AGE-STRUCTURED BIOMASS DYNAMICS OF NORTH ATLANTIC SHORTFIN MAKO WITH IMPLICATIONS FOR THE INTERPRETATION OF SURPLUS PRODUCTION MODELS

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SUMMARY

*The 2017 North Atlantic shortfin mako (*Isurus oxyrinchus*) assessment has resulted in a substantial negative shift in perception of the stock status and future projections, which we summarize here as the "The Good, the Bad and the Ugly". The existence of large mature sharks not caught in ICCAT fisheries has probably retarded the stock collapse ("The Good"). This biomass is as cryptic to the fishery as it is unobservable in the available abundance data ("The Bad"). By ignoring the strong lag effect between exploitable and reproductive biomass, earlier surplus production model assessments have probably contributed to a false perception about the long-term sustainably of the fishery. The inability to predict the long-term impact of unsustainable fishing over the last 30 years has likely created a "time bomb" scenario towards a collapse of the mature biomass ("The Ugly"). While it is probably too late to halt the collapse, rebuilding chances will depend on the time it takes to implement effective management interventions.*

RÉSUMÉ

*L'évaluation de 2017 du requin-taupe bleu de l'Atlantique Nord (*Isurus oxyrinchus*) a entraîné un changement négatif important dans la perception de l'état du stock et des projections futures, que nous résumons ici comme étant « le bon, la brute et le truand ». L'existence de grands requins matures non capturés dans les pêcheries de l'ICCAT a probablement retardé l'effondrement du stock (« le bon »). Cette biomasse est aussi cryptique pour la pêcherie qu'elle est non observable dans les données d'abondance disponibles (« la brute »). En ignorant le fort effet de décalage entre la biomasse exploitable et la biomasse reproductive, les précédentes évaluations du modèle de production excédentaire ont probablement contribué à une fausse perception de la durabilité à long terme de la pêche. L'incapacité à prévoir l'impact à long terme d'une pêche non durable au cours des 30 dernières années a probablement créé un scénario de « bombe à retardement » en vue de l'effondrement de la biomasse mature (« le truand »). S'il est probablement trop tard pour mettre fin à l'effondrement, les chances de rétablissement dépendront du temps nécessaire pour mettre en œuvre des interventions de gestion efficaces.*

RESUMEN

*La evaluación de 2017 del stock de marrajo dientuso del Atlántico norte (*Isurus oxyrinchus*) dio como resultado un importante cambio negativo en la percepción del estado del stock y las proyecciones futuras, que resumimos aquí como «el bueno, el feo y el malo». Probablemente, la existencia de grandes tiburones maduros no capturados en las pesquerías de ICCAT ha retardado el colapso del stock («el bueno»). Esta biomasa es tan críptica para la pesquería que es inobservable en los datos de abundancia disponibles («el malo»). Ignorando el fuerte efecto de desfase entre la biomasa explotable y la biomasa reproductiva, las anteriores evaluaciones del modelo de producción excedente han contribuido probablemente a contar con una falsa percepción acerca de la sostenibilidad a largo plazo de la pesquería. La incapacidad de predecir el impacto a largo plazo de una pesca insostenible durante los últimos 30 años ha creado, probablemente, un escenario de «bomba de relojería» hacia un colapso de la biomasa madura («el feo»). Aunque probablemente es demasiado tarde para detener el colapso, las opciones de recuperación dependerán del tiempo que lleve implementar intervenciones de ordenación eficaces.*

KEYWORDS

JABBA, Stock Synthesis, time-bomb, lag-effects, selectivity

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1. Introduction

The application of recent improvements in assessment methodology via the introduction of the State-Space Bayesian Production Models (SPMs), BSP2 (McAllister, 2014) and JABBA (Winker *et al*., 2018a), and of the integrated stock assessment framework Stock Synthesis (Methot and Wetzel, 2013), resulted in large, troublesome changes of the status and projections for shortfin mako (*Isurus oxyrinchus*) in the North Atlantic in 2017 (ICCAT, 2017). The 2017 pessimistic, results were in sharp contrast to the previous 2012 assessment results (ICCAT, 2013), when estimates from a deterministic Bayesian Surplus Production Model (BSP; McAllister and Babcock, 2006) indicated a healthy stock with a low probability that overfishing was occurring (Babcock and Cortes, 2009). The 2012 BSP assessment model was, however, unable to adequately fit the then "U-shaped" catch-per-unit-effort (CPUE) trend, which attained a minimum around the year 2000 and increased again until 2010, the terminal year assumed in the 2012 stock assessment (**Figure 1**). Since 2010, CPUE trends have been decreasing again (**Figure 2**). Continuity runs with the 2011 BSP model and newly developed model diagnostics for the shortfin mako shark Stock Synthesis (see Courtney *et al*., 2019 for details) showed that is not possible to adequately capture the trends in the updated CPUE indices through 2015 without accounting for process error.

Although the 2017 Bayesian State-Space Bayesian Production Model and Stock Synthesis assessment models were in agreement with regard to the stock status of the North Atlantic shortfin mako shark stock (ICCAT, 2017), concerns were raised about the comparability of those results due to major structural differences between SPMs and the integrated age-structured model Stock Synthesis.

SPMs are age-, size-, and sex-aggregated models that approximate changes in biomass as a function of the biomass of the preceding year, the surplus production in biomass and the removal by the fishery in the form of catch (in biomass). Therefore, SPMs are often referred to as Biomass Dynamics Models (Hilborn and Walters, 1992) to distinguish them from age-structured production models (ASPMs; Hilborn, 1990). Somatic growth, reproduction, natural mortality and associated density-dependent processes are inseparably captured in the surplus production function. The resulted surplus production function is then governed by: (i) the intrinsic rate of population increase r, (ii) the shape parameter m, and iii) virgin biomass K. The r is the slope of the function as biomass approaches zero, and m determines the biomass that produce Maximum Sustainable Yield (BMSY) at equilibrium relative to K (BMSY/K).

State-space SPMs are typically formulated in the form of a discrete process equation to model the aggregated, latent biomass. The process error can account for model structural uncertainty (Thorson *et al*., 2014) as well as natural variability of stock biomass due to stochasticity in recruitment, natural mortality, growth, and maturation (Meyer and Millar, 1999; Punt, 2003). The observation error determines the uncertainty in the observed abundance index due to measurement error, reporting error and other unaccounted variations in catchability (Francis, 2011; Francis *et al*., 2003). Ignoring the observation error easily leads to overfitting and loss of predictive power, whereas ignoring the process error can result in biased stock status estimates and typically poorly estimated precision (Ono *et al*., 2012; Punt, 2003; Thorson and Minto, 2015).

In contrast to SPMs, ASMs allow distinction between spawning-biomass (SSB) (in this case this term is misleading as shortfin mako is a viviparous species, but we keep it for consistency with common stock assessment terminology) and vulnerable biomass (VB), where SSB is the biomass fraction of mature fish (or females) in the population, and VB is the fraction of the total biomass that is vulnerable to the fishery. Modelling the population dynamics using ASMs allows accounting for important age-specific processes, such as size- (or age) dependent selectivity and lags between spawning (here: pupping) and the recruitment into the fishery. In ASMs, density-dependent processes are typically limited to a spawner-recruitment relationship (SRR), and natural mortality (M) is usually assumed to being age- and time invariant (Mangel *et al*., 2013; Thorson *et al*., 2012). Process error in ASMs is typically restricted to recruitment variation of age-0 fish (Thorson *et al*., 2019).

Conventional SPM formulations imply that the modelled biomass will follow the trend of the VB, which is typically assumed to be linear proportional to CPUE (Pedersen and Berg, 2017). Absolute estimates of SSB would therefore be comparable when the fishery selectivity curve is similar to the maturity ogive, so that VB ~ SSB. Increasing divergence between VB and SSB will not only affect the ratio of the absolute quantities of B to SSB, but can also result in B/BMSY being a biased estimator SSB/SSBMSY, because the increasing non-linearity between VB and SSB and associated lag effects can lead to severe distortions in the fitting process of SPMs (Winker *et al*., 2018b).

In this paper, we uncouple the underlying age-structured biomass dynamics from the 2017 Stock Synthesis base-case model (Run 3; Courtney *et al*., 2017; ICCAT, 2017) to explore potential caveats for fitting and interpreting results from SPMs. To do this, we conduct an experiment by fitting JABBA to the total biomass (Age-1+), spawning biomass (SSB, Age-22+) and age-specific biomass trajectories summed over the age groups, which we assess to a JABBA reference model fitted to the CPUE data. For ease of argumentation, we considered the current Stock Synthesis base-case model (Run 3) as the most plausible available hypothesis to describe the age-structured population dynamics of North Atlantic mako shark. We discuss similarities and differences between the JABBA reference model and Stock Synthesis base-case and highlight potential pitfalls for the interpretation of stock status results.

2. Uncoupling age-structured dynamics of the Stock Synthesis base-case model

2.1. Stock Synthesis quantities

To examine the age-structured biomass dynamics of the current Stock Synthesis base-case model, we first extracted a variety of estimated quantities from the Stock Synthesis 'report.sso' file, using the R package 'r4ss'. The extracted data included: (1) CPUE fits by fleet (numbers), (2) age-selectivity by fleet, (3) total catch by fleet, (4) total biomass (age1+), (5) spawning stock fecundity (SSF; in numbers), (6) sex-specific biomass-at-age,(7) sex-specific somatic weight-age, and (8) the estimated recruitment deviations. Age-specific biomass trajectories summed over the age groups from between age-3 and age-10 to age-31+ (plus group) were calculated as the products of

$$B_A = \sum_s \sum_a N_{a,s} w_{a,s}$$

where B_A is the biomass for age groups A, $N_{a,s}$ is number-at-age for age a and sex s and $w_{a,s}$ is the corresponding somatic weight-at-age for sex s. Spawning biomass is calculated as the biomass of females that are 22 years or older (Courtney *et al*. 2017), assuming knife-edge maturity at age-22.

2.2. Driving factors for age-specific biomass dynamics of shortfin mako

The fitted CPUE values (in numbers) show a down-up-down trend with fairly little variation across fleets (**Figure 1**), except for small distortions among aligned indices due to differences in the expected fleet specific selectivity-at-age (**Figure 2**). It can be readily seen that most fleets predominantly catch sub-adults between age-3 and ages of ~ 10-15 years old (**Figure 2**). In Stock Synthesis, fishing mortality is standardized as Fstd = Catch/Bref, where Bref is taken here to correspond to the total biomass (age-1+). Age-specific fishing mortality is strongly influenced by the estimated by steep dome-shaped EU-LL fleet selectivity, which has been responsible for 50%-90% of the annual reported catches since 1990 (**Figure 3**). As a result of the dome-shaped selectivity pattern, VB and SBB are largely disconnected. Once mature, the large, old mature females experience very little risk of being caught and form a mostly 'cryptic' SSB that is essentially 'unobservable' in the CPUE and size composition data. The lag between full vulnerability to the fishery and attaining maturity is about 8-13 years (**Figure 2**).

Another critical component for understanding the biomass dynamics of shortfin mako is recruitment variation, because this is the only source of process error in the Stock Synthesis model to induce divergence in biomass from its deterministic expectation (**Figure 4**). Due to the absence of size information in earlier years, recruitment deviates are only estimated from 1985 onward, so that the early population dynamics are modelled deterministically. The estimated recruitment deviations (1985-2014) are non-random and show a systematic trend, as judged by the significance of a Runs test (Courtney *et al*., 2019). The years 1994-1996 and 2003-2005 demarcate extreme low and high recruitment events, respectively, which fall outside the range of the 3-sigma limits (Anhøj and Olesen, 2014).

The estimated biomass time trends show strong contrasts both in magnitude and direction (**Figure 5**). The unfished female SSB0 represents about 15% of the unfished total biomass. The ratios of SSF/SSF0 (in numbers) and SSB/SSB0 (in weight) showed very similar trends. In contrast to a logistic selectivity pattern, the combination of dome-shape selectivity and very late maturation causes hyperstability in SSB when compared to the total biomass in response to fishing pressure. On closer inspection, the plus group (Age-31+) accounts for 50% of SSB0 and over 70% of SSB2015. This means that most of the remaining SSF relies on females born before 1985 and thus before the sharp increase in fishing mortality caused mainly by the EU-LL fleet.

Importantly, the strong recruitment signal (**Figure 4**) is neither discernible in the total biomass trend nor in the SSB trend. Winker (2018) demonstrated that longevity and fishing mortality are key drivers of process variation in biomass, where long life spans and low fishing mortality are predictably associated with very small process variation in the biomass. On the other hand, high fishing mortality increasingly truncates the age-structure, which results in the loss of the 'buffering' effect and leads to a more pronounced variation in biomass as individual age-classes passing through the population. **Figure 5** demonstrates a similar amplification in the recruitment signal in VB with increasing truncation of the underlying age-structure comprised of fewer age groups due to the shape of the selectivity function. Therefore, dome-shaped selectivity plays a pivotal role in the Stock Synthesis base-case model to propagate the recruitment variation into process variation of the VB. This in turn allows fitting the observed trends in CPUE, which is not possible otherwise within plausible biological limits of shortfin mako.

3. A surplus production model (SPM) perspective

3.1 JABBA reference model

A closer inspection of the JABBA runs from the 2017 North Atlantic shortfin mako assessment in comparison to Stock Synthesis base-case (ICCAT, 2017) revealed a number of differences in some of the general model specifications. We addressed those by revising the JABBA reference case to improve comparability with the Stock Synthesis base-case as follows:

(1) Instead of initiating the process error on the first year of the stock assessment model, process deviations were only estimated for the years of 1985-2015. These are the same years in which recruitment deviations were estimated in the Stock Synthesis model.

(2) For Stock Synthesis, initial biomass was assumed to be equal to the unfished equilibrium. By contrast, the 2017 JABBA runs admitted uncertainty about the initial biomass depletion in 1950 by using an informative lognormal prior for B2015/B0 with a mean of log(1) and a CV of 25% . For more direct comparison, we reduced the CV to 3%.

(3) A CV of 30% was assumed for all CPUE indices, without estimating any additional observation variance within JABBA (for details of variance estimation options see Winker *et al*. 2018a).

(4) In the 2017 JABBA model, there were two alternative shape parameters for the surplus production considered, which are formulated in JABBA as a function of BMSY/ B0 (B0 = K): (i) a Schaefer model with BMSY/ B0 = 0.5 and (ii) a Pella-Tomlinson formulation BMSY/ B0 = 0.66. Here, those scenarios were replaced into a single reference case for BMSY/ B0 = 0.54, which corresponds to the inflection point of the equilibrium yield curve of the Stock Synthesis base-case run (**Figure 6**).

No changes were made for r prior (r ~ LN(0.024 , 0.47), based on r = 0.01-0.66) and the input data series of catch and CPUE compared to the 2017 JABBA shortfin mako models. The JABBA fits and model diagnostics for this study's revised JABBA reference case are provided in **Appendix I.**

3.2 Surplus production model experiment

To explore the impacts of varying the age composition of the VB from a surplus production modelling perspective, we conduct an experiments by fitting JABBA to the total biomass (age-1+), spawning biomass (SSB, Age-22+) and age-specific biomass trajectories summed over the age groups as shown in **Figure 5**, which we assess to a JABBA reference model fitted to the CPUE data. We assume that all biomass indices are known without error and estimate r with minimal prior information using a flat lognormal prior.

The predicted biomass trends shown as B/B0 closely resemble the corresponding Stock Synthesis outputs (**Figure 7**). For the final year 2015, the JABBA reference case and the SSB fit produce very similar biomass depletion levels, and only slightly more optimistic estimates compared to the total biomass. Retrospectively, major differences in B/B0 become apparent (**Figure 7**). For example, in 2000 the estimated B/B0 differed between 0.8 for SSB and around 0.4 for the JABBA reference case, whereas by 2010 the JABBA reference case shows the most optimistic B/B0.

The estimated process error deviations on log(B) amplify with increasing age-truncation of the fished fraction of VB (**Figure 7**). Here, the reference case and the fits to VB for age-classes between age-3 and up to age-10 to age-13 produce similar trends. Fitting the total biomass requires the least process variance; whereas fitting JABBA to the “known” SSB required consecutive positive process error deviates over the period 1985-2000. The large process error from the SSB fit can be interpreted as direct consequence of conflict between the SPM process equation and underlying population dynamics of the Stock Synthesis base-case. The expectation of SPMs is that biomass is a function of surplus production in biomass and the subtracted catch. The age-structured population dynamics of mako shark imply, however, that the removal catch by the fishery will impact the reproductive potential ten years, and more, later. The inability to account for this extreme lag between fishing impact and response in SSF is therefore partially compensated by process error.

The second mechanism to compensate for the lagged response in SSF to increased fishing pressure when fitting SPMs is through overestimating the stock’s productivity in the form r (**Figure 8**). At the other end of the spectrum, fitting total biomass results in a very low r estimate, which may be an underestimate because the SPM cannot account for the reduced fishing mortality on the mostly ‘cryptic’ SSF. Reducing the number of age-classes in the VB produced fits with sequentially higher r. A worrisome consequence is that this also resulted in surplus production, and thus MSY, becoming increasingly overestimated relative to the Stock Synthesis base-case estimate (**Figure 8**). For example, fitting JABBA to a “known” VB that comprised age-classes 3-10 (c.f. **Figure 2**) produced an MSY that exceeded the Stock Synthesis base-case estimate by 350% (**Figure 8**). The JABBA reference case produced a reasonably similar MSY estimate to the Stock Synthesis base-case. Inference about the stock status would lead to comparable classification about the stock status in 2015 between the JABBA reference case and Stock Synthesis base-case model (**Figure 9**). However, we suspect that controlling r by way of an informative prior may have helped counter-balancing the age-truncation in the VB as driver to towards higher productivity in the fitting process (**Figure 8**).

Such biased productivity estimates would have severe implications for inference on stock status, future projections, and ultimately management advice (**Figure 10**). Yet, any SPM-based projections are expected to be fundamentally over-optimistic relative to the Stock Synthesis base-case (Courtney and Rice, 2019). This is because the extreme lag effect between the exploited and reproductive portions of the stock would cause, even under zero fishing, the mature biomass (i.e. SSF) to decline further in years to come as result of severe overfishing of sub-adults over the last two decades.

4. Discussion

In this paper, we have highlighted the key drivers of the biomass dynamics of North Atlantic shortfin mako based on the current Stock Synthesis base-case model. The fishery represents a special case, signified by an extreme lag between the exploitable and reproductive component of a long lived species with low fecundity. As a result of steep dome-shaped selectivity, fisheries mortality predominantly impacts on the sub-adults, but is expected to be relatively low on the mostly cryptic mature females. A secondary effect of the dome-shape selectivity is that it propagates the stochastic recruitment variation into the VB and thus the observed CPUE trends. The underlying mechanism is the strong truncation of the age-structure within exploited part of the biomass, which results in an increased “reactiveness” of the CPUE. Only the combination of systematic variations in recruitment in combination with dome-shaped selectivity makes it possible to fit the pertinent “down-up-down” trend in the observed CPUE series reasonably well, and within plausible biological limits of the shortfin mako Stock Synthesis base-case model.

The consequences of these dynamics have created a new paradigm for the North Atlantic shortfin mako, which could be summarized as: “The Good, the Bad and the Ugly”. The existence of large mature sharks not caught in ICCAT fisheries has probably retarded the stock collapse (“The Good”). This biomass is as cryptic to the fishery as it is unobservable in the available abundance data (“The Bad”). By ignoring the strong lag effect between exploitable and reproductive biomass, earlier surplus production model assessments have probably contributed to a false perception about the long-term sustainably of the fishery, but even the 2017 state-space implementations with informed prior remain at high risk to overestimating the rebuilding potential. The inability to predict the long-term impact of unsustainable fishing over the last 30 years has likely created a “time bomb” scenario towards a collapse of the mature biomass (“The Ugly”). While it is probably too late to halt the collapse, rebuilding chances will depend on the time it takes to implement effective management interventions.

From a technical point of view, we suggest that continuity runs with JABBA and BSP2, as they can be a useful tool to track the rebuilding of sub-adult biomass in response to potential intervention measure. However, for this rather special case of the North Atlantic shortfin mako fishery, we advise against the using SPMs for stock status determination and future projections.

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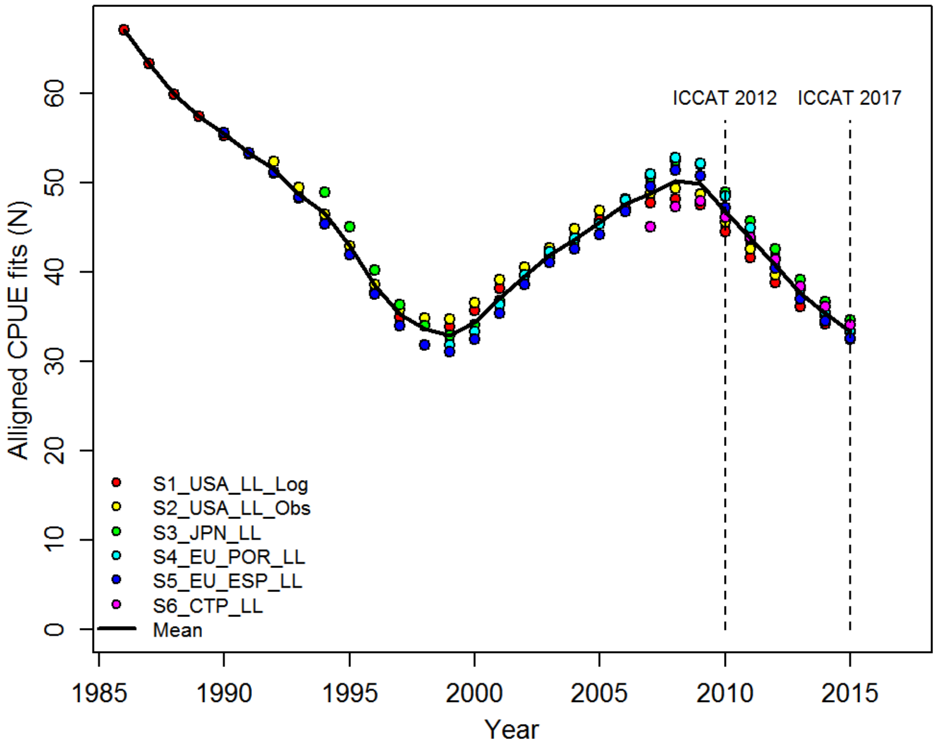

Figure 1. Fitted values for standardized CPUE indices (in numbers) for six longline fleets from the 2017 Stock Synthesis base-case model.

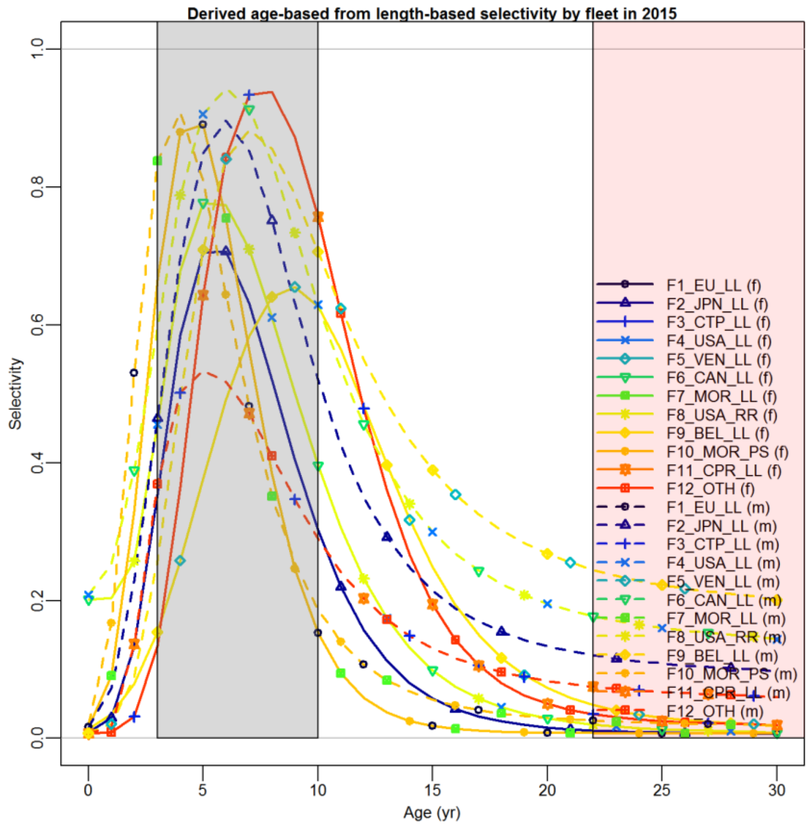

Figure 2. Estimated sex- and fleet-specific selectivity-at-age of North Atlantic shortfin mako shark from the stock synthesis base-base model.

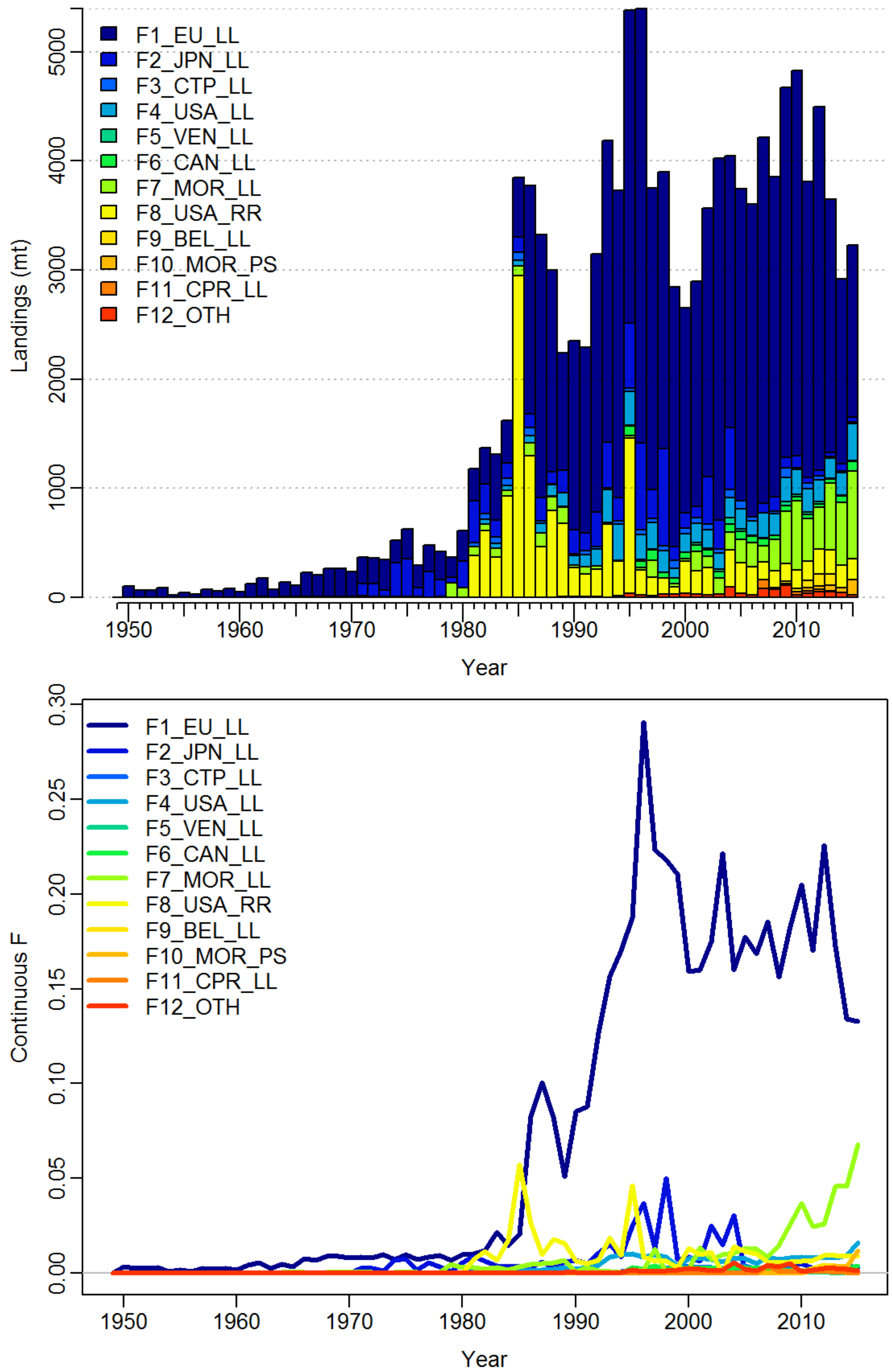

Figure 3. Total catch time series (mt) and estimated fishing mortality by fleet (1950-2015) from the Stock Synthesis base-case model for North Atlantic shortfin mako shark.

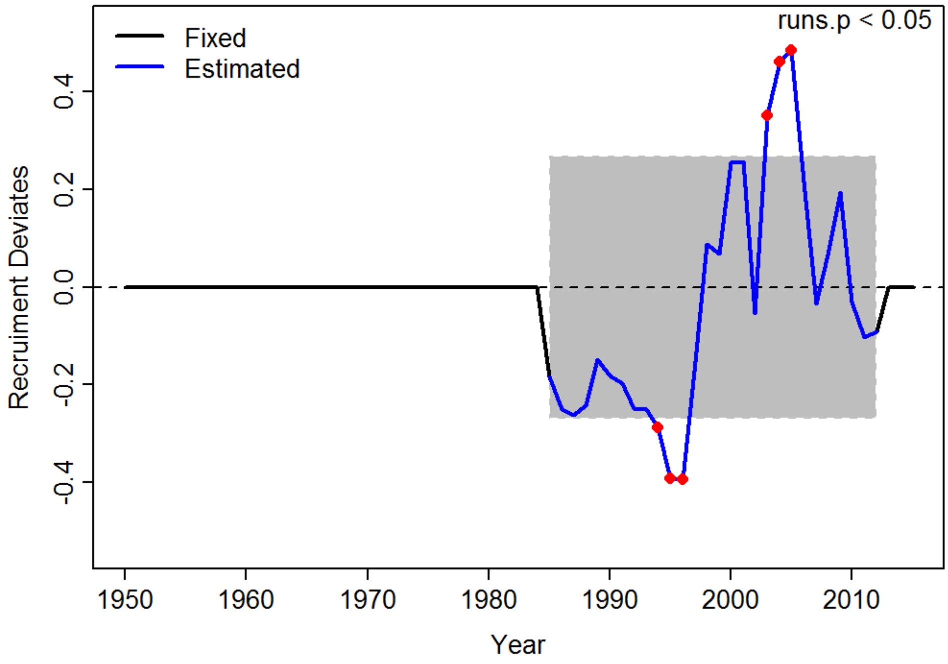

Figure 4. Estimated recruitment deviations for Stock Synthesis base-case model. Grey shaded area represents the 3-sigma limits of the residual time series, while the red circles denote recruitment deviations that fell outside this range. A runs test rejected the hypothesis of randomly distributed estimated recruitment deviations (runs.p < 0.05).

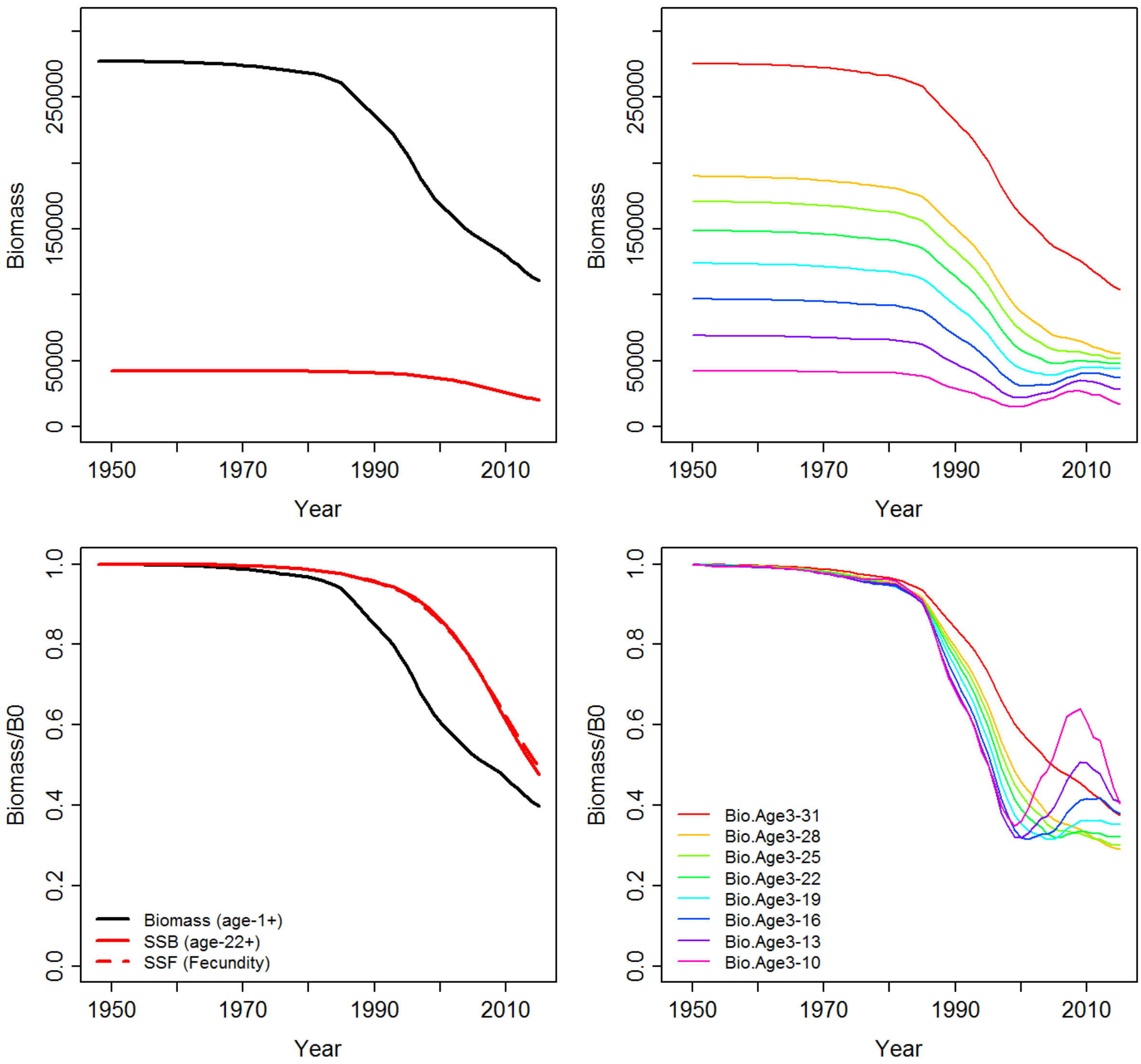

Figure 5. Absolute (top) and relative (bottom) trajectories for total biomass (age-1+), Spawning Stock Biomass (SSB), Spawning Stock Fecundity numbers (SSF) (left), and biomass summed for the age groups between age-3 to age-10 and age-3 to age-31, age-31 representing the plus group (right).

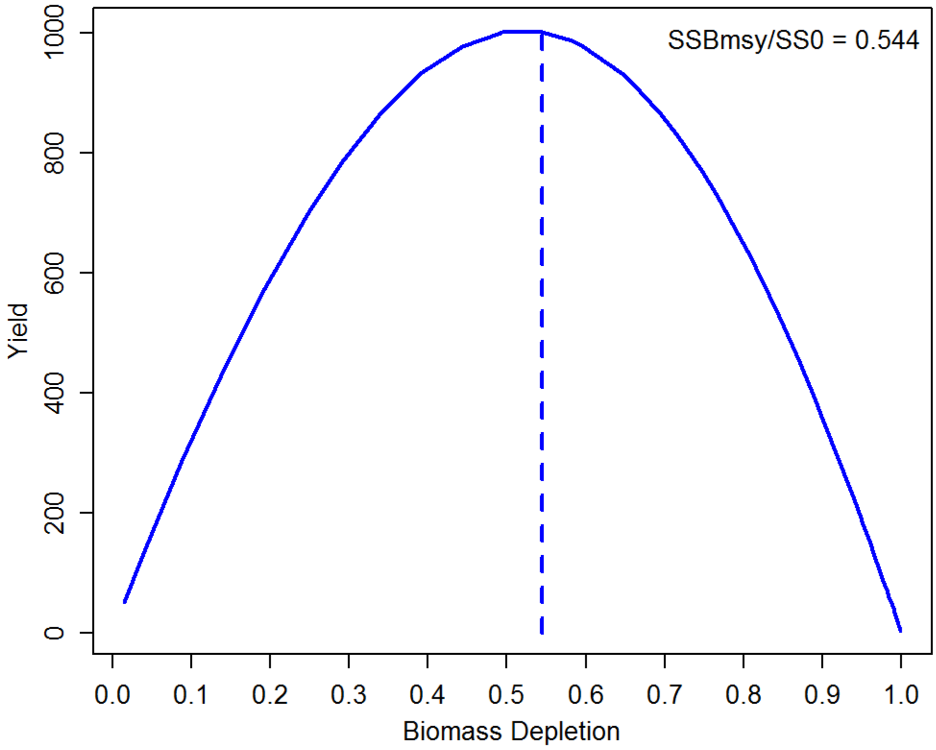

Figure 6. Equilibrium surplus production curve for the Stock Synthesis base-case, showing the equilibrium yield (Surplus Production) as a function of Biomass depletion, with the inflection point considered here as a proxy for BMSY/K in the JABBA model. Note that biomass depletion is expressed in the North Atlantic shortfin mako shark modelling units of SSF/SSF0.

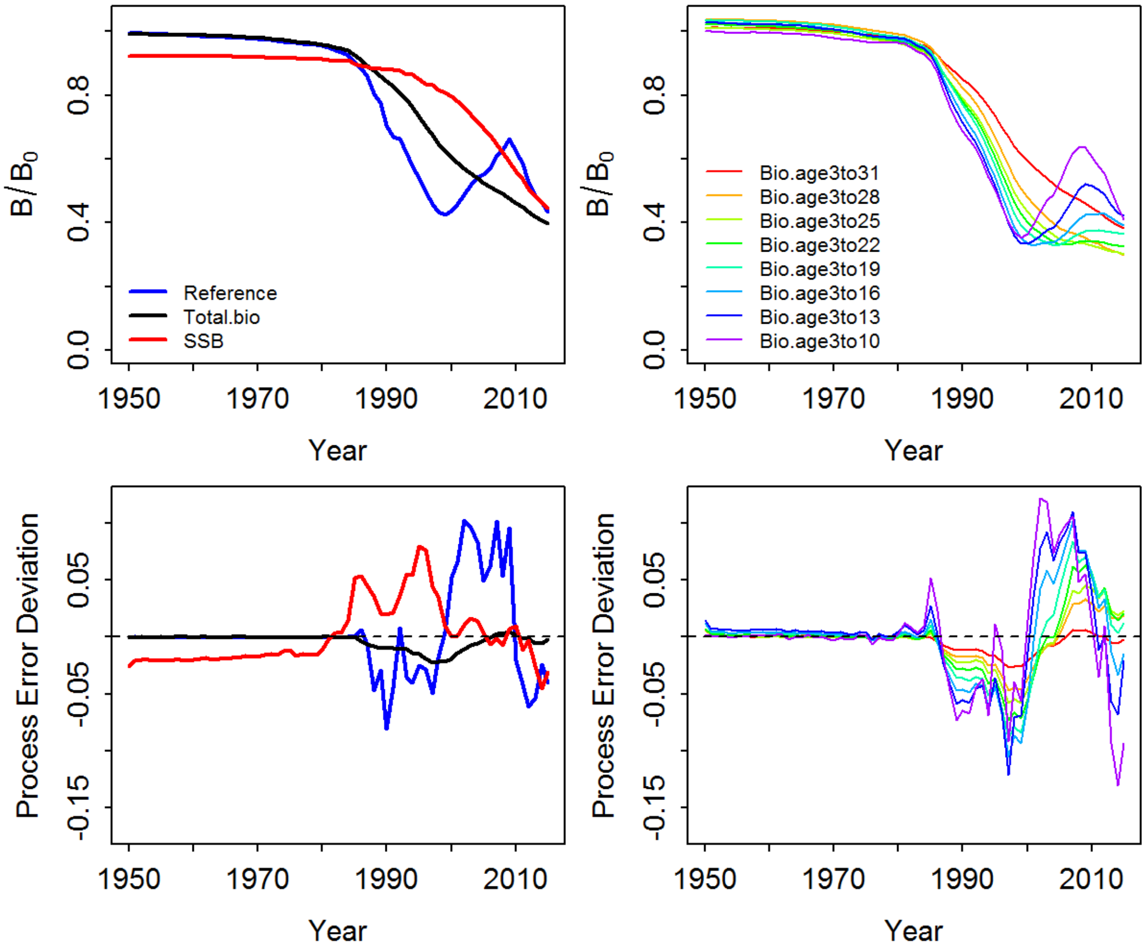

Figure 7. Predicted biomass trajectories of B/B0 and process error deviations of log(Biomass) for the JABBA reference case and JABBA fits to the total biomass (age-1+), spawning biomass (SSB, Age-22+) (left) and biomass summed for the age groups age-3 to age-10 and age-3 to age-31 (right).

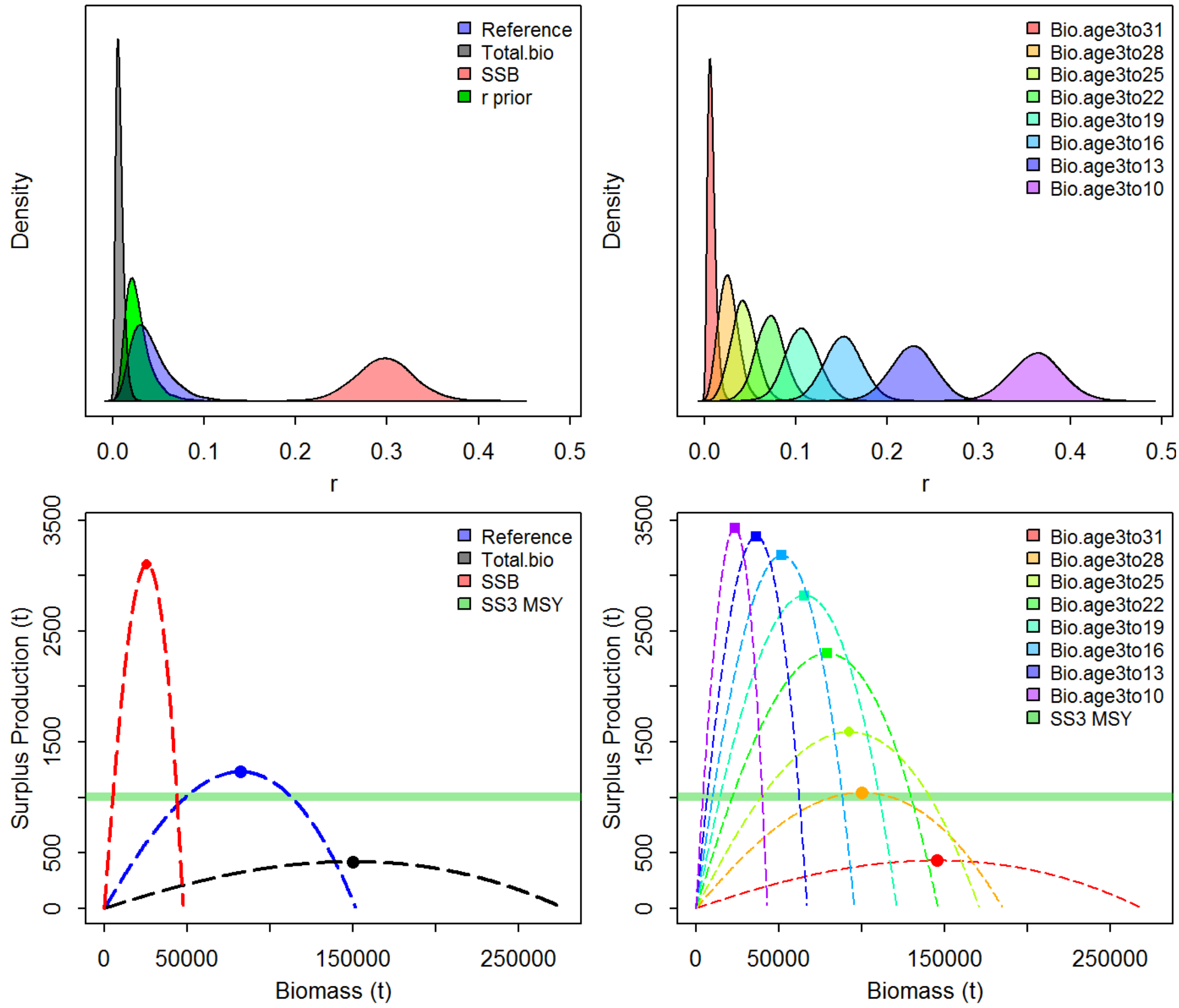

Figure 8. Posterior distributions of r (upper panel). Surplus production functions for the JABBA reference case and JABBA fits to the total biomass (age-1+), and spawning biomass (SSB, Age-22+) (Bottom panel left). Biomass summed for the age groups between age-3 to age-10 and age-3 to age-31 (Bottom panel right). The green horizontal line in the bottom panels denotes the MSY from the Stock Synthesis base-case model.

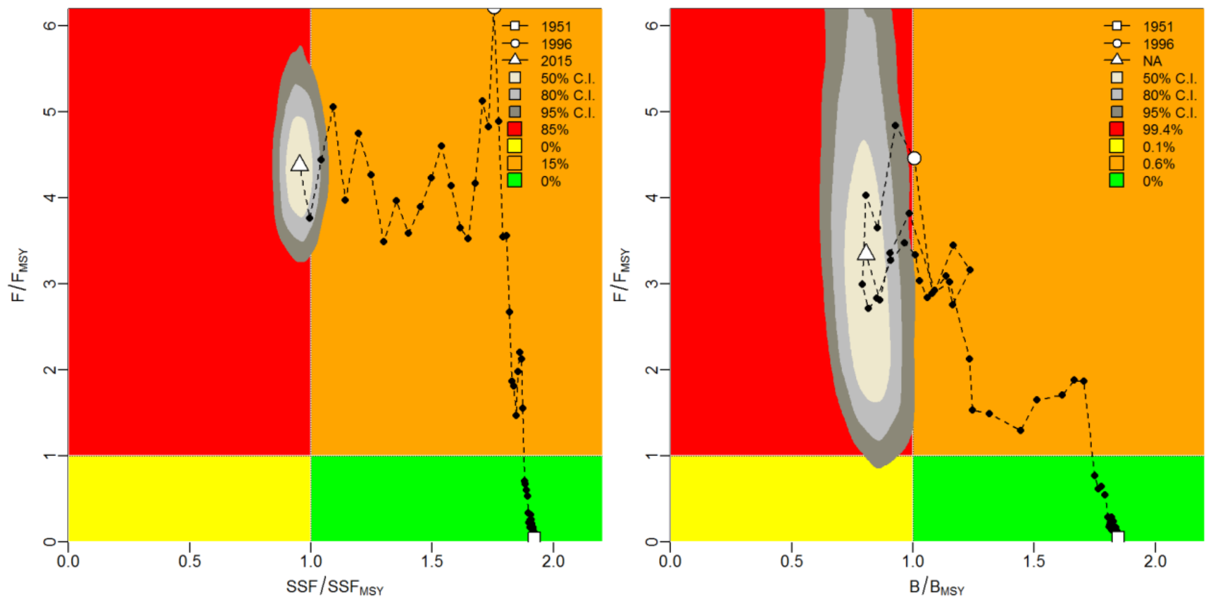

Figure 9. Kobe probability density distributions from the Stock Synthesis base-case and the JABBA reference case run.

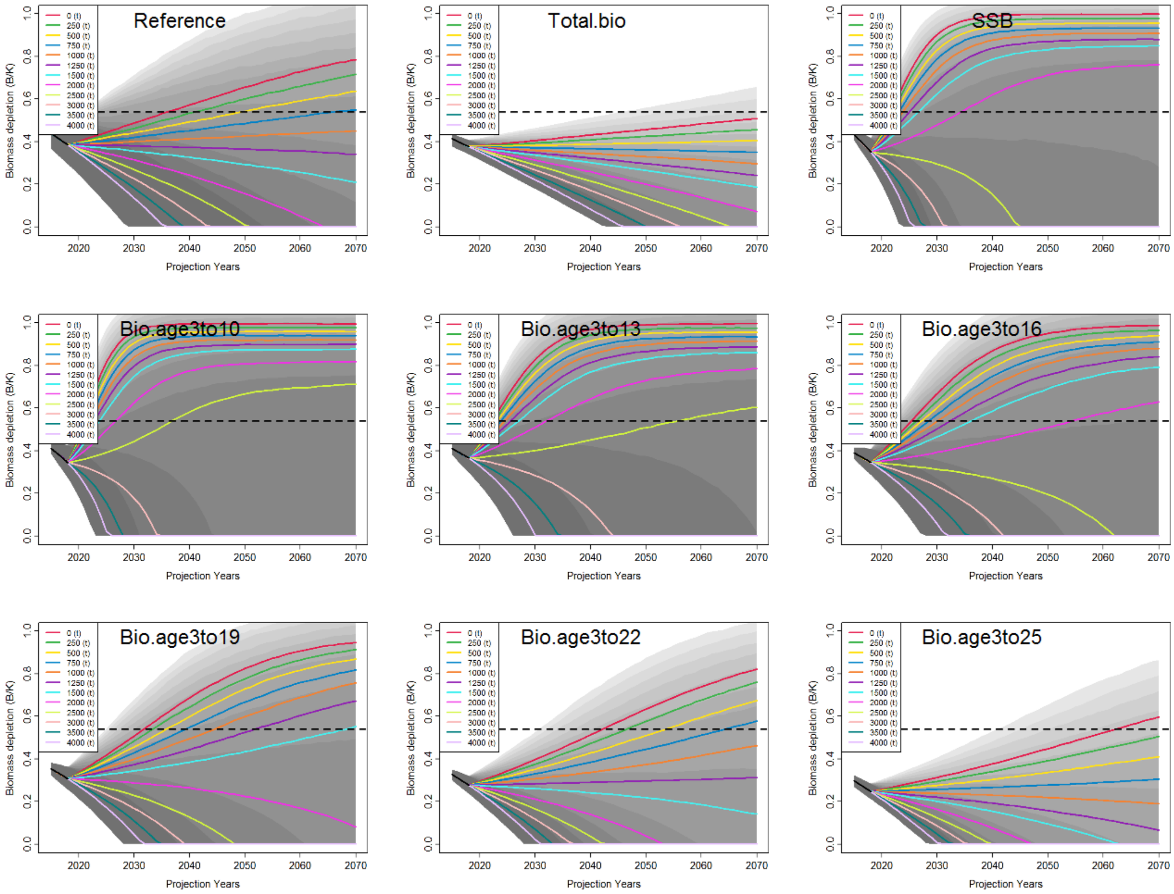

Figure 10. Future projection of B/B0 until 2070 over a range of catch quotas (0 – 4000 mt) for the JABBA reference case and JABBA fits to the total biomass (age-1+), spawning biomass (SSB, Age-22+) and biomass summed for the age groups between age-3 to age-10 and age-3 to age-31.

Table 1. Summary of posterior quantiles of parameters for the Bayesian state-space surplus production models for JABBA reference case run for North Atlantic shortfin mako shark.

Estimates	Median	2.50%	97.50%
K (t)	153027	117820	219953
r	0.036	0.014	0.08
y (psi)	0.998	0.962	1.037
σ_{proc}	0.045	0.045	0.045
m	2.463	2.463	2.463
F_{MSY}	0.014	0.006	0.033
B_{MSY} (t)	82640	63627	118783
MSY (t)	1211	494	2483
B_{1959}/K	0.998	0.958	1.041
B_{2017}/K	0.435	0.358	0.513
$B_{2017}/B_{\mathrm{MSY}}$	0.806	0.664	0.951
$F_{2017}/F_{\mathrm{MSY}}$	3.343	1.554	8.25

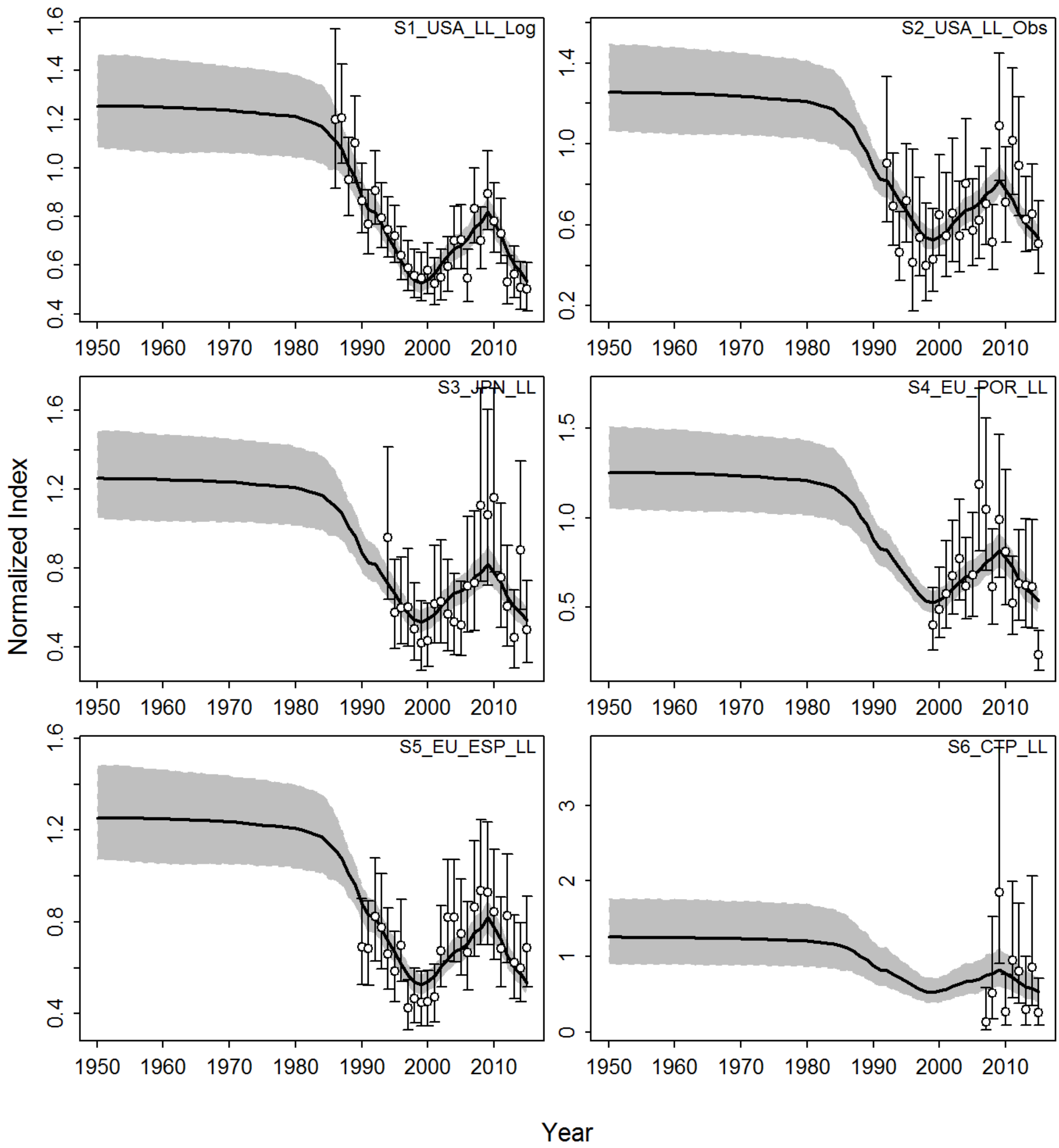

Figure A1. JABBA fits to six standardized CPUE longline indices for JABBA reference case, shown over the entire time series. The solid black line is the model predicted value and the circles are observed data values. Grey shaded area is the estimated 95% confidence intervals, error bars denote the assumed observation variance (in 95% CIs) for the observed CPUE values.

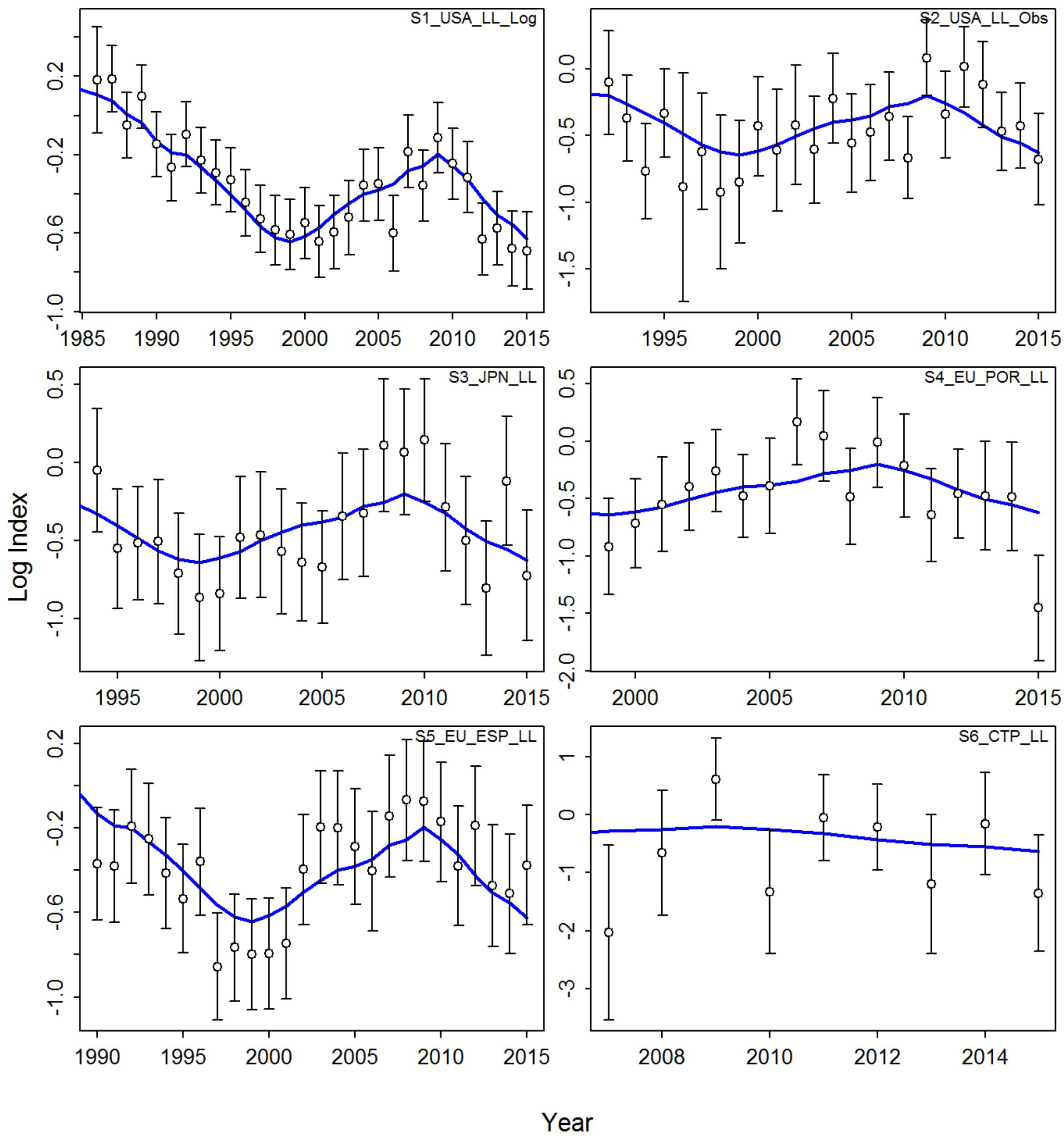

Figure A2. JABBA fits (on log-scale) to six standardized CPUE longline indices for JABBA reference case. The solid blue line is the model predicted CPUE and the circles are observed CPUE values. Error bars denote the assumed observation variance (in 95% CIs) for the observed CPUE values.

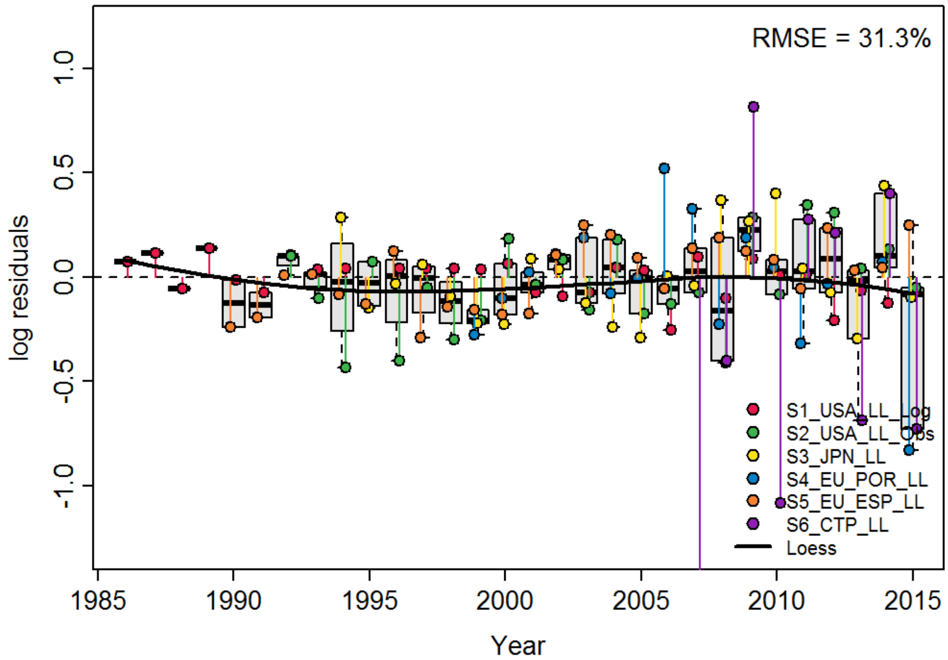

Figure A3. JABBA residual plot for the JABBA reference for North Atlantic shortfin mako shark showing boxplots of combined color-coded residual and a loess smoother fitted through all residual (black line).

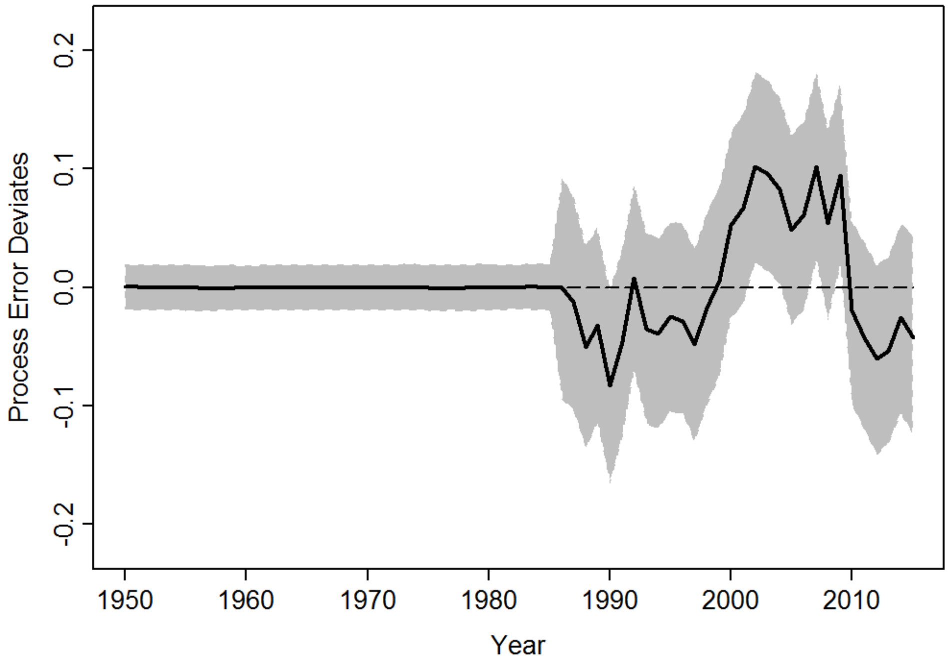

Figure A4. Biomass process error deviates on log-scale for the JABBA reference case for North Atlantic shortfin mako shark.

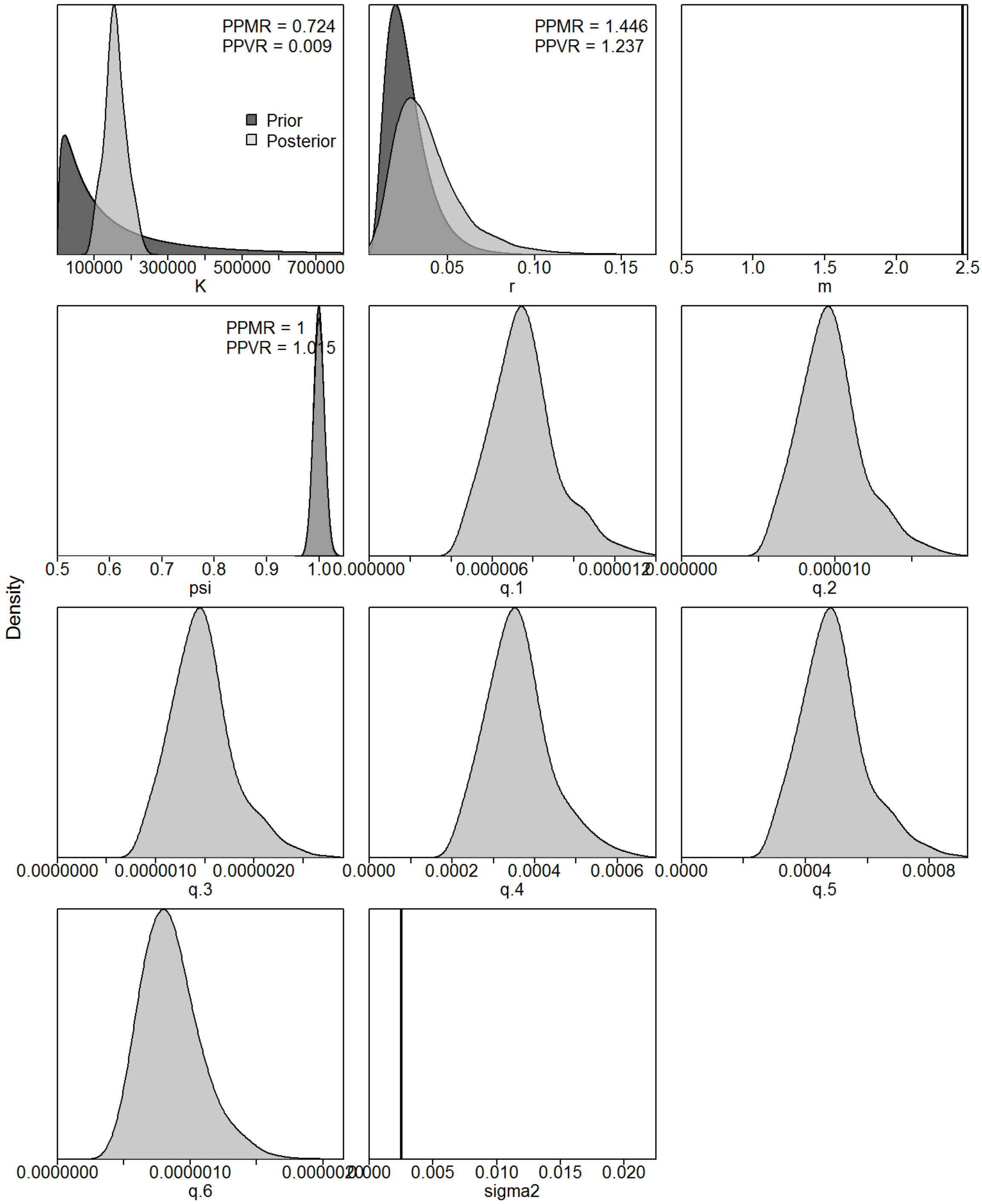

Figure A5. Posterior and prior distributions for all parameters estimated by JABBA reference model fitted to catch and abundance data for North Atlantic shortfin mako shark. PPRM: Posterior to Prior Ratio of Means; PPRV: Posterior to Prior Ratio of Variances.