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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): $L(t) = L_\infty(1-\exp(-k(t-0)))$ 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 $a = 0, 1, \ldots, A_{MAX}$. Baseline: $M_{EL}(d) = 2.2 \times 10^{-4} w_{ELH}(d)^{-0.85}$ $M_J(d) = 5.26 \times 10^{-3} w_{ELH}(d)^{-0.25}$ $M(0) = 0.49$ yr^{-1}, $M(1) = 0.45$ yr^{-1}, $M(j) = 0.40$ yr^{-1}, for $2 \le j \le A_{MAX}$
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:

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

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:

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

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:

$$h = \frac{\alpha_S \cdot SPR_0}{4 + \alpha_S \cdot SPR_0} \tag{3}$$

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 jth randomly selected fish in the kth 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 kth population and dividing by the sampled biomass gives an estimate of