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On the Probable Distribution of Stock-Recruitment Steepness for Western and Central North Pacific Swordfish

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Abstract

The resilience of a stock-recruitment relationship is a key characteristic for modeling the population dynamics and fishery productivity of living marine resources. Steepness determines the expected resiliency of a fish stock to harvest and is important for the estimation of biological reference points such as maximum sustainable yield. Stock-recruitment steepness was a primary uncertainty for the determination of stock status and biological reference points in the most recent stock assessment (ISC 2018) of Western and Central North Pacific swordfish (*Xiphias gladius*). To address this uncertainty, we applied the method of Mangel et al. (2010) and Brodziak et al. (2015) to quantify the probable distribution of steepness for swordfish using new information on the mean batch fecundity, spawning frequency, and spawning season duration. Results indicated that, under an assumption of Beverton-Holt stock-recruitment dynamics, the median steepness of swordfish was 0.95 with a 95% probable range of (0.89, 0.99). This suggested that Western and Central North Pacific swordfish was highly resilient to reductions in spawning potential. Results also indicated that variation in some reproductive and life history parameters had an important influence on the distribution of steepness. In particular, 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.

Introduction

The resilience, or steepness, of the stock-recruitment relationship, is an important factor for assessing stock status of fishery resources. Steepness measures the expected reduction in recruitment when spawning potential declines to 20% of its unfished level. The magnitude of the reduction in recruitment determines the resilience of a fish stock to harvest and is important for estimating biological reference points such as maximum sustainable yield. In this study, we use the individual-based modeling approach of Mangel et al. (2010) as extended by Brodziak et al. (2015) to evaluate the distribution of probable values of stock-recruitment steepness for Western and Central North Pacific (WCNPO) swordfish, *Xiphias gladius*. We applied new information on the mean batch fecundity, spawning frequency, and expected egg size from Sharma and Arocha (2017) along with the best available data on swordfish reproductive ecology and life history parameters including growth, maturity at age, average weight at length, and natural mortality rates to assess the steepness of swordfish (Table 1). We also evaluated the effects of misspecification of swordfish reproductive ecology and life history parameters on steepness by conducting a systematic set of sensitivity analyses.

Materials and Methods

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 the steepness parameter (h) measures the decrease in recruitment as spawning potential decreases. Stocks with higher values of steepness are relatively more productive at lower spawning biomasses than stocks with lower values of steepness. We applied the age-structured simulation model of Mangel et al. (2010) as extended by Brodziak et al. (2015) to assess a baseline prior distribution of steepness for WCNPO swordfish using the best available information on reproductive ecology and life history parameters. It was assumed that recruitment dynamics followed a Beverton-Holt stock-recruitment relationship, which was consistent with the stock assessment model used for WCNPO swordfish (ISC 2018). The expected value of age-0 female recruitment to the population at time *t*, denoted as *N*(0,*t*), was

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

where $B_S(t)$ was spawning biomass at time *t*. In Eqn. 1, the slope-at-the-origin parameter, α_S, has units of new individuals produced per unit of spawning biomass and is a key parameter for constructing estimates of steepness for swordfish. In this context, the individual-based 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 success (Mangel et al. 2010). Given that individual fecundity is proportional to body mass, the female spawning biomass $B_S(t)$ in year *t* is

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

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 directly calculated from the slope at the origin when density-dependent impacts on life history parameters are negligible, which is typically assumed in age-structured assessment models including the Stock Synthesis model used for WCNPO swordfish (ISC 2018). In this context, 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

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

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 probable distribution of values of the slope at the origin α_S.

Slope at the origin

We used Monte Carlo simulation to construct a total of *K* swordfish breeding populations to estimate the distribution of the slope at the origin α_S. Here each breeding population represented the survival and reproductive success of the swordfish population during one annual time cycle under the specific set of simulated environmental conditions experienced by the breeding population. In particular, each population consisted of *n* fish randomly sampled from the probability distributions of reproductive and life history parameters for WCNPO swordfish. The mean values of these parameters were taken from recent literature and the most recent stock assessment information for swordfish in the North Pacific.

To calculate the distribution of probable slope at the origin values over the set of simulated breeding populations, we first simulated the age structure of each population and then simulated the egg production and survivorship of eggs from each individual by cohort. To simulate the age structure of each population, natural mortality rates at age were randomly sampled from their probability distributions to generate survival-to-age distributions for each simulated population. The 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 their population-specific survivorship curve.

To calculate slope at the origin for a given population, let $a_{n,k}$ denote the age of the j^{th} randomly selected female 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 during a single batch 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. Thus, summing the expected fecundity times expected larval survival L_S to the expected weight at age-0 over all fish in the k^{th} population and dividing this sum by the sampled biomass gives an estimate of the number of new recruits produced per unit of spawning biomass, or the slope at the origin $\alpha_S(k)$, in the k^{th} population as

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

For each simulated 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) or McCoy and Gillooly (2008) as described below. Thus, given the relationship between steepness and the slope at the origin in Eqn. 3, a frequency distribution for each possible value of steepness *h* was generated from the observed values in the simulated populations.

Life history parameters

The inputs to the individual-based simulation model included information on growth, length-weight, and other life history parameters gathered from the most recent stock assessment (ISC 2018). Swordfish juvenile and adult growth was simulated using the von Bertalanffy growth curve estimated by DeMartini et al. (2007) with growth parameters of L_{∞} = 230.5 (cm, eye-fork length), k = 0.246 yr^{-1}, and t_0 = -1.24 years (Table 1). For all analyses, the length-weight relationship from Uchiyama et al. (1999) was used to convert length to weight (Table 1). The natural mortality rate at age parameters (Table 1) were gathered from the most recent stock assessment (ISC 2018). In this case, the estimated age-0 value of $M(0) = 0.42$ represented the natural mortality rate experienced by age-0 fish subsequent to survival through the expected early life history stage duration of about 226 days (see below).

Reproductive ecology

The median length at maturity of female swordfish was gathered from DeMartini et al. (2000) and was L_{50} = 143.6 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 DeMartini et al. (2007) to set $a_{50} = 2.725$ yr (Table 1). Sharma and Arocha (2017) reported an average timing between batch spawning events (T_B) of $T_B = 2.6$ days, which was used to characterize the expected batch spawning frequency (Table 1).

Information on swordfish fecundity and spawning season duration was used to estimate total egg production for each simulated population. Sharma and Arocha (2017) reported that the relative fecundity of swordfish averaged 32.2 oocytes per gram of body weight (E_G) and we used the expected batch fecundity of $E_G = 32.2$ eggs per gram as a measure of the central tendency of fecundity for each simulated fish (Table 1). DeMartini et al. (2000) reported that females in spawning condition were observed in April-July in the central Pacific based on observations of hydrated oocytes and this suggested that the length of the swordfish spawning season (S_L) was approximately $S_L = 4$ months (Table 1). Given the uncertainty in this information, sensitivity analyses were conducted to characterize the effects of alternative relative fecundity and spawning season durations on steepness estimates.

The expected durations of the early life history stages of swordfish eggs, larval and juvenile fish were used to calculate the size-specific allometric natural mortality rates and associated survival probabilities of early life history stage females. In this case, it was assumed that individual daily growth was exponential (e.g., Buckley 1981) 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 $L(0) = 60.6$ cm EFL; DeMartini et al. 2007). This value of $L(0)$ indicated that growth through the early life history stages was rapid and was compared to the predicted median size at age 1 of approximately $L(1) = 97.65$ cm EFL. We used the ratio of the size realized at the end of early life history stage growth to the predicted size at age 1 to estimate the expected duration of the early life history stages (D_{ELH}, days) as $D_{ELH} = \frac{L(0)}{L(1)} \cdot 365 \approx 226$ days (Table 1) where the expected size at an age of D_{ELH} days was $L(0)$. Information on mean swordfish egg weight was used to simulate the initial condition for size-specific allometric survival rates of early life history stages. Sharma and Arocha (2017) reported a mean swordfish egg weight (W_E) of $W_E = 6.17 \cdot 10^{-4}$ (Table 1). As with other parameters, we investigated the sensitivity of steepness estimates to early life history stage duration and average egg weight.

Growth and survival of early life history stages

Early life history 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 (Sponaugle et al. 2005) and was parameterized using the expected early stage duration D_{ELH} and the expected weight of an age-0 fish $(W(0) = 3914\ g)$ under the von Bertalanffy growth curve (Figure 1a). The expected body mass (wet weight) at an age of d days $(W_{ELH}(d))$ was calculated from the initial egg weight to the ending age-0 weight as

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

where $K_{ELH} = \log(W(0)/W_E)/D_{ELH}$. Thus, growth of early life history stages of swordfish 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 life history 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 previous modeling of early life history rates for characterizing resilience (Mangel et al. 2010, Brodziak et al. 2015), 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 $\overset{\square}{W}_{ELH}(d)$, where $M_{ELH}(d) = b_0 \cdot \overset{\square}{W}_{ELH}(d)^{b_1}$ for intercept b_0 and slope b_1 and $\overset{\square}{W}_{ELH}(d) = 0.2W_{ELH}(d)$. 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 $W_{CRIT} = 5.04\cdot 10^{-3}$ g with $b_1 = -0.85$ in comparison to the allometric slope of $b_1 = -0.25$ reported by 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 $M_{EL}(d) = 2.2\cdot 10^{-4} W_{ELH}(d)^{-0.85}$ 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 $M_J(d) = 5.26\cdot 10^{-3} W_{ELH}(d)^{-0.25}$ (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.

Individual-based simulation analyses

For each individual-based simulation analysis, we ran a total of 500 simulations for each of 500 populations comprised of 500 individual fish to estimate the empirical probability density function of stock-recruitment steepness. We used a sample size of 500 fish to calculate the expected value of slope at the origin for a relatively small population of swordfish. We also note that the most recent assessment indicated that the unfished swordfish stock size was about five orders of magnitude above this level and that individual-based simulation results were insensitive to population sample sizes ranging from 100 to 1,000 fish in a similar analysis conducted for striped marlin (Brodziak et al. 2015).

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 $I_j = \left(h_j, h_{j+1}\right)$ had a width of 0.01 units with a lower bound of $h_j = 0.2 + 0.01\cdot\left(j-1\right)$. For each population, a simulated value of steepness ($h^{(p)}$) was calculated 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 $h_k < h^{(p)} \le h_{k+1}$. 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 $H^{(s)} = \left\{p^{(s)}(I_1),\ p^{(s)}(I_2),\ldots,\ p^{(s)}\left(I_{n_h}\right)\right\}$, where $p^{(s)}(I)$ denoted the observed probability that h was in interval I. The overall empirical distribution of steepness (H) was then calculated from the set of simulated densities generated from the total of n simulations. In particular, the distribution H was given by $H = \left\{p(I_1),\ p(I_2),\ldots,\ p\left(I_{n_h}\right)\right\}$ 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

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

We also fitted a beta density to the empirical distribution of steepness as described in Mangel et al. (2010).

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). This was in effect an assumption about the potential strength of changes in reproductive and life history parameters due to phenotypic plasticity, regardless of the causal mechanism, which in practice may be difficult to discern (i.e., Ghalambor et al. 2007, Auld et al. 2010). 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 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 a 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 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 parameter misspecification.

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

(7) $$e(\theta_k) = \frac{\partial h}{\partial \theta_k}(\underline{\theta})\frac{\theta_k}{h}$$

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.

Two additional one-off sensitivity analyses were conducted to assess model robustness. First, we conducted a sensitivity analysis using the allometric scaling of natural mortality reported by McCoy and Gillooly (2008) for early life history stage swordfish instead of the McGurk (1986) scaling. This was done to examine whether the model results were sensitive to the form of allometric scaling of swordfish natural mortality rate with body mass. Second, we conducted a sensitivity analysis where the simulated process error for several life history parameters was set equal to the reported observation error for each parameter instead of using the assumption that the process error CV was 10%. In this case, the observed CVs for the set of life history parameters $\{L_\infty, k, t_0, A, B, a_{50}\}$ were $\{2\%, 8\%, 13\%, 23\%, 1\%, 1\%\}$ respectively, and the question was what would be the effect on results if the observation errors were equal to the process errors for these parameters where some information on the likely observation error was available.

Results

Results of the baseline steepness model indicated that the distribution of steepness was left skewed (Fig. 2a) with a median steepness of *h*=0.95 and a 95% probable range of (0.89, 0.99). The mean steepness was 0.98 with a coefficient of variation of 0.05 (Fig. 2a) and the fitted beta density parameters were a_β = 0.975 and b_β = 4.665 (i.e., Eqn 7 in Brodziak et al (2015)). The median steepness value was 8% higher than the metaanalysis estimate of *h*=0.88 from Myers et al. (1999) and was 3% higher than the individual-based simulation analysis estimate of *h*=0.92 from Sharma and Arocha (2017). Overall, the results of the baseline model indicated that the stock-recruitment dynamics of Western and Central Pacific North Pacific swordfish were likely highly resilient to declines in spawning potential.

The sensitivity analysis comparing the baseline results with those obtained using the early life history natural mortality rate relationship from McCoy and Gillooly (2008) showed that the baseline results were robust to the assumed natural mortality allometry (Figure 2b). Results using the McCoy and Gillooly mortality allometry also showed that the distribution of steepness was left skewed (Fig. 2b) with a median steepness of *h*=0.98 and a 95% probable range of (0.91, 0.99). In this case, the mean steepness was also 0.98 with a coefficient of variation of 0.05 (Fig. 2a) and the fitted beta density parameters were a_β = 0.977 and b_β = 4.927. Thus, using the alternative natural mortality rate relationship from McCoy and Gillooly produced similar results and suggested slightly higher stock-recruitment resilience for WCNPO swordfish.

Similarly, the sensitivity analysis comparing the baseline results with those obtained using the observed CVs of life history parameter estimates for the simulated process errors showed that the baseline results were robust to the process error assumption (Figure 2b). Results using the observed CVs produced a probable distribution of steepness that was left skewed with a median steepness of *h*=0.98 and a 95% probable range of (0.94, 0.99). The mean steepness using the observed CVs was also 0.98 with a coefficient of variation of 0.04 and the fitted beta density parameters were a_β = 0.980 and b_β = 7.335.

Overall, using the observed CVs of life history parameter estimates produced similar results with a slightly higher implied steepness for WCNPO swordfish.

The systematic sensitivity analyses showed the effects of related types of reproductive and life history parameters on the probable distribution of WCNPO swordfish steepness. Growth parameters had a moderate impact on steepness. Of the three growth parameters, the one with the strongest influence was the asymptotic length L_∞ which had an increasing effect on steepness over the sensitivity interval (Fig. 3a). The elasticity of L_∞ was $e\left(L_\infty\right)=0.05$ for the baseline, which indicated that a 10% increase in L_∞ would be expected to produce a 0.5% increase in steepness. The next most important growth parameter was the Brody growth coefficient *k* (Fig. 3b) for which the elasticity was $e\left(k\right)=0.02$. The least influential growth parameter was the age at zero length t_0 (Fig. 3c) with an elasticity of $e\left(t_0\right)$ = 0.02. For each growth parameter, the variability of the steepness estimate decreased as the value of the growth parameter increased (Fig. 3).

Length-weight parameters had a somewhat stronger impact on steepness. The length-weight scaling parameter *A* had a minor impact on steepness (Fig. 4a) with an elasticity of $e\left(A\right)$ = 0.02. In contrast, steepness was more sensitive to the length-weight exponent *B* (Fig. 4b) where increases in the exponent *B* produced notable increases in steepness with an elasticity of $e\left(B\right)$ = 0.3, indicating that a 10% change in *B* would produce a 3% change in steepness. Overall, 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).

For the mortality rate parameters, it was apparent that changes in the egg and larval mortality rate had a more important impact on steepness with an elasticity of $e\left(M_{EL}\right)$ = -0.15 (Fig. 5a). In comparison, the juvenile and adult natural mortality rates had minor effects on steepness with elasticities of $e\left(M_J\right)$ = -0.02 (Fig. 5b) and $e\left(M\right)$ = -0.02 (Fig. 5c). Overall, the variability in the estimates of steepness showed an increasing trend for the natural mortality rate parameters (Fig. 5).

In terms of reproductive parameters, changes in the female maturity at age ogive had a minor effect on steepness. In particular, the median age of maturity had an elasticity of $e\left(a_{50}\right)$ = 0.02 which suggested that increases in the age of female maturity would have little impact on steepness. The estimates of steepness showed a range of effect sizes for the reproductive parameters of spawning season, fecundity, and early life history stage duration. The average time between spawning events parameter T_B had a minor negative impact on steepness (Fig. 6b) with $e\left(T_B\right)$ = -0.01. In contrast, the length of spawning season S_L had a negligible effect on steepness (Fig. 6c) with $e\left(S_L\right)$ = -0.00. Similarly, the mean number of eggs per gram of body weight parameter E_G had a negligible impact on steepness (Fig. 6d) with $e\left(E_G\right)$ = -0.00. The duration of early life history stage had a minor negative impact on steepness (Fig. 6e) with an elasticity of $e\left(D_{ELH}\right)$ = -0.08. In contrast, the mean egg weight W_E had a minor positive effect on steepness (Fig. 6f) with an elasticity of $e(W_E)$ = 0.08. The variability in estimated steepness had a decreasing trend for the mean egg weight parameter W_E (Fig. 6f) and an increasing trend for the early life history duration parameter D_{ELH} (Fig. 6e) but showed little or no trend for the other reproductive ecology parameters (Fig. 6). Overall, the most important reproductive parameters were the mean egg weight and early life history stage duration parameters.

A comparison of the estimated elasticity of steepness across reproductive life history parameters shows differences in both the direction and magnitude of the parameter effects (Figure 7). Two parameters, the length-weight exponent B and the egg-larval natural mortality M_{EL} had the strongest effects on steepness with elasticities of greater than 0.1. The rest of the parameters had minor or negligible impacts on steepness. It is notable that all of the natural mortality parameters had a negative impact on steepness, as expected (Mangel et al. 2010) while each of the growth parameters had a positive impact (Fig. 7). Overall, the steepness of WCNPO swordfish appeared to be relatively inelastic to changes in reproductive or life history parameters compared to North Pacific striped marlin (Brodziak et al. 2015).

Discussion

The basic result of this study is that the stock-recruitment resilience of WCNPO swordfish is relatively high and as a result, it can be expected that this stock has the capacity to rebound from high exploitation rates. This result is not surprising based on the rapid growth rate and relatively high fecundity of swordfish (e.g., Collette and Graves 2019) which has a median age of maturity of about 3 years and a mean generation time of about 9 years in the western and central north Pacific Ocean (ISC 2018, unpublished data). Our results are also consistent with estimates of swordfish resilience derived from meta-analyses (Myers et al. 1999) and individual-based simulation analyses (Sharma and Arocha 2017). Sensitivity analyses also support the result that WCNPO swordfish resilience is relatively high ($h \geq 0.9$) even when accounting for potential misspecification or plasticity of reproductive or life history traits.

The individual-based simulation approach used here to characterize the resilience of swordfish is based on the simplifying assumption that life history parameters are effectively density-independent over the range of stock sizes examined. This assumption is typically made in integrated age-structured stock assessments and seems plausible for swordfish, a fast-growing apex predator. However, it may not be an accurate approximation for small pelagic species with high turnover rates, such as sardines. Regardless, we recognize that this assumption is an approximation and note that if density-dependence were substantial, then precaution would be warranted in applying our results as density-dependence in growth and maturation can produce slower rebuilding times for depleted stocks and more optimistic scientific advice on stock status (i.e., Helser and Brodziak 1998).

We also comment that results of the sensitivity analyses showing the effects of variation in reproductive ecology and life history parameters are consistent with expectations. In particular, larger asymptotic fish length will lead to larger average body weight and increase reproductive output as a function of body weight. Similarly, larger values of the Brody growth coefficient *k* imply a more rapid approach to asymptotic size and a higher probability of increased reproductive output, all else being equal. Increases in body girth, as measured by the length-weight exponent B, will increase the average weight of fish at a given length and the expected reproductive output of the stock. Larger egg sizes will also generally produce higher survival probabilities for larval fish and improve net reproductive output and stock resiliency, e.g., the big old fat fecund female fish hypothesis (Marteinsdottir and Steinarsson, 1998; Longhurst, 2002; Berkeley et al., 2004). In contrast, increases in the natural mortality rate have the opposite effect of decreasing reproductive potential, especially increased mortality rates for larval fish. Overall, the observed effects of variation in life history parameters on estimates of steepness were generally consistent with the expected effects of increases or decreases in population egg production.

While our results suggested that the probable distribution of steepness for WCNPO swordfish was relatively robust to reproductive parameters, we note that there was some sensitivity to mean egg weight W_E, early life history stage duration D_{ELH}, and egg and larval survival M_{EL}. Reproductive ecology of swordfish is a source of uncertainty for evaluating the probable distribution of steepness and it would be useful to consider collecting more field data to empirically refine our understanding of these parameters. It would also be useful to consider additional information on density-dependent processes for successive early life history stages for swordfish, because in our case, estimates of resilience are contingent on the representativeness of the available metaanalytic information on the likely distribution of early life history survival rates from McGurk (1986) or McCoy and Gillooly (2008).

The individual-based simulation approach applied here (e.g., Mangel et al. 2010, Simon et al. 2012, Brodziak et al. 2015) provides a means to directly estimate stock-recruitment resilience that is complementary to meta-analytical approaches (e.g., Myers et al. 1999, Shertzer and Conn 2012, Punt and Dorn 2014) or more recently developed hybrid approaches (Munyandorero 2019). All of these approaches, in turn, provide a framework to characterize how much recruitment is influenced by the stock size and address the management question, how much exploitation can the stock withstand with a low risk of stock depletion? On the other hand, the assumption that recruitment is effectively "environmentally driven" over observed stock sizes has empirical support in many cases (i.e., Vert-pre et al. 2013, Szuwalski et al. 2014). Future work may need to account for the impacts of autocorrelation on recruitment success, as suggested by the positive impact of ENSO on observed recruits per spawner (ISC 2018), and in general, address the likely impacts of a changing and nonstationary climate (WMO 2019) on swordfish fishery productivity.

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Table 1. Mean values of swordfish 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): $L(t) = L_\infty\left(1-\exp\left(-k\left(t-t0\right)\right)\right)$ Baseline: L_∞ = 230.5, *k* = 0.246, t_0 = -1.24
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: $A = 1.2988\cdot10^{-5}$ and $B = 3.0738$
$M_{EL}(d), M_J(d)$, $M(a)$	**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, …, A_{MAX}. Baseline: $M_{EL}(d) = 2.2\cdot10^{-4} W_{ELH}(d)^{-0.85}$ $M_J(d) = 5.26\cdot10^{-3} W_{ELH}(d)^{-0.25}$ $M(0)=0.42$ yr^{-1}, $M(1)=0.37$ yr^{-1}, $M(2)=0.32$ yr^{-1}, $M(j)=0.22$ yr^{-1}, for $3 \le j \le A_{MAX}$
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.

	$\Pr\left(mature\,at\,age\,a\right) = \dfrac{\exp\left(\dfrac{a-a_{50}}{\sigma_M}\right)}{1+\exp\left(\dfrac{a-a_{50}}{\sigma_M}\right)}$ Baseline: $a_{50} = 2.725$, $\sigma_M = 0.67$
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 = 2.6, S_L = 4, E_G = 32.2, $D_{ELH} = 226$, $W_E = 6.17 \cdot 10^{-4}$

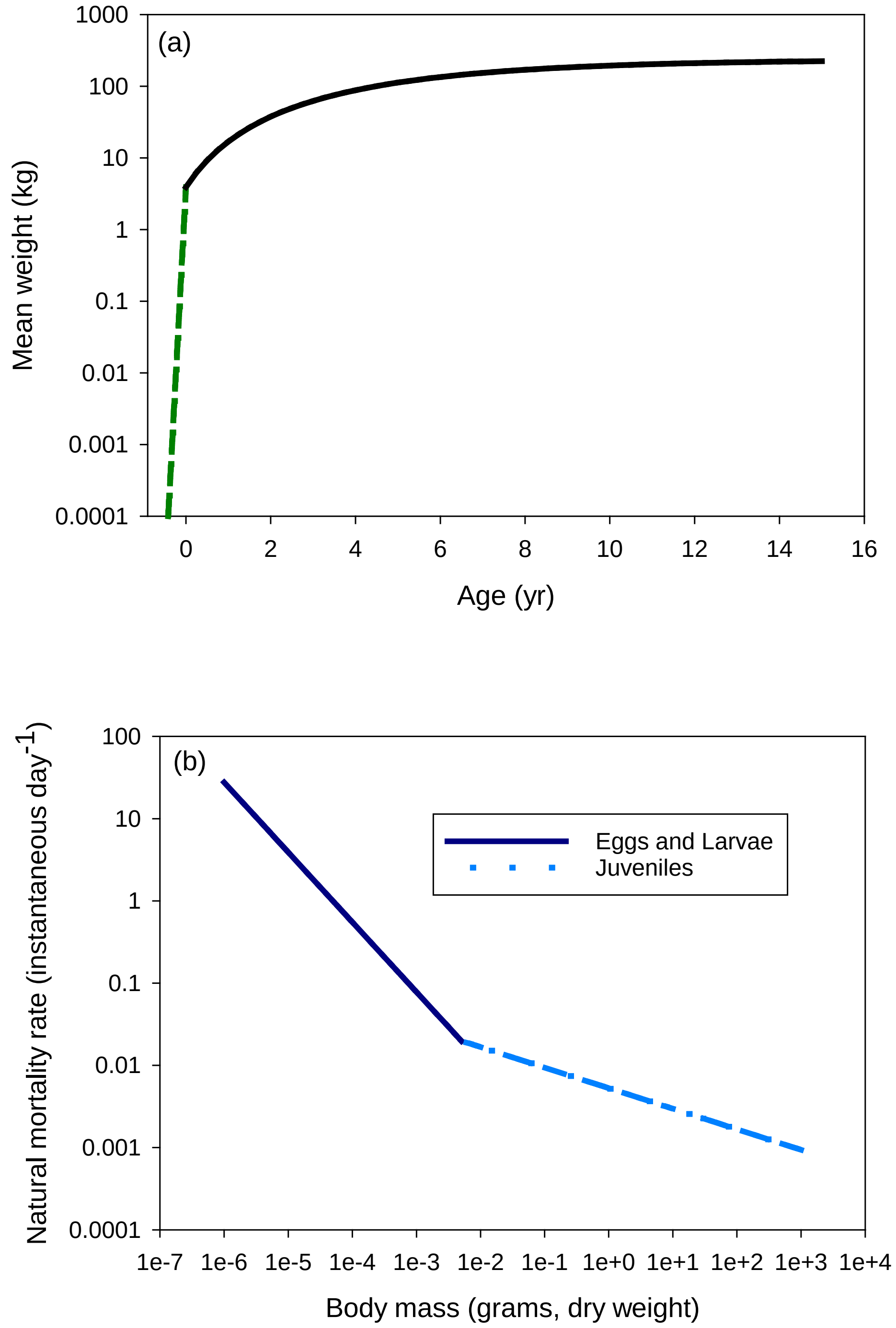

Figure 1. Growth of early life history stage and adult WCNPO swordfish (a) and the allometry of weight-specific natural mortality rates as a function of body mass (b).

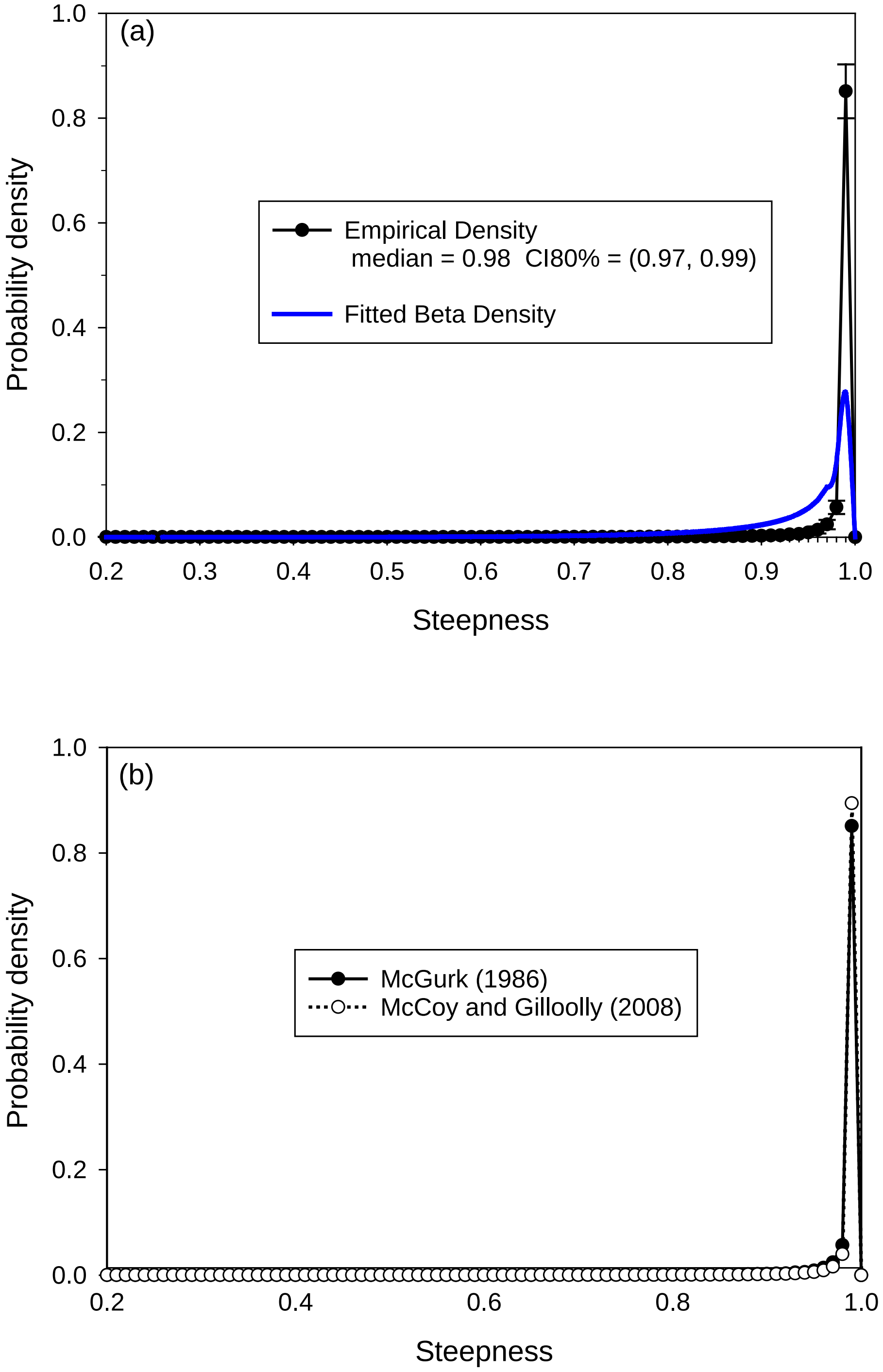

Figure 2. Baseline estimate of the empirical probability density of stock-recruitment steepness for Western and Central North Pacific swordfish along with fitted beta density (a) and sensitivity analysis showing the effect of weight-specific allometry of natural mortality rate as a function of body mass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

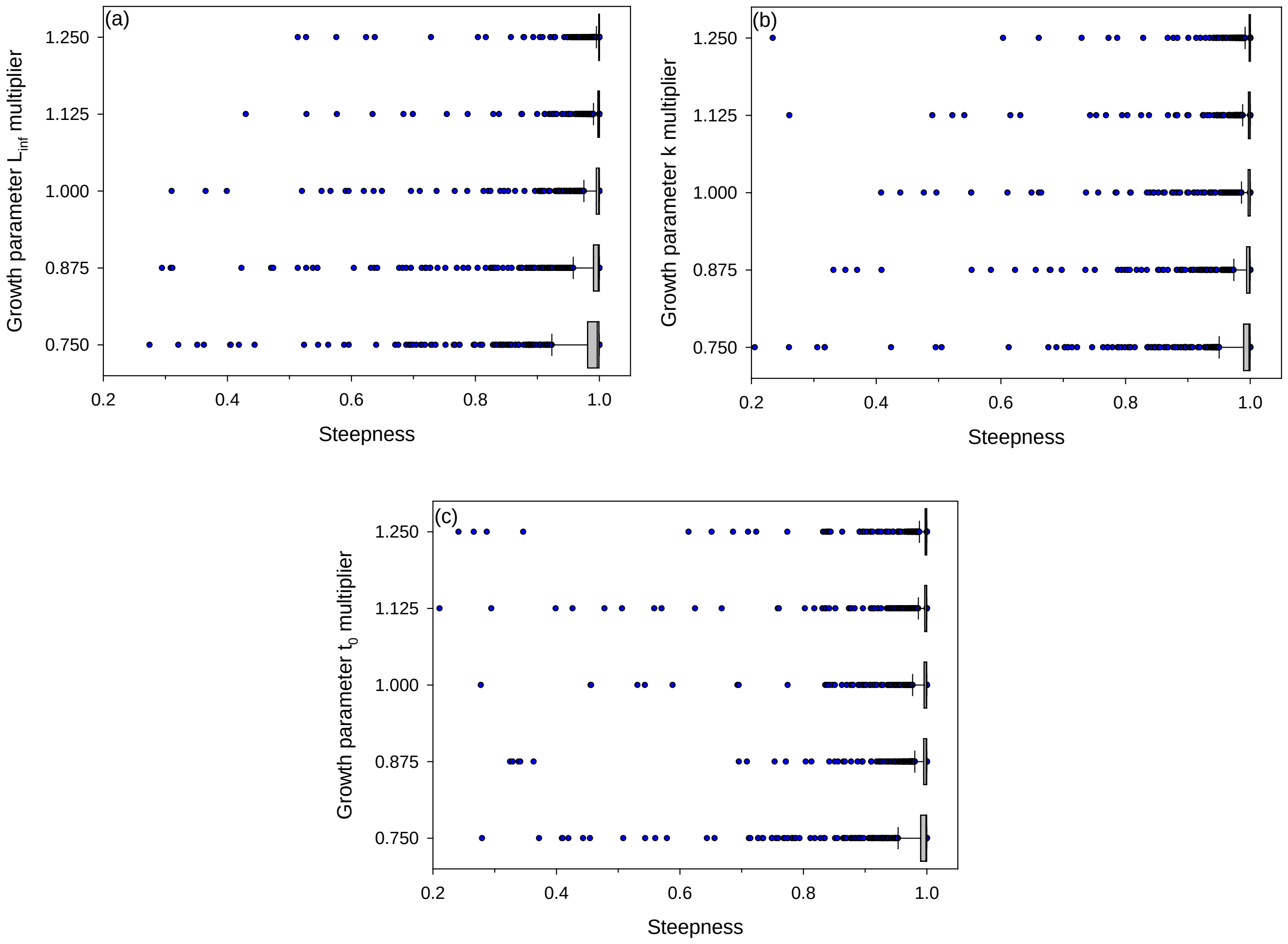

Figure 3. Sensitivity analyses showing boxplots for the effects of changes in the growth parameters (a) asymptotic length (L_∞), (b) Brody growth coefficient (k), and (c) age at zero length (t_0) on median steepness (solid line inside box), its interquartile range (bottom and top of the box), and its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

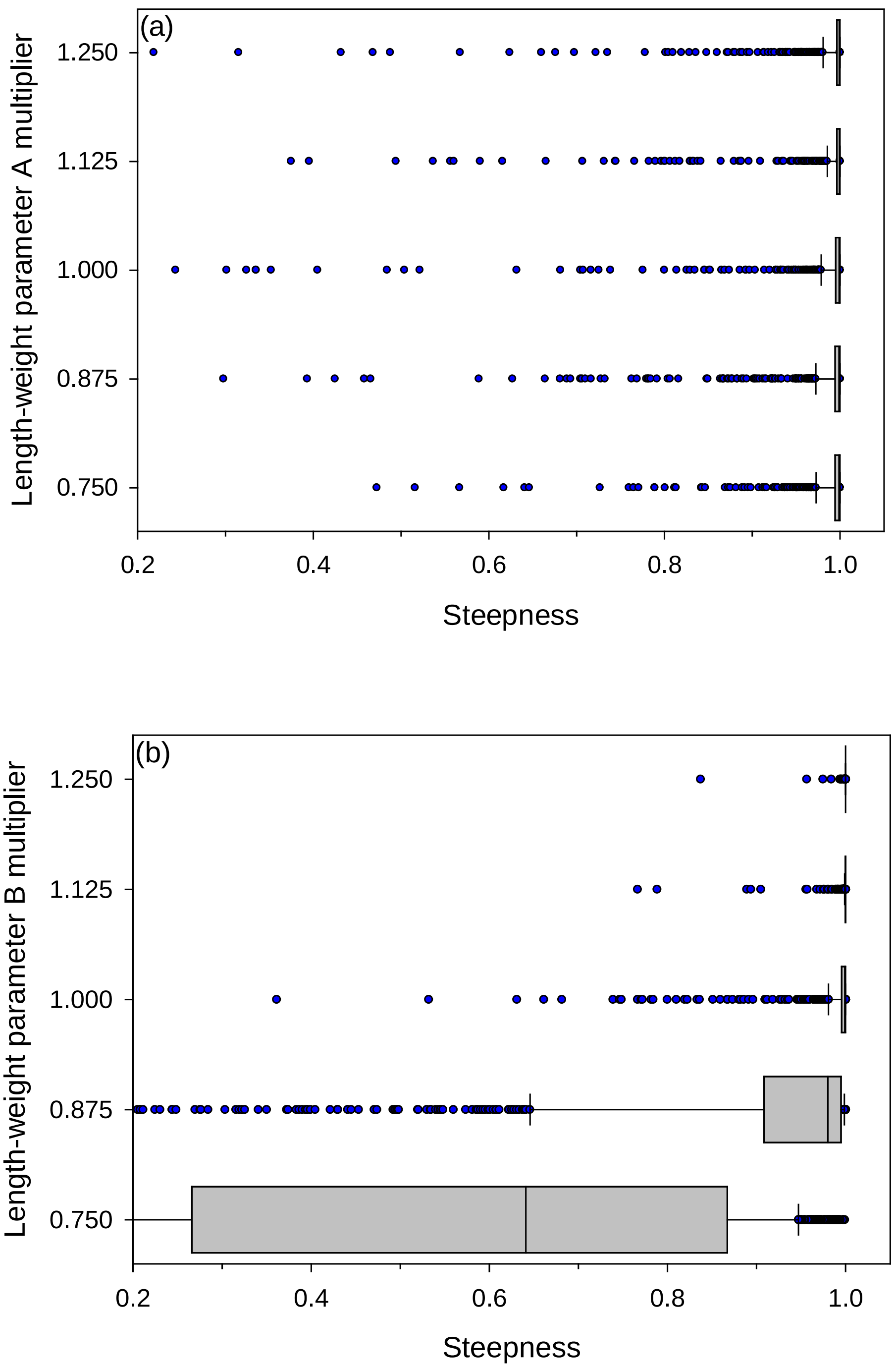

Figure 4. Sensitivity analyses showing boxplots for the effects of changes in length-weight parameters for (a) scale (A) and (b) exponent (B) on median steepness (solid line inside box), its interquartile range (bottom and top of the box), and its 10th and 90th percentiles (bottom and top whiskers).

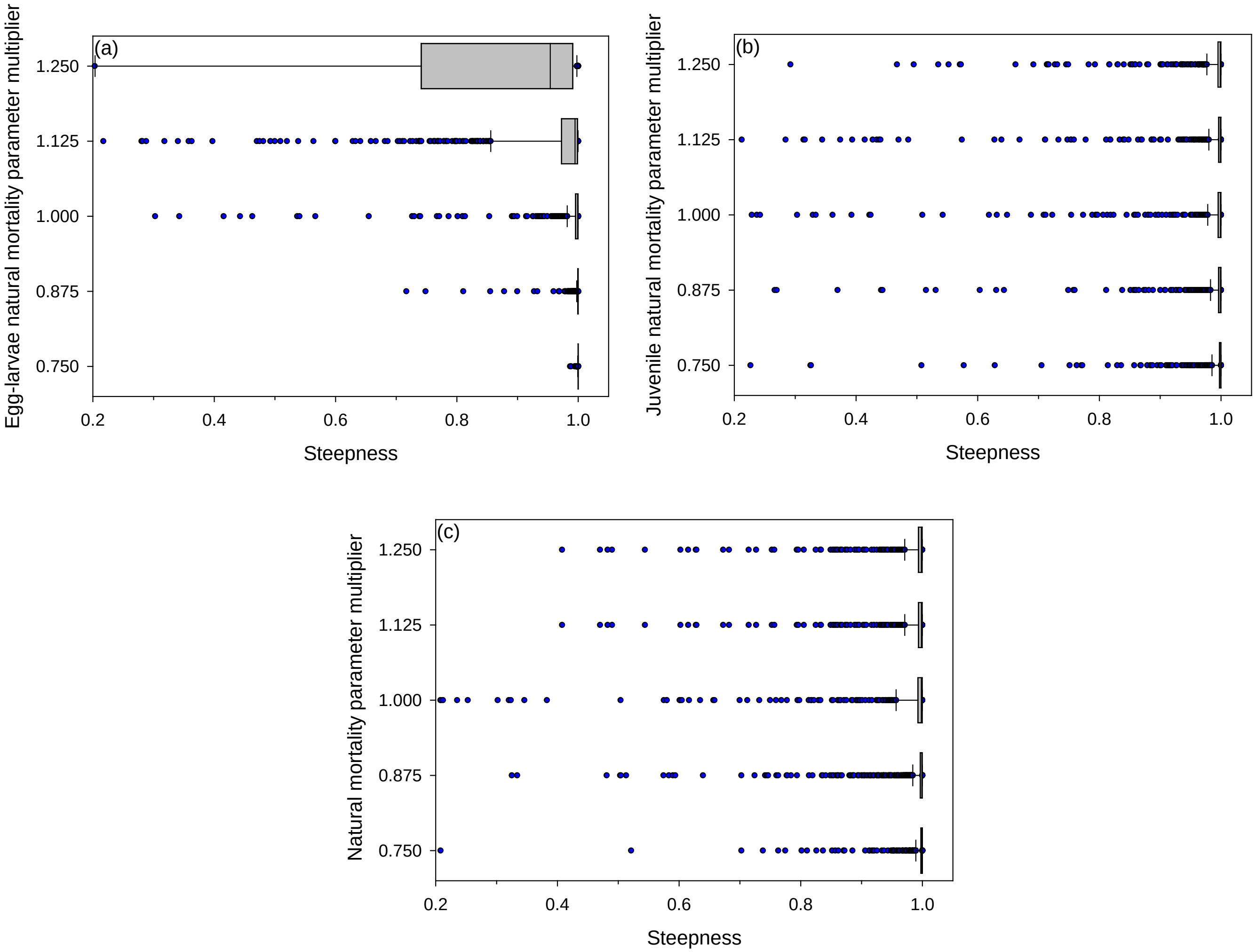

Figure 5. Sensitivity analyses showing boxplots for the effects of changes in the slope of the egg-larval natural mortality rate (a), the slope of the early life history juvenile natural mortality rate (b), and the natural mortality rate at age parameters (c), on median steepness (solid line inside box),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

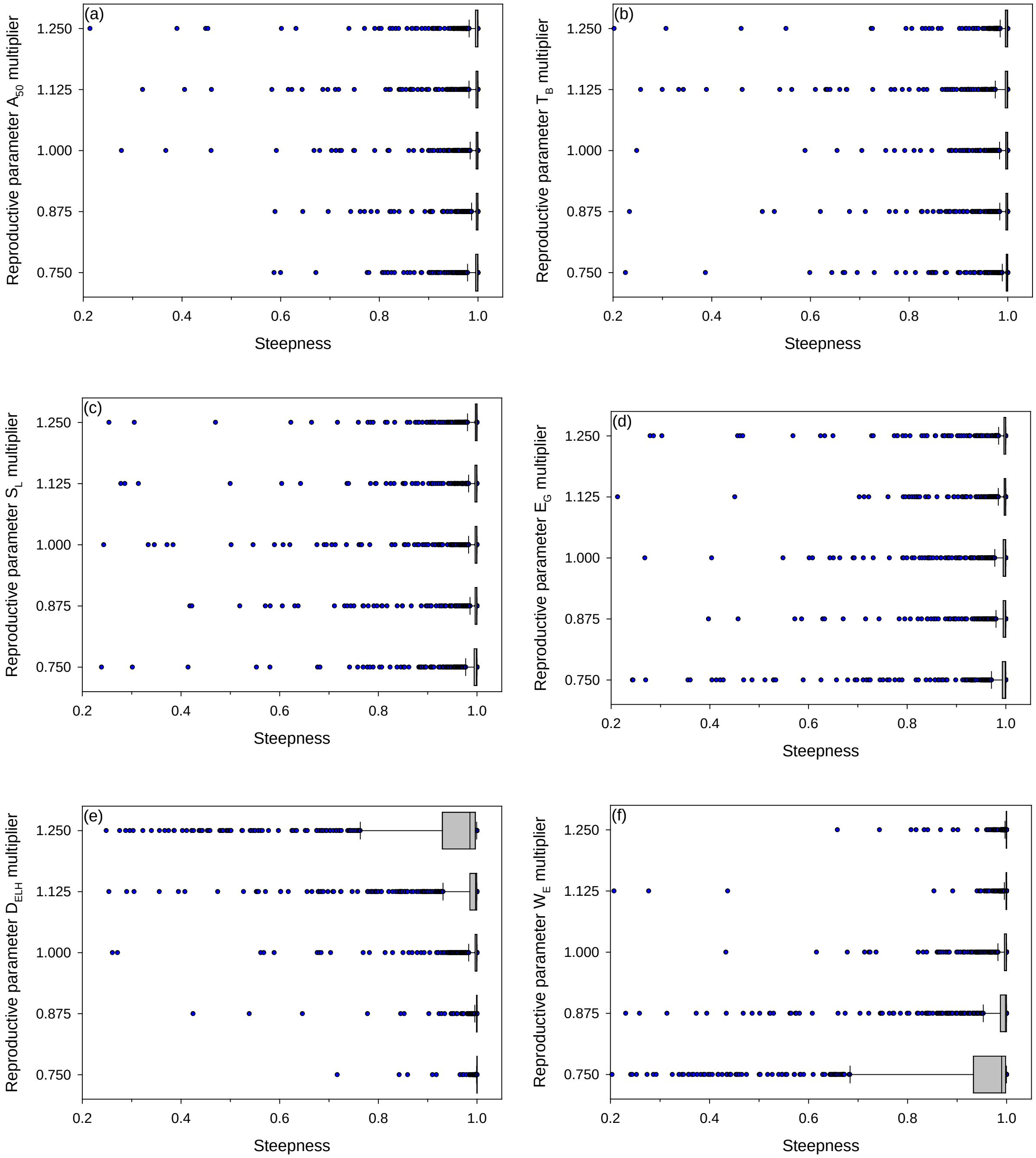

Figure 6. Sensitivity analyses showing boxplots for the effects of changes in reproductive ecology parameters on steepness for female age at 50% maturity (a), average time between spawning events (b), spawning season length (c), mean number of eggs per gram of body weight (d), early life history stage 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).

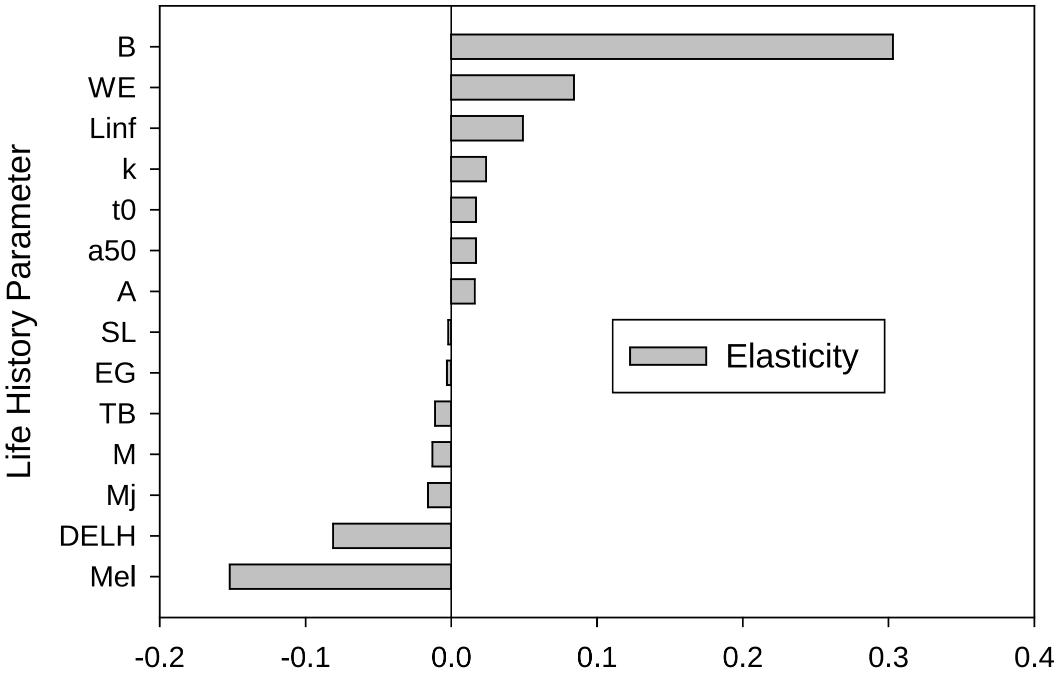

Figure 7. Comparison of the elasticity of steepness evaluated at the baseline parameter values with respect to the daily natural mortality rates of eggs and larval fish (M_{el}), the early life history stage duration (D_{ELH}), the mean number of eggs per gram of body weight (E_G), the Brody growth coefficient (k), the average time between spawning events (T_B), the daily natural mortality rates of juvenile early life history stage fish (M_{ej}), 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 median at maturity (A_{50}), the mean egg weight (W_E), and the length-weight exponent parameter (B).