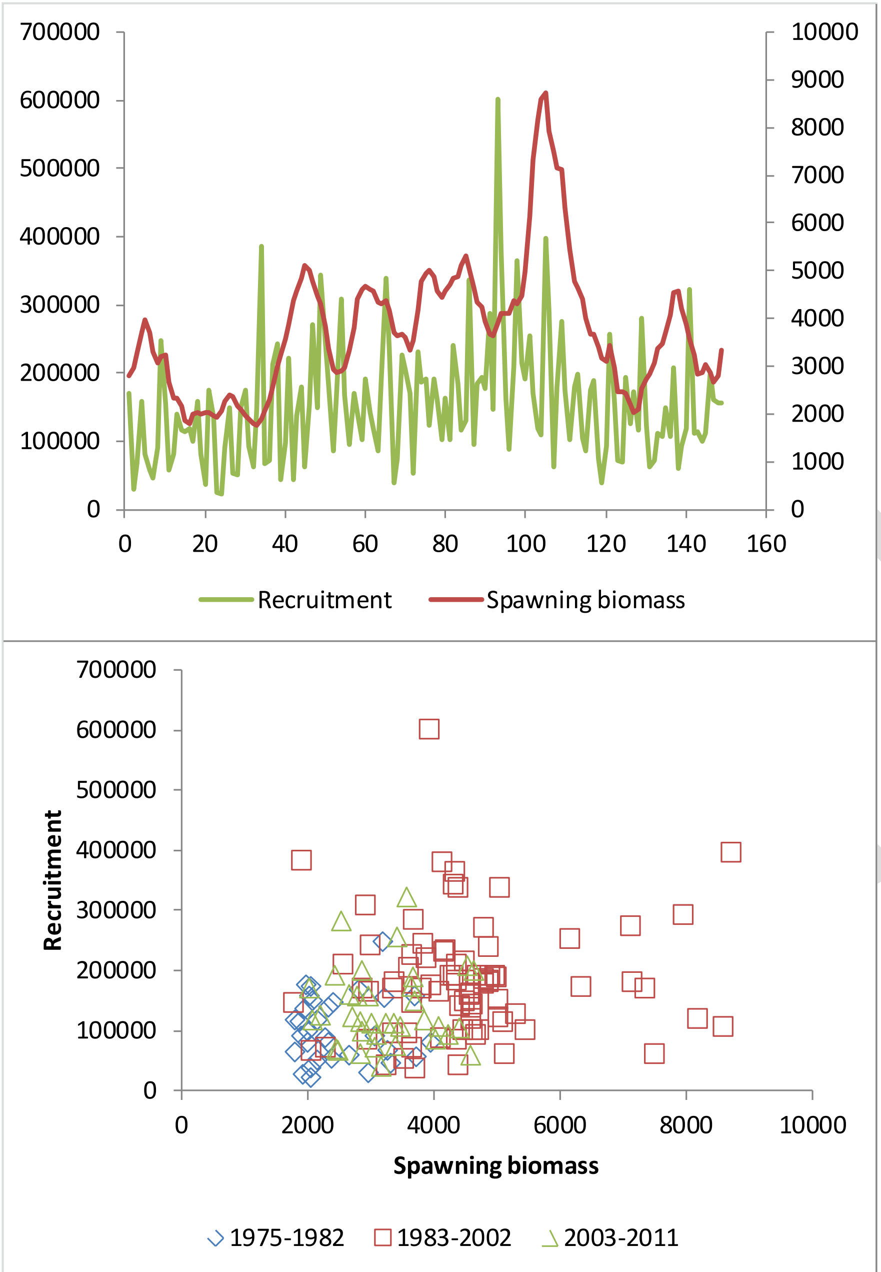

Figure 1. Estimates of quarterly spawning biomass and recruitment for yellowfin tuna in the EPO.

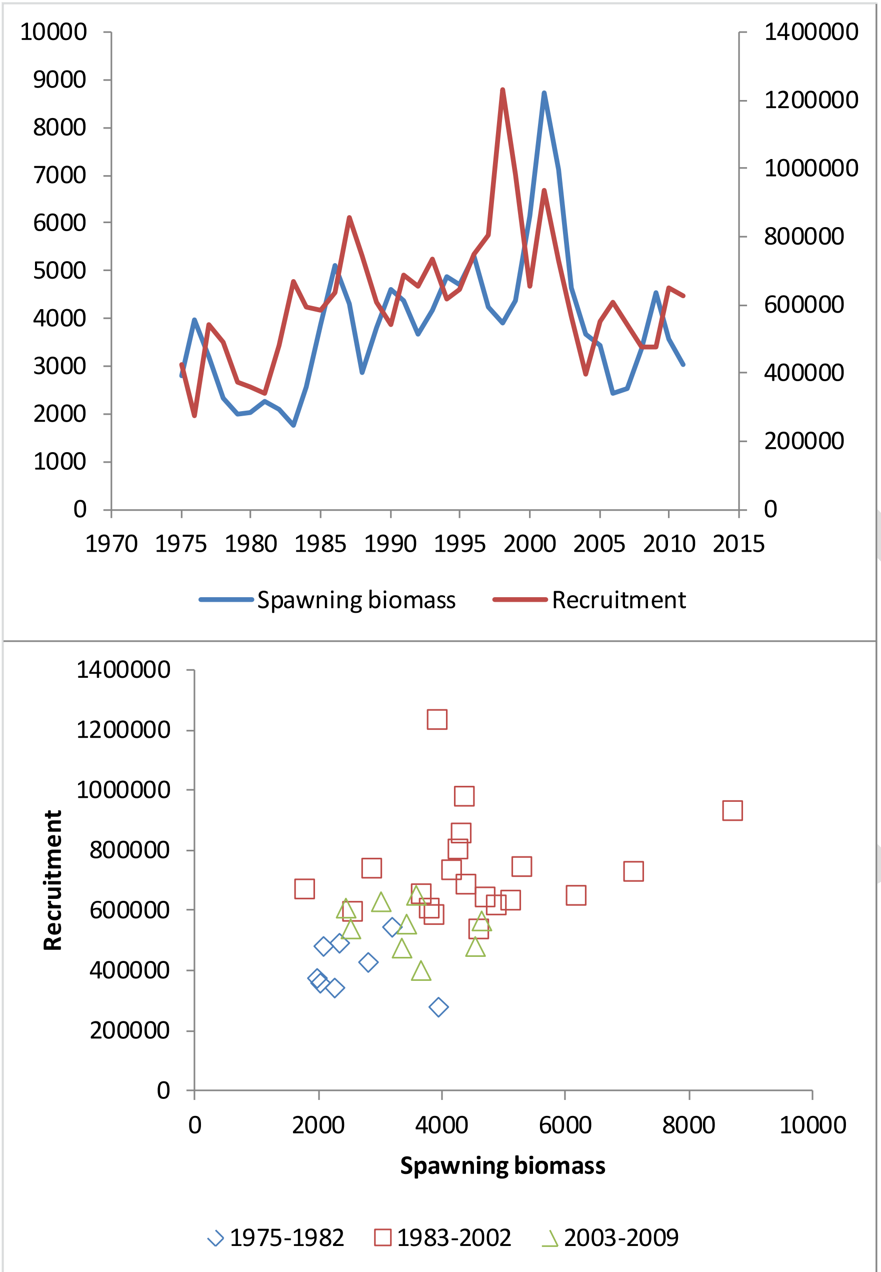

Figure 2. Estimates of annual spawning biomass (start of year) and recruitment (total) for yellowfin tuna in the EPO.

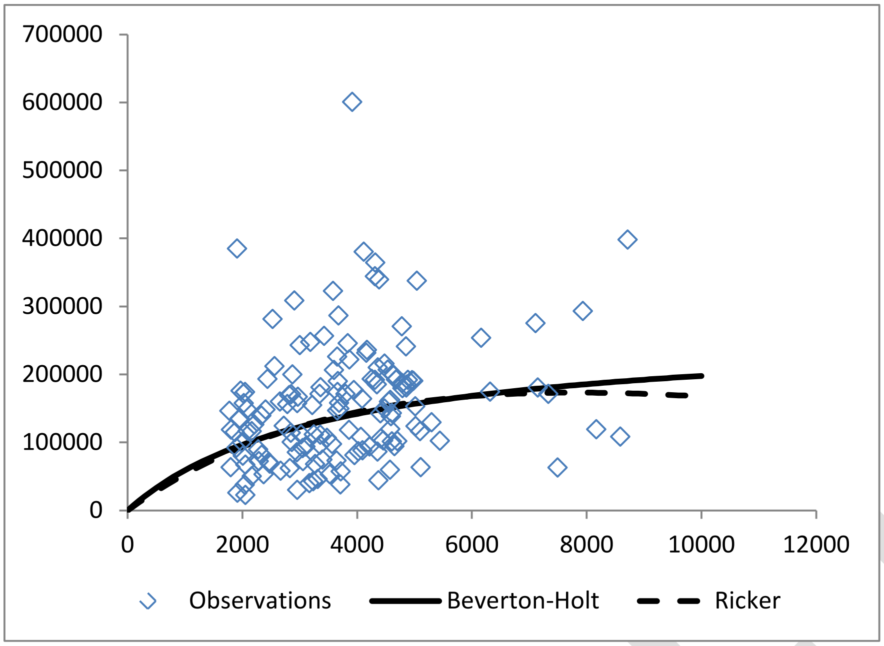

Figure 3. Beverton-Holt and Ricker stock-recruitment models fit to the stock and recruitment data for yellowfin tuna in the EPO.

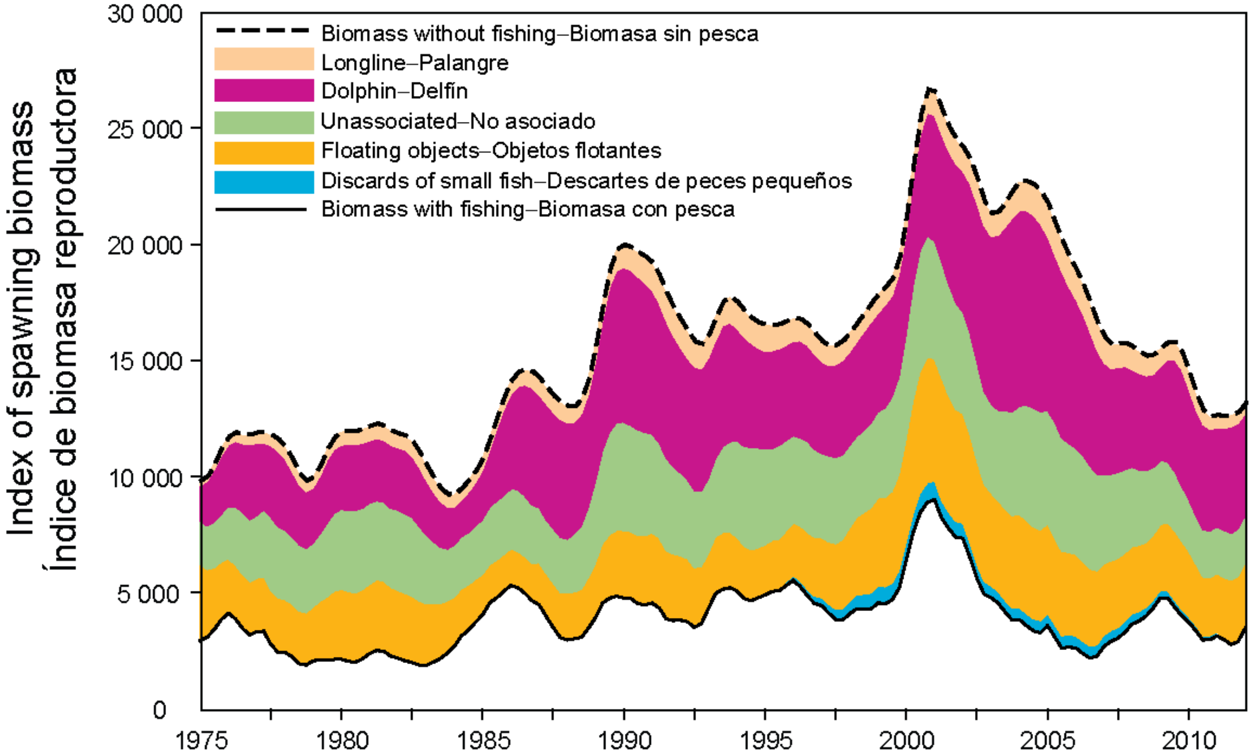

Figure 4. Fishery impact plot for yellowfin tuna in the EPO showing dynamic B_0 (dB_0). Biomass trajectory of a simulated population of yellowfin tuna that was never exploited (dashed line) and that predicted by the stock assessment model (solid line). The shaded areas between the two lines show the portions of the fishery impact attributed to each fishing method.

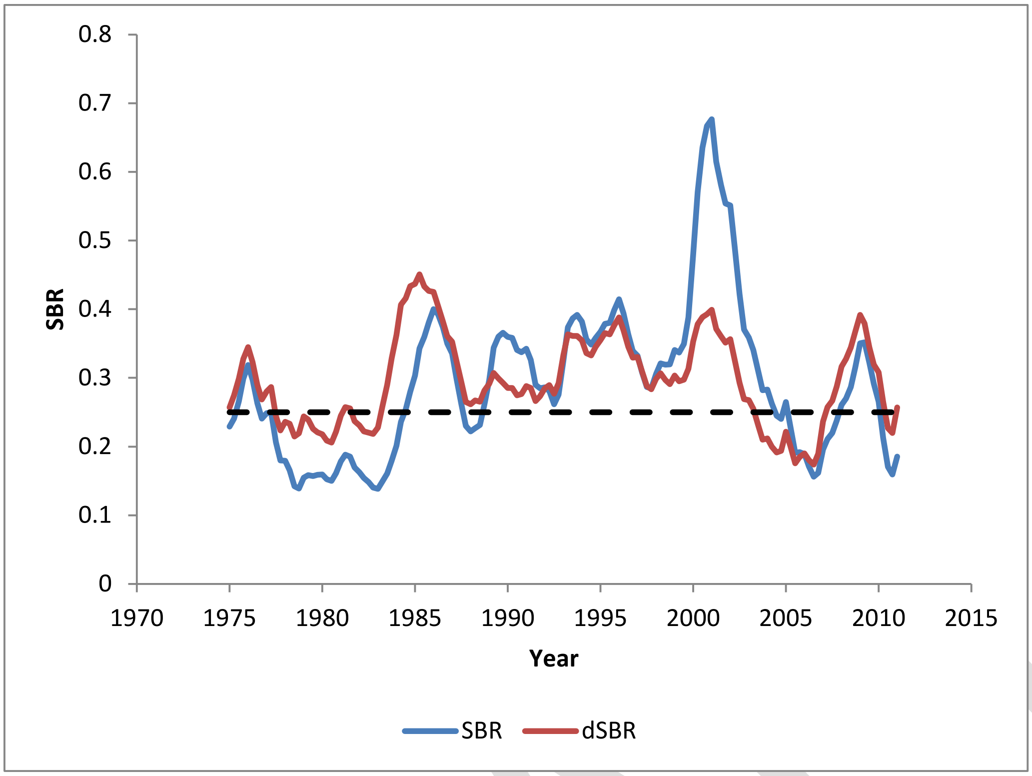

Figure 5. Spawning biomass ratio (SBR) and dynamic spawning biomass ratio (dSBR; estimated spawning biomass in a given year divided by the dynamic B0 in the same year) for yellowfin tuna in the EPO. The dashed horizontal line (at about 0.25) identifies the SBR at MSY.

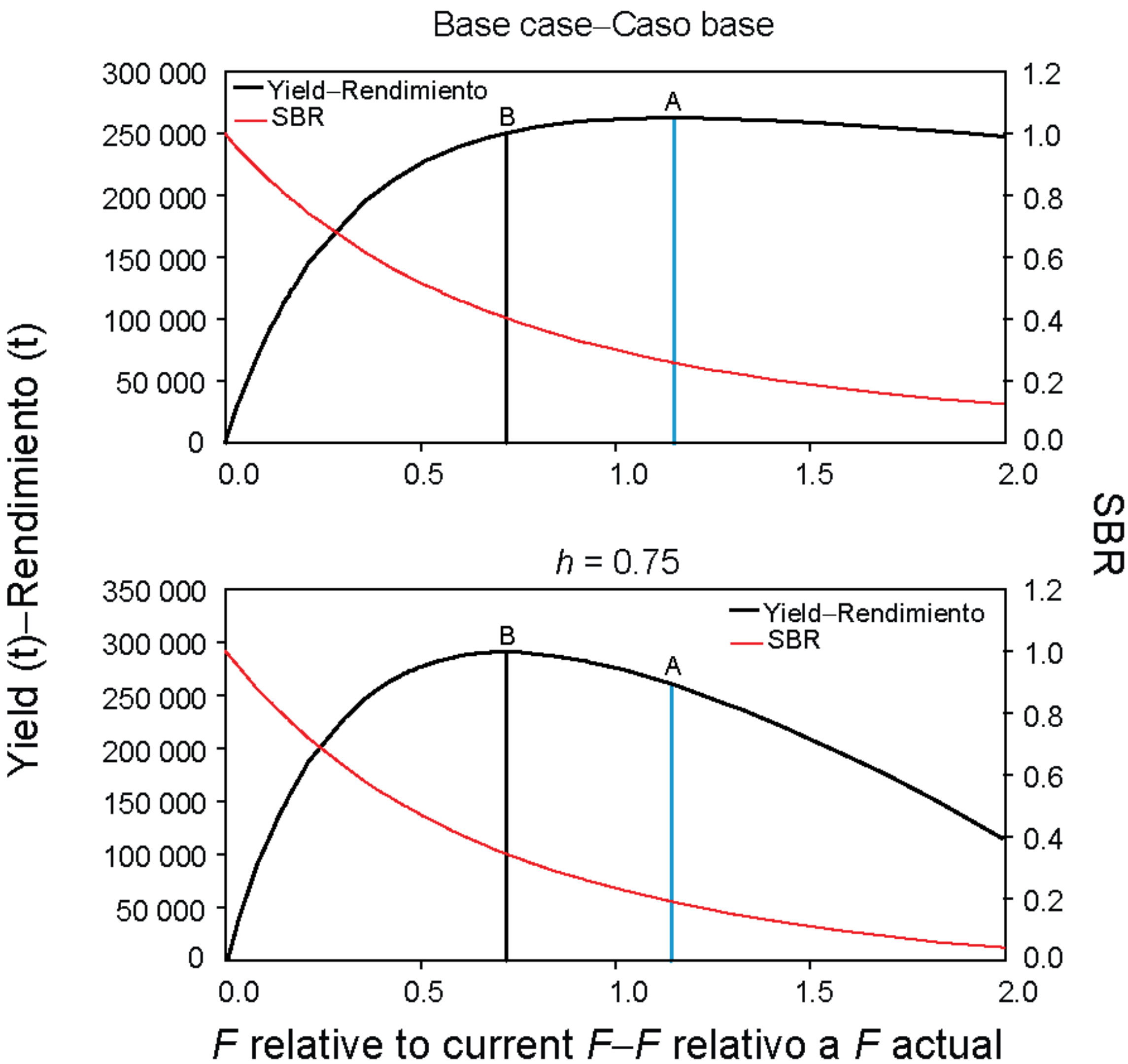

Figure 6. The tradeoff in lost equilibrium yield between different levels of misspecification of steepness of the Beverton-Holt stock-recruitment relationship. Yield and spawning biomass ratio (SBR) as a function of fishing mortality relative to the current fishing mortality. The vertical lines represent the fishing mortality corresponding to MSY for the base case and the sensitivity analysis that uses a stock-recruitment relationship (h = 0.75). The vertical lines A and B represent the fishing mortality corresponding to MSY for the base case and h = 0.75, respectively.

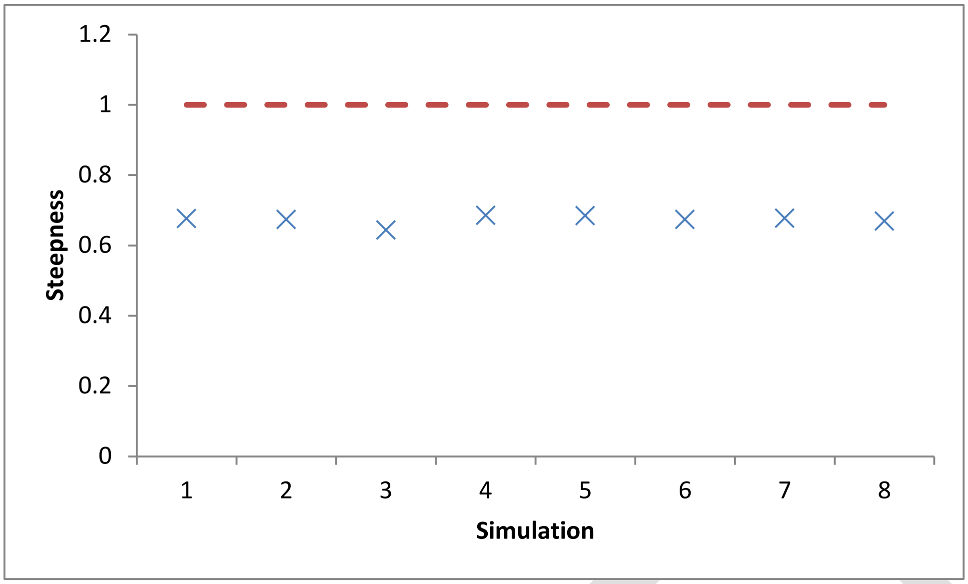

Figure 7. Estimates of steepness from the simulation scenario where steepness = 1 and the recruitment deviates used in the simulator were taken from the original estimates.

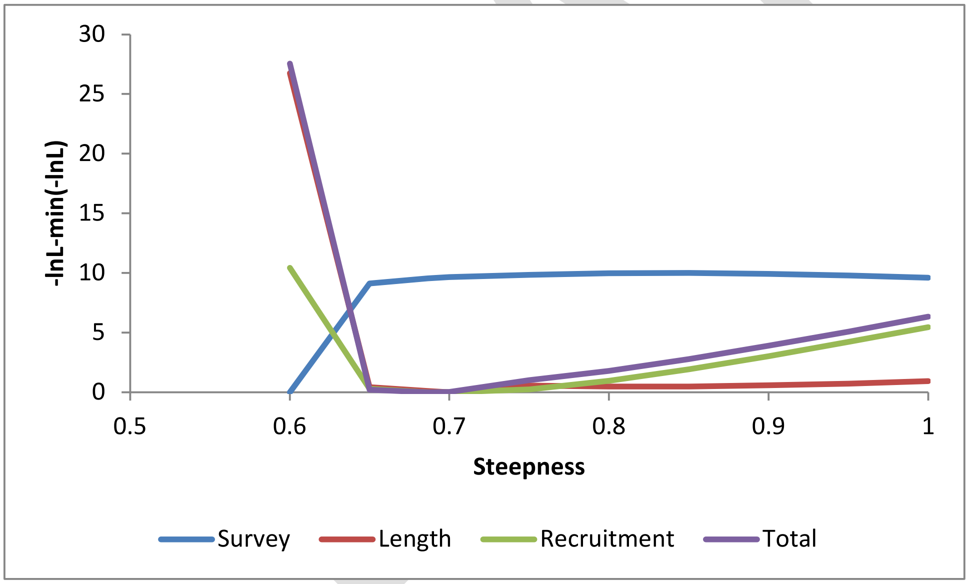

Figure 8. The component negative log-likelihoods for different values of the steepness of the stock-recruitment relationship.

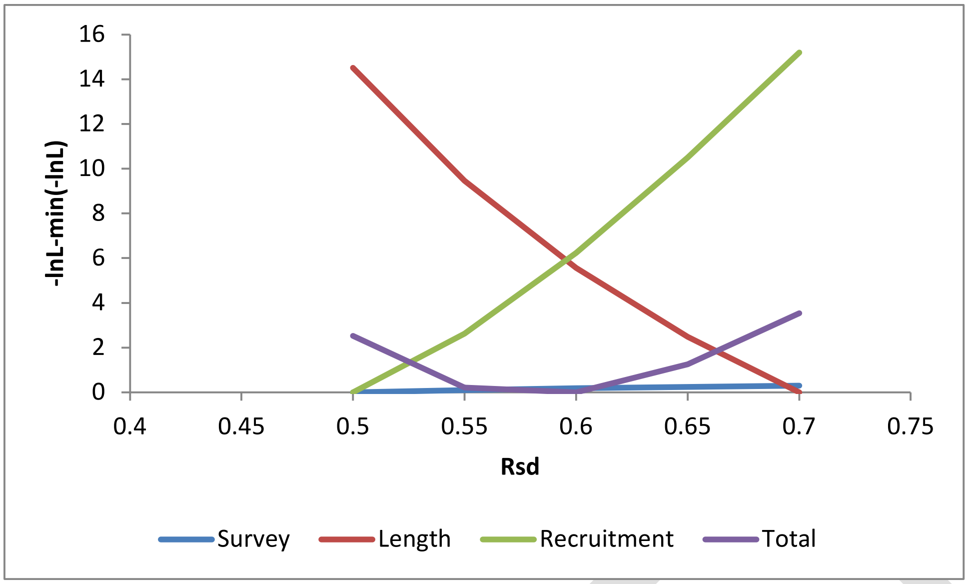

Figure 9. The component negative log-likelihoods for different values of the standard deviation used in the lognormal distribution penalty for recruitment deviates.

Table 1. Estimates of steepness for Scombridae from Myers et al (1999).

Species	Number of stocks	Median steepness
Scombridae	8	0.52
Atlantic bluefin tuna (*Thunnus thynnus*)	1	0.56
Bigeye tuna (*Thunnus obesus*)	2	0.57
Chub mackerel (*Scomber japonicus*)	1	0.38
Atlantic mackerel (*Scomber scombrus*)	2	0.81
Southern bluefin tuna (*Thunnus maccoyii*)	1	0.42
Yellowfin tuna (*Thunnus albacares*)	1	0.70

Table 2. Management quantities and the component negative log-likelihoods for different values of the steepness of the stock-recruitment relationship.

H	0.6	0.65	0.686501 (estimated)	0.7	0.75	0.8	0.85	0.9	0.95	1
Management quantities										
Msy	351142	335698	312660	306168	290680	278728	271046	266243	263563	262642
Bmsy	871271	750893	660324	633578	560354	502291	457241	420141	387629	356682
Smsy	9616	8250	7182	6864	6013	5294	4720	4230	3782	3334
Bmsy/Bzero	0.39	0.38	0.37	0.37	0.37	0.36	0.35	0.34	0.33	0.31
Smsy/Szero	0.38	0.37	0.36	0.36	0.35	0.33	0.32	0.3	0.28	0.26
Crecent/msy	0.59	0.61	0.66	0.67	0.71	0.74	0.76	0.77	0.78	0.79
Brecent/Bmsy	0.43	0.47	0.54	0.56	0.63	0.71	0.78	0.85	0.92	1
Srecent/Smsy	0.37	0.41	0.47	0.49	0.56	0.63	0.71	0.79	0.89	1
Fmultiplier	0.6	0.62	0.66	0.67	0.72	0.78	0.85	0.93	1.03	1.15
Negative log likelihoods										
Survey	-158.53	-149.39	-148.99	-148.87	-148.68	-148.54	-148.52	-148.60	-148.74	-148.93
Length	8469.65	8443.31	8442.98	8442.89	8443.46	8443.36	8443.37	8443.47	8443.62	8443.82
Recruitment	-0.42	-10.56	-10.85	-10.85	-10.60	-9.89	-8.93	-7.82	-6.64	-5.41
Total	8310.72	8283.37	8283.17	8283.19	8284.19	8284.95	8285.94	8287.06	8288.26	8289.50

Table 3. Management quantities and the component negative log-likelihoods for different values of the standard deviation used in the lognormal distribution penalty for recruitment deviates.

Rsd	0.5	0.55	0.6	0.65	0.7
Management quantities					
msy	251633	256665	262642	269590	277546
Bmsy	341715	348557	356682	366122	376932
Smsy	3195	3258	3334	3422	3523
Bmsy/Bzero	0.31	0.31	0.31	0.31	0.31
Smsy/Szero	0.26	0.26	0.26	0.26	0.26
Crecent/msy	0.82	0.8	0.79	0.76	0.74
Brecent/Bmsy	1.05	1.02	1	0.98	0.95
Srecent/Smsy	1.05	1.03	1	0.98	0.95
Fmultiplier	1.15	1.15	1.15	1.15	1.15
Negative log likleihoods					
Survey	-149.11	-149.01	-148.93	-148.87	-148.81
Length	8452.77	8447.72	8443.82	8440.74	8438.26
Recruitment	-11.64	-9.02	-5.41	-1.14	3.56
Total	8292.03	8289.71	8289.50	8290.76	8293.03