



Stock-recruitment resilience of North Pacific striped marlin based on reproductive ecology

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ABSTRACT

The resilience of a stock-recruitment relationship is a key characteristic for modeling the population dynamics of living marine resources. Steepness determines the expected resiliency of a fish stock to harvest and is fundamentally important for the estimation of biological reference points such as maximum sustainable yield. Stock-recruitment steepness was the primary uncertainty for the determination of stock status and biological reference points in recent stock assessments of Western and Central North Pacific striped marlin (*Kajikia audax*). We therefore applied the method of Mangel et al. to estimate probable values of steepness for striped marlin using new information on the mean batch fecundity, spawning frequency, and spawning season duration under an assumption of Beverton–Holt stock-recruitment dynamics. Results indicated that the median steepness was 0.87 with an 80% probable range of (0.38, 0.98). It is very likely that North Pacific striped marlin is highly resilient to reductions in spawning potential. Variation in reproductive and life history parameters had an important influence on the distribution of steepness. Sensitivity analyses showed that steepness was most sensitive to body girth, mean egg weight, and most importantly, early life history stage survival. Sensitivity analyses also confirmed that the effects of changes in life history parameters on steepness were consistent with expected increases or decreases in reproductive output due to changes in body weight or fecundity. Our approach can be applied to pelagic fish species to directly assess the probable distribution of stock-recruitment resiliency when sufficient information on reproductive ecology and life history parameters is available.

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1. Introduction

The resilience, or steepness, of a stock-recruitment relationship is a key factor for assessing the status of fishery resources. Steepness measures the expected reduction in recruitment when spawning biomass declines to 20% of its unfished level. This reduction determines the resilience of a fish stock to harvest and is fundamentally important for the estimation of biological reference points such as maximum sustainable yield. In the 2007 stock assessment of the striped marlin (*Kajikia audax*) population in the North Pacific, a lack of information on stock-recruitment steepness was identified as the primary uncertainty for determining stock status and biological reference points (Piner et al., 2007; Brodziak and Piner, 2010). To address this uncertainty for the 2012 stock assessment of the western and central North Pacific Ocean

(WCNPO) striped marlin stock (*Kajikia audax*), the individual-based simulation method (Mangel et al., 2010) was applied in 2011 to characterize the probable distribution of steepness values under a Beverton–Holt stock-recruitment assumption, consistent with the assessment modeling (Brodziak and Mangel, 2011). In this case, the WCNPO stock is defined as the striped marlin population inhabiting the North Pacific Ocean west of 140° W. This population is considered to be a unit stock based on analyses of fishery catch and effort patterns and two recent genetic studies (McDowell and Graves, 2008; Purcell and Edmans, 2011).

In this study, we extended our 2011 analyses using information on the mean batch fecundity, spawning frequency, and spawning season duration of striped marlin from Sun et al. (2011a) and new information on expected egg size and early life history duration from Kopf et al. (2012). The best available information on striped marlin reproductive ecology and life history parameters included new set of information on growth, maturity at age, average weight at length, and natural mortality rates of striped marlin (Table 1). We characterized the effects of reproductive ecology and life

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Table 1
Mean values of striped marlin life history and reproductive ecology parameters used to calculate distributions of stock-recruitment steepness.

Life history and reproductive ecology parameters	Description and parameter values
L_∞, k, t_0	Growth Parameters: The asymptotic length parameter (L_∞) for the von Bertalanffy growth curve (cm, eye-fork length)-at-age (t , years), the Brody growth coefficient parameter (k , yr^{-1}), and the value of age at length zero parameter (t_0 , years): $L(t) = L_\infty(1 - \exp(-k(t - t_0)))$ Baseline: $L_\infty = 203.2$, $k = 0.34$, $t_0 = -1.9$
A, B	Length-Weight Parameters: The scale (A) and exponent (B) parameters of the length (cm, eye-fork length)-weight (kg, wet weight) equation: $W = A \cdot L^B$ Baseline: $A = 4.68 \times 10^{-6}$ and $B = 3.16$
$M_{EL}(d), M_j(d), M(a)$	Daily and Annual Natural Mortality Parameters: The daily instantaneous natural mortality rates of eggs and larval fish ($M_{EL}(d)$ d^{-1}) and early life history stage juveniles ($M_j(d)$ d^{-1}) as well as instantaneous annual natural mortality rates at age for ages $a = 0, 1, \dots, A_{MAX}$. Baseline: $M_{EL}(d) = 2.2 \times 10^{-4} W_{ELH}(d)^{-0.85}$ $M_j(d) = 5.26 \times 10^{-3} W_{ELH}(d)^{-0.25}$ $M(0) = 0.49 \text{ yr}^{-1}$, $M(1) = 0.45 \text{ yr}^{-1}$, $M(j) = 0.40 \text{ yr}^{-1}$, for $2 \leq j \leq A_{MAX}$
A_{50}, σ_M	Maturity Parameters: The female age at 50% maturity (A_{50} yr^{-1}) and shape parameters (σ_M yr^{-1}) of the logistic probability of maturity-at-age (units are years) function. $Pr(\text{mature at age } a) = \frac{\exp((a - A_{50})/\sigma_M)}{1 + \exp((a - A_{50})/\sigma_M)}$ Baseline: $A_{50} = 2.3$, $\sigma_M = 0.58$
$T_B, S_L, E_G, D_{ELH}, W_E$	Spawning, Fecundity, and Early Life History Stage Parameters: The average time between batch spawning events (T_B days), the length of the spawning season (S_L months), the mean number of oocytes per gram of body weight (E_G g^{-1}), the early life history stage duration (D_{ELH} days), and the mean egg weight (W_E g). Baseline: $T_B = 3.4$, $S_L = 4$, $E_G = 53.6$, $D_{ELH} = 281$, $W_E = 4.88 \times 10^{-4}$

history parameters on steepness by conducting a systematic set of sensitivity analyses.

2. Materials and methods

2.1. Stock-recruitment steepness

Stock-recruitment steepness is the fraction of unfished recruitment produced when spawning biomass has been reduced to 20% of its unfished level (Mace and Doonan, 1988). The value of steepness (h) characterizes the drop-off in recruitment as spawning potential decreases. Stocks with higher values of steepness are relatively more productive at lower spawning biomasses than stocks with lower steepness. We applied the age-structured simulation model of Mangel et al. (2010) to assess a baseline prior distribution of steepness using reproductive ecology and life history parameters for WCNPO striped marlin. It was assumed that recruitment dynamics followed a Beverton–Holt stock-recruitment relationship, consistent with the stock assessment model used for striped marlin (Piner et al., 2007). The expected value of age-0 female recruitment to the population at time t , denoted as $N(0, t)$, was:

$$N(0, t) = \frac{\alpha_S B_S(t)}{1 + \beta B_S(t)} \quad (1)$$

where $B_S(t)$ was spawning biomass at time t . In Eq. (1), the slope-at-the-origin parameter, α_S , has units of new individuals produced per unit of spawning biomass and is the key to constructing estimates of steepness for striped marlin. In this context, the simulation

model keeps track of the spawning biomass of females under the assumption that the abundance of adult males is not a limiting factor in determining reproductive outcomes (Mangel et al., 2010). Given that individual fecundity is proportional to body mass, the female spawning biomass $B_S(t)$ at time t is:

$$B_S(t) = \sum_{a \leq A_{MAX}} N(a, t) \cdot W_f(a) \cdot p_{f,m}(a) \quad (2)$$

where A_{MAX} is the maximum age, $W_f(a)$ is the average body mass of an age- a female, and $p_{f,m}(a)$ is the probability that an age- a female is mature.

Steepness can be calculated from the slope at the origin. Mangel et al. (2010) show that steepness h for the Beverton–Holt curve is a function of the expected surviving spawning biomass per recruit in the absence of fishing, which we denote here as SPR_0 , and the slope at the origin α_S by:

$$h = \frac{\alpha_S \cdot SPR_0}{4 + \alpha_S \cdot SPR_0} \quad (3)$$

Each steepness value will generate a single Beverton–Holt curve with an associated value of unfished recruitment R_0 for a fixed SPR_0 value. The value of R_0 is uniquely determined by the intersection of the stock-replacement line going through the origin with a density-independent slope equal to $1/SPR_0$ and the Beverton–Holt stock-recruitment curve. Thus, it is possible to generate an associated distribution for h given SPR_0 and the distribution of probable values for α_S .

2.2. Slope at the origin

We used Monte Carlo simulation to construct a total of K striped marlin breeding populations to obtain estimates of the slope at the origin α_S . Each breeding population represented the survival and reproductive success of the striped marlin population during one annual time period with the specific set of environmental conditions experienced by the breeding population. Each population consisted of subsample of n fish randomly sampled from distributions of reproductive ecology and life history parameters of striped marlin. Mean values of these parameters were taken from recent literature and the most recent stock assessment information for striped marlin in the North Pacific.

To compute a distribution of probable slope at the origin values over the simulated breeding populations, we first simulated the age structure of each population and then simulated the egg production and survivorship of eggs from each cohort. To simulate the age structure of each population, values for natural mortality rate at age were randomly sampled from distributions to generate survival to age distributions for each simulated population. Individual fish in each population were randomly assigned an age based on their realized age-specific survivorship. Consequently, each population had its own randomly generated survivorship to age curve and the age of each fish was randomly sampled from the population-specific survivorship curve with interpolation.

To compute slope at the origin for a given population, let $a_{n,k}$ denote the age of the j th randomly selected fish in the k th population and let its mass be $W(a_{j,k})$. It follows that one can compute the expected egg production of this female in a single spawning event as $E(W(a_{j,k}))$, where $E(w)$ is the expected batch fecundity as a function of body mass w . Multiplying the expected batch fecundity by the expected number of spawning events, N_S gives the expected egg production of each individual. Similarly, summing the expected fecundity times expected larval survival L_S to the expected weight at age-0 under von Bertalanffy growth for all fish in the k th population and dividing by the sampled biomass gives an estimate of

new recruits per spawning biomass, or the slope at the origin $\alpha_S(k)$ in the k th population as

$$\alpha_S(k) = \frac{L_S \sum_j N_S \cdot E(W(a_{j,k}))}{\sum_j W(a_{j,k})} \quad (4)$$

For each population, we calculated stochastic realizations of the larval survival rate using the allometries between mass and natural mortality rate of early life history stages from McGurk (1986) and McCoy and Gillooly (2008) as described below in Section 2.6. Thus, based on the relation between steepness and the slope at the origin, a frequency distribution for each possible value of steepness from $h = 0.2$ to $h = 1$ was generated from the observed values in the simulated populations.

2.3. Life history parameters

The simulation model inputs included new information on growth, length-weight, and other life history parameters in comparison to the 2007 stock assessment. Striped marlin juvenile and adult growth was simulated with the von Bertalanffy growth curve estimated by Sun et al. (2011b) with growth parameters of $L_\infty = 234.9$ (cm, lower jaw-fork length), $k = 0.34 \text{ yr}^{-1}$, and $t_0 = -1.9$ years (Table 1). The asymptotic length L_∞ was converted to eye-fork length (EFL) using the linear relationship estimated by Sun et al. (2011b). This led to a value of $L_\infty = 203.2$ (cm, EFL). For all analyses, the length-weight relationship from Sun et al. (2011b) was used to convert length to weight (Table 1). Natural mortality rate at age parameters (Table 1) were gathered from the most recent stock assessment (Lee et al., 2012a). In this case, the estimated age-0 value of $M(0) = 0.49$ represented the natural mortality rate experienced by age-0 fish subsequent to survival through the expected early life history stage duration of about 281 days (see below).

2.4. Reproductive ecology

The median length at maturity of female striped marlin from Sun et al. (2011a) is $L_{50} = 179.0$ cm EFL. This estimate of L_{50} was converted into a median age of female maturity (a_{50}) using the von Bertalanffy growth curve parameters from Sun et al. (2011b) (Table 1). Sun et al. (2011a) reported an average timing between batch spawning events (T_B) of $T_B = 3.4$ days, which was used to characterize the expected batch spawning frequency.

Information on striped marlin fecundity and spawning season duration was needed to estimate total egg production for each simulated population. Sun et al. (2011a) reported that the relative fecundity of striped marlin averaged 53.6 oocytes per gram of body weight (E_G) with a range of 30.3–78.3 eggs per gram. We used the expected batch fecundity of $E_G = 53.6$ eggs per gram as a measure of the central tendency of fecundity for each simulated fish (Table 1). Sun et al. (2011a) reported that females in spawning condition were observed in May–July based on examination of postovulatory follicles and in April–August based on observations of hydrated oocytes. This information suggested a spawning season duration of mid-April through mid-August. As a result, the length of the spawning season (S_L) was assumed to average $S_L = 4$ months in the baseline model (Table 1). Previous studies in the North Pacific suggested that the spawning season of striped marlin ranged from May–June (Kume and Joseph, 1969), June–July (Eldridge and Wares, 1974), and July–August (Armas et al., 2006). Given this information, sensitivity analyses were used to characterize the effect of alternative average spawning season durations on steepness estimates.

An estimate of the expected duration of early life history stages of eggs, larval and juvenile fish was needed to compute the size-specific allometric natural mortality rates and associated survival

probabilities of early life history stage females. It was assumed that individual daily growth was exponential prior to the onset of a von Bertalanffy growth pattern, which began at size $L(0)$, the calculated length at age-0 under the von Bertalanffy curve (about $L(0) = 97$ cm EFL; Sun et al., 2011b). This value of $L(0)$ indicated that growth through the early life history stages was very rapid and was compared to the observed median size at age 1 of approximately $L(1) = 126$ cm EFL reported by Kopf and Humphries (2012, available at <http://www.soest.hawaii.edu/pfrp/nov12mtg/nov12mtg.htm>). We used the ratio of the size realized at the end of early life history stage growth to the empirical size at age 1 observed by Kopf and Humphries to estimate the expected duration of the early life history stages (D_{ELH} , days) as $D_{ELH} = \frac{L(0)}{L(1)} \cdot 365 \approx 281$ days (Table 1) where the expected size at an age of D_{ELH} days was $L(0)$.

Information on mean egg weight was used to simulate the initial condition for size-specific allometric survival rates of early life history stages. Very little information on striped marlin egg size was available until Kopf et al. (2012) provided direct field measurements of egg diameters collected from the Southwest Pacific striped marlin population. We assumed that the expected egg diameter of North Pacific striped marlin was approximately equal to the median egg diameter (D_S) of actively spawning females reported by Kopf et al. (2012) to be $D_S = 978 \mu\text{m}$. Given this diameter, spherical egg volume was computed as $V = \frac{4}{3}\pi\left(\frac{D_S}{2}\right)^3$ and the average egg weight was computed from the associated water mass expected at a temperature of 25 °C. This led to a mean egg weight (W_E) of $W_E = 4.88 \times 10^{-4}$ (Table 1). As with other parameters, we investigated the sensitivity of steepness estimates to average egg weight.

2.5. Growth and survival of early life history stages

Early growth, expressed as the daily increase in the body mass of eggs, larvae, and juveniles, was modeled as an exponential function with a constant daily rate of increase in body mass (K_{ELH}). This pattern is characteristic of early life history stage growth of billfishes (e.g., Sponaugle et al., 2005) and was parameterized using the expected early stage duration D_{ELH} and the expected weight of an age-0 fish ($W(0) = 8792.7$ g) under the von Bertalanffy growth curve (Fig. 1a). The expected body mass (wet weight) at an age of d days ($W_{ELH}(d)$) was computed from the initial egg weight to the ending age-0 weight as

$$W_{ELH}(d) = W_E \cdot \exp(K_{ELH} \cdot d) \quad (5)$$

where $K_{ELH} = \log(W(0)/W_E)/D_{ELH}$. Thus, growth of early life history stages of striped marlin was effectively determined by the initial egg weight, the mean weight at age corresponding to the mean length at age 0 from the von Bertalanffy growth curve, and the duration of the early life history stages.

Survival rates of early stages were characterized assuming an allometric scaling of natural mortality as a decreasing function of body mass. Allometric scaling of mortality rate with mass has been observed in a number of ecological studies (McGurk, 1986; Pepin 1991, McCoy and Gillooly, 2008) and is a fundamental principle of metabolic theories of ecology (Schmidt-Nielsen, 1984; Brown et al., 2004; McCoy and Gillooly, 2008). As in our previous modeling of early life history rates for characterizing resilience (Mangel et al., 2010), we employed stochastic realizations of the allometric relationships between natural mortality rate and body mass reported by McGurk (1986). In this case, the predicted daily natural mortality rate ($M_{ELH}(d)$) on the d th day of life was an allometric function of dry weight body mass $w_{ELH}(d)$ where $M_{ELH}(d) = b_0 \cdot w_{ELH}(d)^{b_1}$ for intercept b_0 and slope b_1 and $w_{ELH}(d) = 0.2W_{ELH}(d)$. McGurk (1986) reported a significant difference in the estimated log-scale regression slope for natural mortality rates of animals below a critical weight (W_{CRIT}) of $W_{CRIT} = 5.04 \times 10^{-3}$ g with $b_1 = -0.85$ in

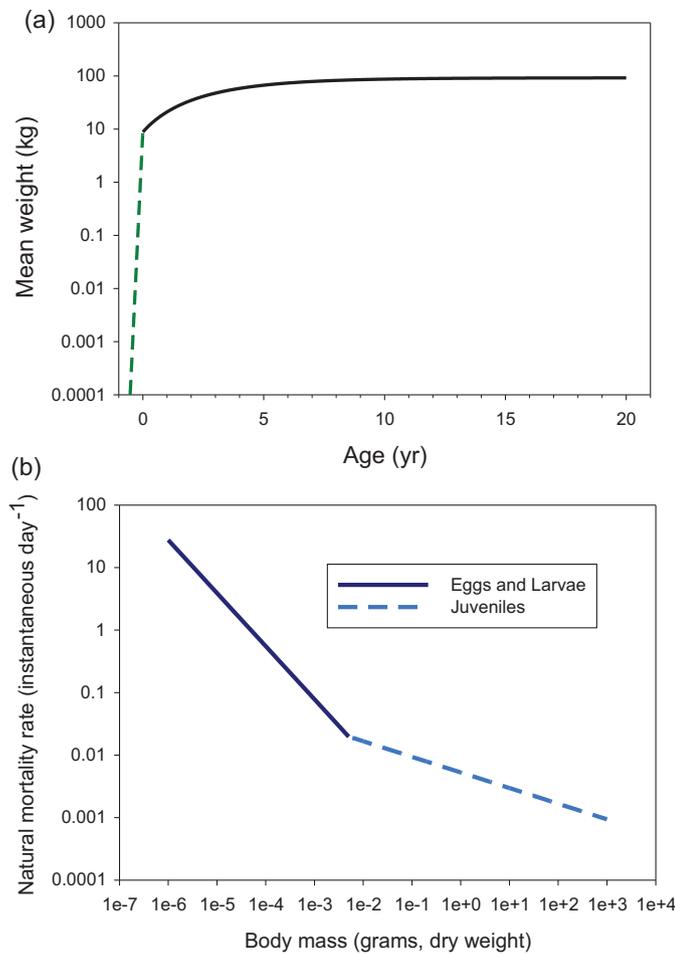


Fig. 1. Growth of early life history stage and adult striped marlin (a) and the allometry of weight-specific natural mortality rates as a function of body mass (b).

comparison to the allometric slope of $b_1 = -0.25$ reported by Peterson and Wroblewski (1984). McGurk attributed this difference in slopes to the observed patchiness of the distribution of eggs and larvae below the critical weight. In reviewing the information for early life history stage survival, we noted that the Peterson and Wroblewski allometry was based on the assumption that energy flow in the pelagic marine system depended predominantly on the size of uniformly shaped biomass particles and not on taxonomy (Peterson and Wroblewski, 1984). As a result, for dry weight body masses less than the critical weight, the expected daily natural mortality (McGurk, 1986) of eggs and larvae were estimated as $M_{EL}(d) = 2.2 \times 10^{-4} w_{ELH}(d)^{-0.85}$ while for body masses greater than or equal to the critical weight, the expected daily natural mortality of early life history stage juveniles was estimated as $M_J(d) = 5.26 \times 10^{-3} w_{ELH}(d)^{-0.25}$ (Table 1). Stochastic realizations of daily values of the intercept and slope parameters of the allometric relationship for natural mortality rate were generated for each simulated population.

2.6. Simulation analyses

For each simulation analysis, we ran a total of 250 simulations for each of 500 populations comprised of 500 individual fish to estimate the empirical probability density function of stock-recruitment steepness. We used 500 fish to characterize the probable value of slope at the origin for a relatively small population of striped marlin, noting that the most recent assessment indicated that the unfished stock size was about five orders of

magnitude above this level. The number of simulations (n) conducted was based on achieving a 95% confidence interval for the grand mean estimate of steepness (μ_h) that was less than $\varepsilon = 0.05$ units wide given the assumed process errors for reproductive ecology and life history parameters. Based on preliminary analyses, an estimate of the standard deviation of steepness from 250 simulations was about $\sigma_h = 0.18$, and as a result, at least $n > (4\sigma_h/0.05)^2 \approx 250$ simulations were used to achieve the target precision for μ_h and $n = 250$. These choices of the number of simulated populations and fish were similar to those used in a resiliency analysis (Mangel et al., 2010) of Pacific bluefin tuna (*Thunnus orientalis*). More importantly, we note that the estimated distributions of steepness were not sensitive to alternative values of 100 or 500 simulations, or to the number of populations or fish ranging from 100 to 1000 (Appendix).

The goal of the simulation analyses was to estimate the empirical probability density function of steepness. For each simulation, the empirical density ($H^{(s)}$) was calculated from the set of simulated population steepness values. We used a grid of $n_h = 80$ possible intervals (I_j , indexed by j) to cover the set of possible steepness values (0.2 to 1). Each steepness interval $I_j = (h_j, h_{j+1})$ had a width of 0.01 units with a lower bound of $h_j = 0.2 + 0.01 \cdot (j - 1)$. For each population, a simulated value of steepness ($h^{(p)}$) was computed from the set of simulated individual fish and the associated slope at the origin. Given a simulated population value $h^{(p)}$, the frequency of counts in the appropriate interval I_k was increased by 1 where $h_k < h^{(p)} \leq h_{k+1}$. After looping through the set of populations, the simulation algorithm produced a frequency distribution of steepness for the entire simulation. This frequency distribution was normalized to generate the empirical probability density function for each simulation s , as $H^{(s)} = \{p^{(s)}(I_1), p^{(s)}(I_2), \dots, p^{(s)}(I_{n_h})\}$, where $p^{(s)}(I)$ denoted the observed probability that h was in interval I .

The overall empirical distribution of steepness (H) was calculated from the set of simulated densities generated from the total of n simulations. In particular, the distribution H was given by $H = \{p(I_1), p(I_2), \dots, p(I_{n_h})\}$ where $p(I)$ was the empirical probability that h was in interval I and $p(I)$ was calculated as the average probability over the n simulations

$$p(I) = \frac{\sum_s p^{(s)}(I)}{n} \quad (6)$$

Given the overall empirical distribution of steepness, several statistics were calculated to describe the central tendency and dispersion of the distribution. In particular, the mean value of steepness was $\mu_h = \sum_{j=1}^{n_h} h_j \cdot p(I_j)$ and its variance (σ_h^2) was calculated as $\sigma_h^2 = \sum_{j=1}^{n_h} h_j^2 \cdot p(I_j) - (\mu_h)^2$. The median value ($\mu_{1/2}$) and percentiles of steepness were also calculated from the empirical cumulative distribution function using linear interpolation.

Process errors were incorporated into each simulated population and set of individual fish. We assumed that the coefficient of variation of the process error for each input parameter ($CV(\theta)$) was approximately an order of magnitude smaller than the mean parameter value. That is, we set $CV(\theta) = 10\%$ for each of the input parameters (Table 1). Each process error was simulated using an independent multiplicative lognormal distribution with a mean of unity and a coefficient of variation of 10% with the exception of adult natural mortality rates which were assumed to have a gamma distribution with mean values at age taken from the most recent stock assessment (Table 1) and had a coefficient of variation of 10%. The use of a common CV across parameters was made to facilitate comparisons of the sensitivity or relative influence of each parameter on steepness, as shown by the uncertainty importance described below. Sensitivity of results to alternative coefficients of variation for process errors of 1%, 5%, and 25% were also evaluated.

We estimated parameters of a beta density for steepness $f(h)$ that provided the maximum likelihood fit to the empirical steepness distribution given the population simulations. The form of the fitted density with beta density parameters a_β and b_β was

$$f(h) = \frac{\Gamma(a_\beta + b_\beta)}{\Gamma(a_\beta)\Gamma(b_\beta)} h^{a_\beta-1}(1-h)^{b_\beta-1} \quad (7)$$

The fitted parameters a_β and b_β can be used to select a parametric prior distribution for stock-recruitment steepness of striped marlin assuming a Beverton–Holt stock-recruitment curve.

2.7. Sensitivity analyses

Sensitivity analyses were conducted to measure the relative importance and directional effects of changes in each reproductive ecology or life history parameter (θ_k) on steepness. The relative sensitivity of steepness to parameter (Table 1) was assessed by re-estimating the empirical steepness distribution across a set of alternative input values ranging from -25% to $+25\%$ of θ_k in 12.5% increments. For the natural mortality at age parameters, the relative sensitivity was assessed by making the same incremental change for all age-specific parameters at once. Overall, the results of the sensitivity analyses showed the sign, magnitude, and shape of changes in the steepness distribution that would be expected if reproductive ecology or life history parameters varied from their expected values due to changes in environmental conditions or other factors.

The importance of uncertainty associated each parameter was characterized using the elasticity of steepness (U) for the k th parameter evaluated at the baseline set of reproductive ecology and life history parameter values ($\underline{\theta}$), where

$$U(\theta_k) = \frac{\partial h}{\partial \theta_k}(\underline{\theta}) \frac{\theta_k}{h} \quad (8)$$

The elasticity of steepness provided a normalized measure of the effect of a one percent in life history parameter value on the percent change in steepness. As a relative measure of uncertainty importance, the elasticity accounted for differences in both the scale of the parameters and the central tendency of steepness. In this case, the partial derivative of steepness as a function of θ_k was numerically evaluated using a first order central-difference approximation.

3. Results

Results of the baseline steepness model indicated that the distribution of steepness was left skewed (Fig. 2a) with a median steepness of 0.87 and an 80% probable range of (0.38, 0.98). The mean steepness was 0.78 with a coefficient of variation of 0.29 (Fig. 2a) and the fitted beta density parameters were $a_\beta = 0.72$ and $b_\beta = 1.44$. The median steepness value was intermediate to the two values of steepness assumed for separate assessment scenarios (0.75 and 1) in the 2007 North Pacific striped marlin assessment and was lower than the meta analytic point estimate of 0.9 for swordfish reported by Myers et al. (1999). Overall, our results suggested that the stock-recruitment dynamics of North Pacific striped marlin were probably highly resilient to declines in spawning potential.

The distributions of steepness were less diffuse with process error values of 1% and 5%. Shrinking the process error to be negligible at 1% produced a highly peaked distribution with positive probability for h in the interval (0.97, 0.99) and a median of 0.98 with $p(h \in (0.98, 0.99)) = 0.85$. In contrast, increasing process error to be 25% spread out the distribution of steepness with a median of 0.80 and an 80% probable range of (0.28, 0.98). The sensitivity analysis comparing the baseline results with those obtained using the natural mortality rate relationship from McCoy and Gillooly (2008)

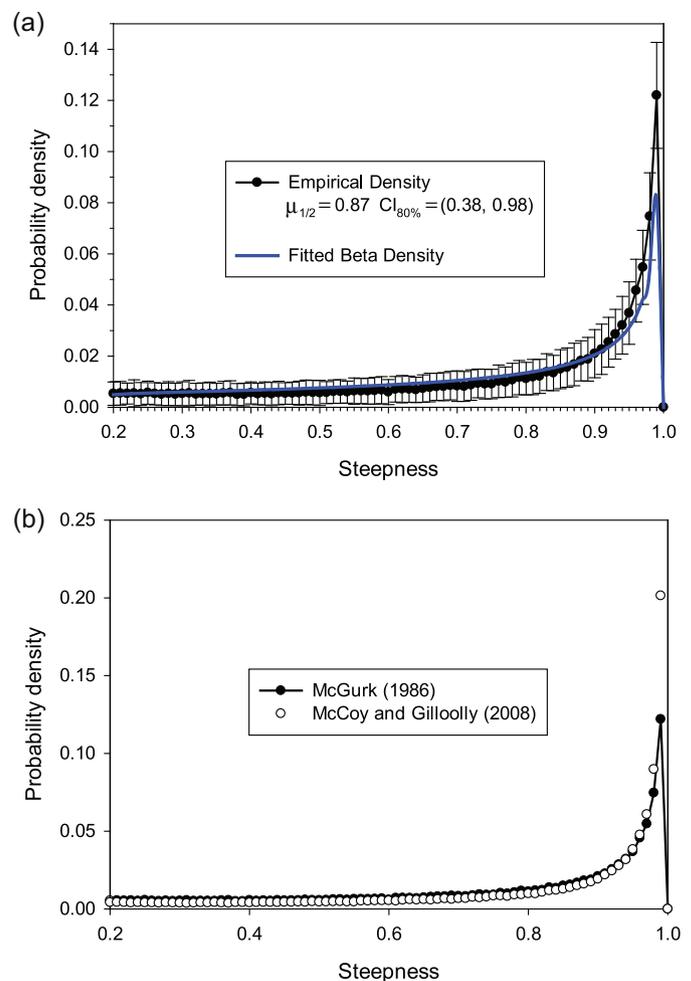


Fig. 2. Baseline estimate of the empirical probability density of stock-recruitment steepness for Western and Central North Pacific striped marlin along with fitted beta density (a) and sensitivity analysis showing the effect of weight-specific allometry of natural mortality rate as a function of body mass from McCoy and Gillooly (2008).

showed that this relationship implies a slightly higher average estimate of stock-recruitment steepness (Fig. 2b), i.e. mean steepness estimate of 0.82 (Fig. 2b) with beta density parameters of $a_\beta = 0.77$ and $b_\beta = 1.39$.

Growth parameters had an important effect on steepness. Of the three growth parameters, the one with the strongest influence was the asymptotic length L_∞ which had a nonlinear impact on steepness over the sensitivity interval (Fig. 3a). The elasticity of $U(L_\infty)$ was about 0.40% for the baseline which indicated that a 1% increase in L_∞ would be expected to produce a less than 1% increase in steepness. The next most important growth parameter was the Brody growth coefficient k which had a nearly linear impact on steepness over the sensitivity interval (Fig. 3b) and for which the elasticity $U(k)$ was -0.36% . The least influential growth parameter was the age at zero length t_0 (Fig. 3c) with increases in t_0 from the baseline value producing moderate increases in steepness. Elasticity for t_0 was $U(t_0) = 0.26$. For each growth parameter, the variability of the steepness estimate decreased as the value of the growth parameter increased (Fig. 3).

Steepness was very sensitive to the length-weight exponent B (Fig. 4b) In contrast, the scale parameter A had a negligible impact on steepness (Fig. 4a) and for which the elasticity was $U(A) = 0.02\%$. In comparison, increases in the exponent B produced substantial increases in steepness and the elasticity for B was $U(B) = 1.68\%$, indicating that steepness was very sensitive to mis-specifying B .

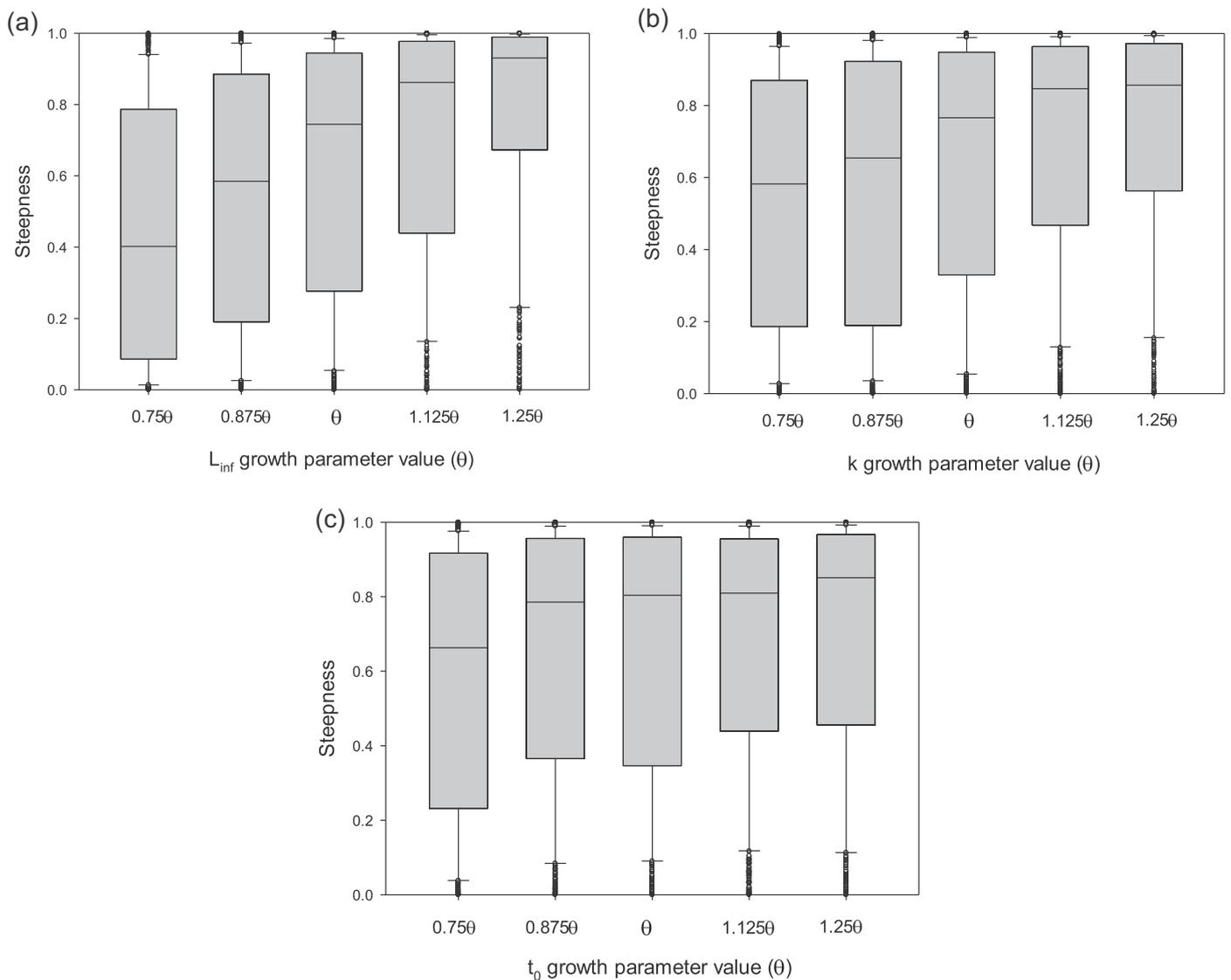


Fig. 3. Sensitivity analyses showing boxplots for the effects of changes in the growth parameters (a) asymptotic length (L_{∞}), (b) Brody growth coefficient (k), and (c) age at zero length (t_0) on median steepness (solid line inside box), its interquartile range (bottom and top of the box), and its 10th and 90th percentiles (bottom and top whiskers).

The length-weight scale parameter exhibited a slight decreasing trend in variability while the variability of the exponent parameter decreased as B increased (Fig. 4).

Changes in the juvenile and adult natural mortality rate had a moderate effect on steepness. The adult natural mortality rate at age had a nearly linear effect on steepness over the sensitivity interval (Fig. 5a) and changes in the $M(a)$ values had a moderate impact on steepness with an elasticity of $U(M) = -0.22\%$. Similarly the juvenile natural mortality rate had a flat impact on steepness (Fig. 5b) with an elasticity of $U(M_j) = -0.31\%$. In contrast, the egg and larval mortality rate had a substantial impact on steepness with an elasticity of $U(M_{EL}) = -6.57\%$ (Fig. 5c). The variability in the estimates of steepness showed an increasing trend for the natural mortality rate parameters.

Changes in the female maturity at age-0 give also had a moderate effect on steepness. The median age of maturity had a nearly linear effect on steepness over the sensitivity interval (Fig. 6a), but the A_{50} value had a minor impact on steepness with an elasticity of $U(A_{50}) = 0.55$. Overall, the estimated steepness had little trend in variability (Fig. 6), and the results suggested that decreases in the age of female maturity would have a modest effect on stock-recruitment steepness for striped marlin.

The estimates of steepness showed a range of effect sizes for the life history parameters for spawning season, fecundity, and early life history stage duration. The average time between spawning events parameter T_B had a minor decreasing impact on steepness (Fig. 6b) (elasticity $U = -0.32$). The length of spawning season S_L also had a minor increasing effect on steepness (Fig. 6c) (elasticity $U = -0.18\%$). Similarly, the mean number of eggs per gram of body weight parameter E_G had a limited impact on steepness (Fig. 6d) (elasticity $U = -0.38$). The duration of early life history stage had a strong negative impact on steepness (Fig. 6e) with an elasticity of $U(E_G) = -0.81$. In contrast, the mean egg weight W_E had a strong positive effect on steepness (Fig. 6f) with decreases in W_E producing marked declines in steepness. Elasticity for W_E was 0.94% . The variability in estimated steepness had a substantial decreasing trend for the mean egg weight parameter W_E but showed little or no trend for the other reproductive ecology parameters (Fig. 6). Overall, the most important reproductive ecology parameter was the mean egg weight parameter.

A comparison of the estimated elasticity of steepness across life history parameters shows differences in both the direction and size of parameter effects (Fig. 7). A majority of the parameters (57%) had a decreasing directional effect on steepness, while the remainder

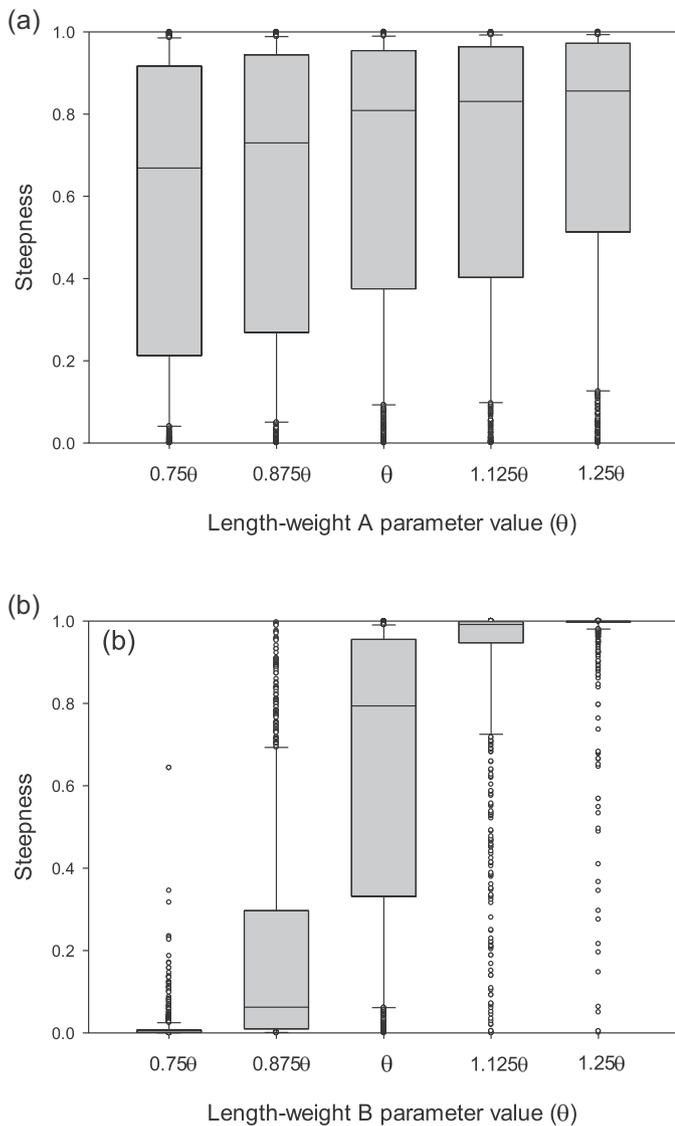


Fig. 4. Sensitivity analyses showing boxplots for the effects of changes in length–weight parameters for (a) scale (A) and (b) exponent (B) on median steepness (solid line inside box), its interquartile range (bottom and top of the box), and its 10th and 90th percentiles (bottom and top whiskers).

had a negative effect. Three of the parameters (A , M , SL) had a negligible effect on steepness with elasticities of less than 0.25 and two parameters (B , $b_{1,el}$) had very strong effects on steepness with elasticities of greater than 1. Of the two parameters with a strong effect, the egg–larval natural mortality slope parameter $b_{1,el}$ had the largest magnitude on estimated steepness while the length–weight exponent B , which provides a measure of body girth, had an important but smaller effect on steepness. All of the remaining nine parameters had a moderate and less important effect on steepness (L_{∞} , k , t_0 , TB , E_G , S_L , A_{50} , W_E , $DELH$), as measured by the elasticity of h .

4. Discussion

The stock–recruitment resilience of WCNPO striped marlin, a fast-growing apex predator, is relatively high and this stock is likely to have the capacity to rebound from high exploitation rates. This is not surprising given the rapid growth and biomass turnover rate of WCNPO striped marlin which has a mean generation time of about 7 years. Due to its high resilience, the WCNPO striped marlin

stock was able to maintain a spawning potential of 35% of SB_{MSY} , the female spawning biomass corresponding to produce MSY , in recent years despite high exploitation rates. In particular, current fishing mortality was estimated to exceed F_{MSY} by about 25% where the F_{MSY} value was calculated based on steepness of $h = 0.87$ (Lee et al., 2012b). Given this information, the stock would currently be classified as overfished and experiencing overfishing if it were managed using the MSY -based limit reference points as employed by the USA fishery management system.

The simulation approach used here to characterize resilience of striped marlin includes several important simplifying assumptions. One important assumption is that density-dependence is negligible in the juvenile and adult life history stages, and as a result, growth, maturation, and natural mortality rates are effectively density-independent. While this assumption is consistent with common assessment practice to model the population dynamics of exploited stocks as density-independent and time-invariant, we recognize that density-dependent effects may have a strong influence for species with higher turnover rates, such as small pelagic fishes and squids. The expected differences among taxonomic groups points to the need for species-specific analyses of stock–recruitment resilience to account for life history invariants (e.g., Beverton, 1992), and in this context, there are density-dependent analogs of our current simulation approach that warrant future study.

The sensitivity analyses show that the effects of variation in reproductive ecology and life history parameters are consistent with current understanding of the relationship between steepness and these parameters (Mangel et al., 2010). Increases in body girth, as indexed by the length–weight exponent B , will increase the reproductive output of the stock. Larger egg sizes, consistent with favorable environmental conditions or expanded age structure due to reduced exploitation rates, will produce higher survival probabilities for larval fish. Increases in asymptotic size will increase average body weight and hence increase reproductive output as a function of body weight. Larger values of the Brody growth coefficient imply a faster approach to asymptotic size and will produce a higher probability of increased reproductive output. Increases in the scale parameter of the length–weight relationship also imply greater weight at a given length. Similarly, increases in mean eggs per unit body weight and duration of the spawning both have a positive impact on egg output and expected lifetime reproductive success. Increases in median age at maturity and natural mortality rate have the opposite effect of decreasing reproductive potential while increasing the age at zero length, a quantity related to early life history stage duration, can be expected to reduce the overall survival probability of larval fish. Overall, the observed effects of variation in life history parameters on estimates of steepness were consistent with the expected effects of increases or decreases in egg production.

Our results also show that the estimate of steepness for WCNPO striped marlin was strongly influenced by reproductive ecology parameters. Currently limited information is available for some of these parameters, namely mean egg weight W_E , early life history stage duration $DELH$, and egg and larval survival. While reproductive ecology is an important source of uncertainty for the baseline assessment of the probable distribution of steepness, it is important to recognize that estimates of reproductive parameters can be empirically measured and refined through direct field research. For example, Simon et al. (2012) developed a more detailed model of early life history stage dynamics of Atlantic bluefin tuna (*Thunnus thynnus*) based on empirical observations and applied this information in a simulation model to characterize the distribution of stock–recruitment steepness. While the steepness model for Atlantic bluefin tuna steepness model developed by Simon et al. (2012) included more data on early life history stage processes,

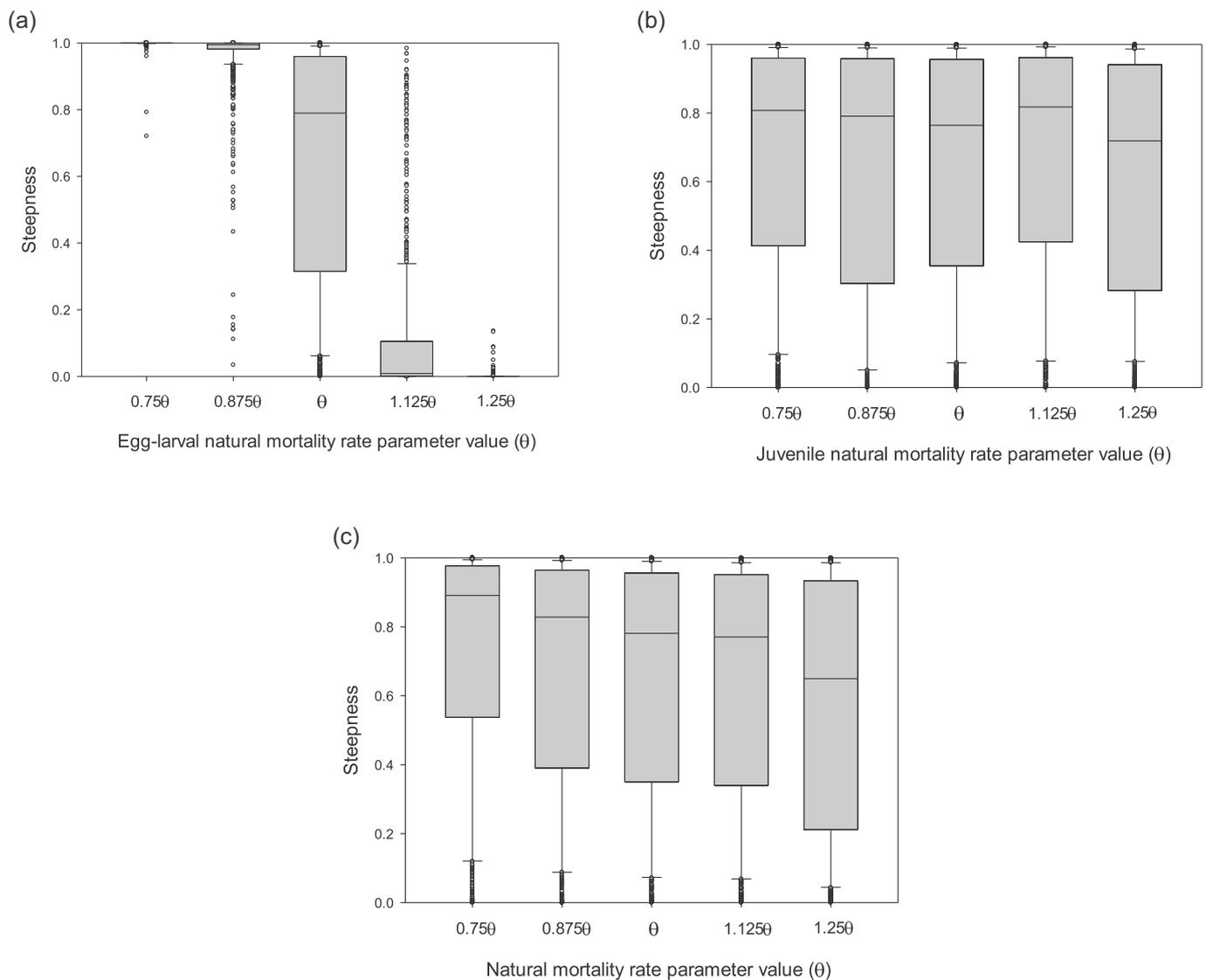


Fig. 5. Sensitivity analyses showing boxplots for the effects of changes in the slope of the egg-larval natural mortality rate (a), the slope of the early life history juvenile natural mortality rate (b), and the natural mortality rate at age parameters (c), on median steepness (solid line inside box), its interquartile range (bottom and top of the box), and its 10th and 90th percentiles (bottom and top whiskers).

it is notable that their estimates of stock-recruitment resilience of Atlantic bluefin tuna were similar to the estimates for Pacific bluefin tuna (Mangel et al., 2010). Overall, this suggested that the two approaches produced consistent results for bluefin tuna species.

The ability to directly collect information on reproductive ecology to characterize stock-recruitment resilience is an important contrast to attempting to estimate steepness through the post hoc analysis of stock-recruitment data from assessment analyses. Typically, several decades of stock-recruitment data would be needed for an accurate characterization of steepness due to the expected variability in recruitment success under environmental forcing. However, it should be noted that simulation and meta analytic approaches to estimate steepness both require an expected form of density-dependence in the stock-recruitment relationship and that this form will likely be an important source of uncertainty for some species. Finally, there may be insufficient statistical information or contrast in the observed spawning biomass levels to accurately estimate steepness, even with a several decades of stock-recruitment data.

In this study, the McGurk (1986) meta analytic estimates of early life history stage survival rates of teleosts have been applied

to characterize the average egg to juvenile survival of WCNP striped marlin. The McGurk allometry can be considered to be a first approximation of the early life history stage mortality processes. McGurk's estimates were based on analyses of field and laboratory data from populations that were experiencing density-dependent and density-independent effects on mortality (McGurk, 1986). Clearly, this approximation is a key assumption for our analysis and it would be desirable to conduct further research to update and improve McGurk's data set and analyses with more recent data sources describing larval fish survival rates, especially at low and high stock densities where density-dependent processes may be strongly influential.

While the assumption that steepness is unity is not biologically possible, (Brodziak et al., 2002; Mangel et al., 2010), this simplifying approximation has and very likely will be continue to be used in stock assessments. In this context, our approach to directly estimating stock-recruitment resilience provides a general framework to characterize how much recruitment is influenced by stock size and address the question, do the data support an assumption that the stock is resilient or not? Setting steepness to unity in the absence of knowledge is inconsistent with the principle of

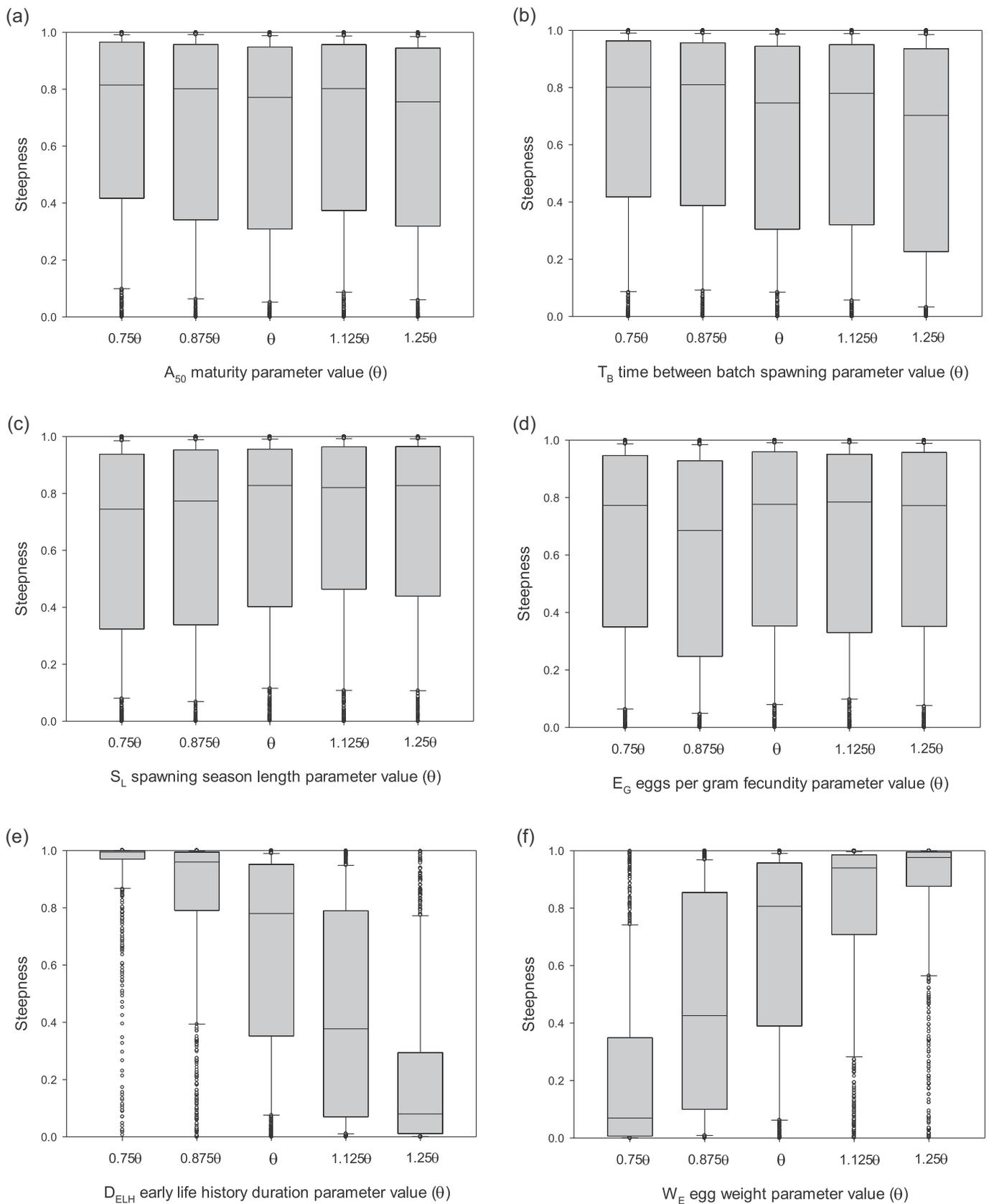


Fig. 6. Sensitivity analyses showing boxplots for the effects of changes in reproductive ecology parameters on steepness for female age at 50% maturity (a), average time between spawning events (b), spawning season length (c), mean number of eggs per gram of body weight (d), early life history stage duration (e), and mean egg weight (f) on median steepness (solid line inside box), its interquartile range (bottom and top of the box), and its 10th and 90th percentiles (bottom and top whiskers).

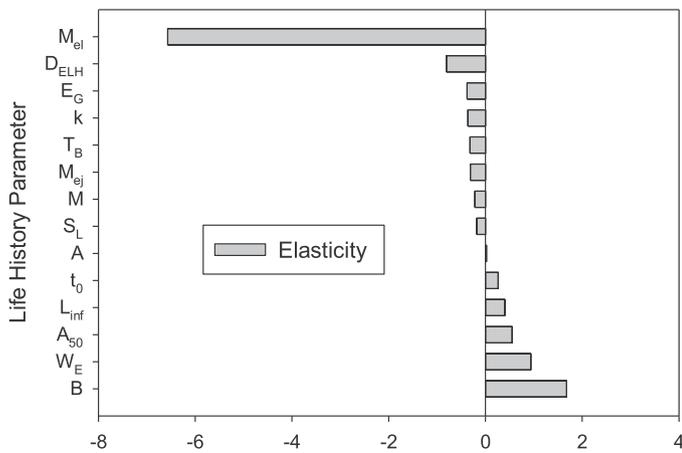


Fig. 7. Comparison of the elasticity of steepness evaluated at the baseline parameter values with respect to the daily natural mortality rates of eggs and larval fish (M_{el}), the early life history stage duration (D_{ELH}), the mean number of eggs per gram of body weight (E_G), the Brody growth coefficient (k), the average time between spawning events (T_B), the daily natural mortality rates of juvenile early life history stage fish (M_{el}), the annual natural mortality rate parameter for juvenile and adult fish (M), the spawning season length (S_L), the length–weight scale parameter (A), the age at zero length (t_0), the asymptotic length (L_{inf}), the female age at 50% maturity (A_{50}), the mean egg weight (W_E), and the length–weight exponent parameter (B).

indifference (Edwards, 1992), and if one really had no prior belief about steepness, then any value of h in the interval (0.2, 1) would be equally probable, assuming Beverton–Holt stock-recruitment dynamics. On the other hand, the assumption that recruitment is effectively “environmentally driven” over observed stock sizes can be supported in many cases (i.e., Vert-pre et al., 2013; Zuwalski et al., 2014). In such cases, assuming steepness is unity may be unimportant if the stock is relatively abundant because the amount of approximation error from assuming there is no curvature in the stock-recruitment relationship is acceptably small. Regardless, avoiding a priori assumptions about stock-recruitment steepness will likely be important for depleted stocks where assessment results are highly scrutinized and subject to being supported by data and accepted by stakeholders.

Treating steepness as a numerical parameter to be estimated in a statistical meta analytical framework is a natural alternative to the reproductive ecology and life history-based estimation approach applied in this study. The use of meta analyses to estimate steepness provides a practical and objective means to using the information in multiple stock-recruitment data sets to gain precision and accuracy (Myers et al., 1999), but this approach also has potential weaknesses. These include the potential lack of a set of representative stocks, the lack of independence among multiple stock responses to environmental variation, inherent measurement error in estimates of both stock and recruitment, and possibly an implicit bias toward selection of a common set of exploited stocks for which assessment data are available. Of these, selection bias of stock-recruitment data sets can have an important potential impact on inferences about a credible range for steepness. For example, meta analytic estimates of the central tendency of steepness reported by Rose et al. (2001) and Shertzer and Conn (2012) are very similar, and on this basis, one might conclude that this was strong evidence for a similar central tendency. But as Shertzer and Conn (2012) note, this similarity can be explained by the selection of common data sets for their meta analyses. Regardless, the meta analytic approach ignores relevant information on resilience that is inherent in a stock’s reproductive and life history parameters and this may lead to biased estimates of steepness. In general, steepness is a function of many parameters and analyses that aim to determine the relationship between steepness and only one of these parameters (e.g. natural mortality or age

at maturity) are implicitly projecting from a multidimensional set of parameters to a single parameter for prediction of steepness. In this context, important biological variation may end up being characterized as statistical noise.

For some marine resources, it will not be possible to estimate steepness within a statistical stock assessment model (Conn et al., 2010). For example, even if a stock is well-managed and spawning biomass has fluctuated around B_{MSY} through time, there still may be little or no information on the expected decrease in recruitment as spawning biomass declines. The same lack of data contrast may be true for poorly managed stocks that have been persistently overfished and that have few observations of stock-recruitment dynamics at high spawning biomasses. In effect, many stock-recruitment data sets may not have sufficient contrast in the range of spawning biomass to estimate steepness. In these cases, it is unlikely that steepness can be freely estimated, as suggested in the simulation analyses of Lee et al. (2012).

In essence, one might view our approach to estimating steepness as replacing one difficult to estimate parameter with others, namely reproductive ecology and larval survival. However, the key difference is that data on reproductive ecology and larval survival can be directly collected, subject to cost, while information on stock-recruitment data accrues on an annual basis over a longer time scale. As a result, our approach to estimating steepness provides a potentially more general and tractable means, rooted in population biology, of quantifying the probable resiliency of stocks for which life history data are sufficient.

There are a number of extensions to this work that may be fruitful for future investigation. In particular, it seems important to assess whether information on egg quality at size or age can be used to account for the possible effects of the big old fat fecund female fish hypothesis (Marteinsdottir and Steinarsson, 1998; Longhurst, 2002; Berkeley et al., 2004) on stock resiliency. We also suggest that it may be essential to incorporate additional information on density-dependent processes for successive early life history stages for some species. Unfortunately, such information is not available for striped marlin, and in this case, our estimates of resilience are contingent on the representativeness of the available information on the distribution of early life history survival rates. On the other hand, density-independent environmental effects on early life history survival can be characterized using Paulik diagrams (Paulik, 1973; Payne et al., 2009) to further refine understanding of the causes of stanzas of recruitment success or failure and this information can be used to improve estimates of early life history dynamics. Thus, while our approach to estimating steepness underscores the practical value of field research on the life history and reproductive ecology of fishes, there is clearly more work to be done on characterizing the resilience of fish stocks to recruitment overfishing.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fishres.2014.08.008>.

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