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Reference Points for Eastern Georges Bank Atlantic Cod

AM Cook, D Hardie, AJF Gibson

Fisheries and Oceans Canada
1 Challenger Drive
Dartmouth, Nova Scotia, B2Y4A2
Canada

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Abstract

3 A VPA model (VPA.8) that incorporates recent increasing natural mortality (M) with age is currently
used to provide stock assessment advice for Eastern Georges Bank cod. This model sets M at 0.2
for all ages except for ages 6+ beginning in 1994 for which M is 0.8. In the past, a loess smoothed
6 stock recruitment relationship (SR) in the Sissenwine-Shepard production model yielded F_{msy}
 $=0.125$, but $F_{90\%FMSY}=0.11$ was chosen as F_{ref} due to uncertainty around the SRR and the high M.
We use the VPA output from the VPA.8 model to estimate several F_{refs} by applying yield per recruit,
9 spawner per recruit and producton models in a Sissensine-Shepard approach using a number of
SR fits, and use profile likelihoods to assess plausibility of F_{msy} reference points. There was
considerable uncertainty in the maximum likelihood point estimates for the SR and F_{refs} . A decision
12 theoretic approach was used to estimate F_{refs} by maximising the expectation of catch by integrating
across the likelihood surface of the SR parameters. Attempts to model the SR in ways that reflect
apparent productivity changes did not improve the ability to predict productivity, so the full time
15 series of data is considered for defining F_{refs} . $F_{maxE(C)}$, or the F that maximises the expectation of
catch, which is thought to be less variable and to lessen the risk of overexploitation relative to F_{msy} ,
was 0.097 (~0.1), and is proposed as F_{ref} for Eastern Georges Bank cod.

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INTRODUCTION

3 Limit reference points consistent with the Precautionary Approach (PA) were developed for NAFO
Division 5Zjm at a zonal science advisory process in 2010. A limit reference point (LRP) based on
6 a Beverton-Holt (BH) stock-recruitment (SRR) model was calculated as $B_{lim} = 21,000t$. At the time,
spawning stock biomass (SSB) was estimated to have been below the limit reference point (LRP)
9 since 1994 and was 9,260 t (Clark et al. 2011). Although recruitment had been consistently low
since 1993, there was no evidence to suggest that recruitment could not return to higher levels with
higher biomass and that there had been an irreversible change in productivity, so the full (1978-
2009) time series of recruitment data was used.

12 Since that time, various assessment formulations have been used to provide stock assessment
advice for Eastern Georges Bank (EGB) cod. At the 2013 Benchmark Meeting for this stock it was
15 agreed that high total mortality (Z) for ages 6+ relative to ages 4-5, coupled with declining relative
exploitation (catch/survey), implied the natural mortality had increased since the mid-1990s and that
natural mortality (M) was higher for ages 6+ (REF Benchmark proceedings). This recognition led to
18 the acceptance of the "M 0.8" VPA model (herein VPA.8), which sets M at 0.2 for all ages in all
years except for ages 6+ beginning in 1994 which have M set to 0.8 (Wang and O'Brien, 2013). At
this time a loess smoother was fitted to the data to describe the SRR, as has been done for EGB
haddock (Wang and Van Eeckhaute 2012).

21 The estimation of a fishing mortality reference point (F_{ref}) in this situation of increasing M was
identified as problematic. Broadly, under a yield-per-recruit (YPR) approach, F_{ref} will increase with
24 higher M, to catch the cod before they die, while under a maximum sustainable yield (MSY)
approach, F_{ref} would decrease to offset the increase in M (Legault and Palmer, 2013). The F_{ref} for
EGB cod, previously negotiated at 0.18 (an F_{msy} proxy $F_{40\%} = 0.18$) based on VPA with $M=0.2$. This
27 F_{ref} was suggested to be inconsistent with the VPA.8 model, and a lower F_{ref} was recommended
(TRAC, 2013).

30 The VPA.8 model run for 2013 yielded $F_{0.1}$ and $F_{40\%}$ of 0.46 and 0.53, respectively. Applying the
loess-smoothed SRR in the Sissenwine-Shepard production model estimated F_{msy} at 0.125. Due to
33 uncertainty in the SRR and the high M, $F_{90\%FMSY}$ was suggested ($F=0.11$) as a F_{ref} for EGB cod
(Wang and O'Brien, 2013). Concerns with this approach included the arbitrary nature of the choice
of $F_{90\%FMSY}$ (and therefore, $F_{ref}=0.11$), the variation around the calculation of $F_{ref}=0.1$ and the
goodness of fit of the loess smoothed SRR.

36 Using the output from the VPA.8 model we estimate several F reference points for the Eastern
George's Bank Cod stock. Specifically we apply yield per recruit (YPR), spawner per recruit (SPR)
39 and production models in a Sissenwine-Shepard type analysis. Several stock recruitment
relationships were fit to data to determine the best fit model. Common F reference points were
estimated using SPR and YPR methods. For the production modelling, profile likelihoods were
42 used to assess the plausibility of values for F_{msy} reference points. There was considerable
uncertainty in the maximum likelihood point estimates (MLEs) of the SRR parameters and hence
the estimates of F_{ref} . Following Ianelli and Heiflitz (1995) as well as Gibson and Myers (2004) we
45 applied a decision theoretic approach to estimating reference points which maximises the
expectation of catch by integrating across the likelihood surface of the SRR parameters. One
advantage of this approach is that it incorporates the uncertainty in stock recruitment parameters
48 into the estimation of reference points.

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METHODS

3 The merits of the accepted M0.8 model will not be considered here and results were produced
using the accepted output from the model. As the model formulation and SRR data showed a two –
6 phase paradigm (Figure 1), with an upper attractor in the pre-1993 period and a lower less
productive attractor post 1993 we performed the analyses described below for each of the two time
blocks separately (not including the transition year 1993 in either block) as well as the full time
series of data (1978-2010).

9

Stock recruitment Relationships

12 We explored several hypotheses on the relationship between SSB and R for this stock by fitting
different models to the data. Parametric stock and recruitment relationships are often suggested to
show compensatory mechanisms, such that recruitment decreases monotonically as stock size
15 increases through a range of processes including density dependence. A Beverton-Holt (BH)
relationship (Eq 1) follows this pattern with the largest increase in recruits per spawner at the origin
(α), and compensatory decreases in slope to an asymptotic level of recruitment (R_a).

$$R_t = \frac{\alpha SSB_t}{1 + (\alpha SSB_t / R_a)} \quad \text{Eq.1}$$

18

A Ricker model (Eq 2) also follow this similar form, but also includes a decrease in recruitment with
stock size through over-compensatory mechanisms such as increased natural mortality or
21 competition.

$$R_t = \alpha SSB_t e^{-\beta SSB_t} \quad \text{Eq.2}$$

24 Additionally, a density-independent, or zero intercept model was used to determine if any evidence
of compensatory mechanisms could be determined. The α parameter in Eq. 3 is essentially a slope
of the origin with no evidence of an asymptote in recruitment.

27

$$R_t = \alpha SSB_t \quad \text{Eq.3}$$

30 We also evaluated nonparametric models (NPM; such as loess or cubic spline smoothers) as they
do not force a functional form. The difficulty with NPMs are that they often result in multiple
equilibria, biologically unreasonable functional forms, such as recruitment >0 as spawning stock
biomass approaches 0, and the choice of smoothing level is subjective. Here the loess smoother
33 was combined with a wild bootstrapping technique to show 95% confidence bounds around the
relationship (Liu 1988). Recent work by Cadigan (2013) has suggested the use of shape
constrained additive models (SCAM) may provide a nonparametric method to overcome the
36 difficulty fitting SRs to a functional shape. Briefly, SCAM models are a type of general additive
models, which combine a series of B-spline basis functions centered between a series of knots or
divisions across the data space. The shape constraint component of these additive models are the
39 key to using SCAMs for SRs as during the fitting procedure a monotonic concave or convex shapes
can be specified in order to maintain the biological realism of the fits. Moreover, constraints can be
included to force the nonparametric relationship through the origin.

42

Parametric models were compared using a delta AIC approach, where AIC incorporated the finite
45 sample size correction (often termed AICc).

Likelihood Profiling of BH SRR

3 Maximum likelihood estimates (MLE) of BH parameters were obtained using a lognormal error structure for recruitment (Myers et al. 1995) in which the log-likelihood is given by:

$$\ell(\alpha, R_a, \sigma) = -n \log \sigma \sqrt{2\pi} - \sum \log r_i - \frac{1}{2\sigma^2} \sum \log \left(\frac{R_i}{g(SSB_i)} \right)^2 \quad \text{Eq.4}$$

6 Here, SSB_i and R_i are the spawner biomass and recruitment data in year i , $g(SSB_i)$ is the BH function, σ is the shape parameter and n is the number of paired SRR observations. The log profile likelihood for α (denoted $\ell_p(\alpha)$), is:

$$\ell_p(\alpha) = \max_{R_a, \sigma} \ell(\alpha, R_a, \sigma) \quad \text{Eq.5}$$

12 The MLE for α occurs where $\ell_p(\alpha)$ is at its maximum value. The plausibility of individual parameter estimates, given the observed data, was done using profile likelihoods, specifically, by comparing their log likelihoods with the maximised log likelihood. A likelihood ratio based 95% confidence interval for α was calculated as:

$$\{\alpha : 2[\ell_p(\alpha^{\text{MLE}}) - \ell_p(\alpha)] \leq \chi_1^2(0.95)\} \quad \text{Eq.6}$$

18 The profile likelihood and the associated 95% confidence interval for R_a were found similarly.

21 Per Recruit Analysis

24 Yield per recruit (YPR) and spawner per recruit (SPR) analysis were performed following methods of Gabriel et al. (1989) across a range of fishing mortality values (F) incorporating the information outlined in Table 1. The same information was used for the full time series as well as the late period (1994-2010) whereas previously published information was used for the 1978-1992 time block (Working Group on Re-Evaluation of Biological Reference Points for New England Groundfish, 2002).

30 Production Model

33 The SPR , YPR and SRR were combined to generate a production model. Specifically, for a given value of F , the spawning biomass produced by the number of recruits in year t is $SSB = SPR_F \cdot R_t$. Equilibrium spawning biomasses (SSB^*) and recruitment levels (R^*) were found by solving R_t , and substituting into the BH (Quinn and Deriso 1999) as:

$$\frac{SSB^*}{SPR_F} = \frac{\alpha SSB^*}{1 + \frac{\alpha SSB^*}{R_a}} \quad \text{Eq.7}$$

39

Rearranging, the equilibrium spawning biomass (SSB^*) becomes:

$$SSB^* = \frac{(\alpha SPR_F - 1)R_a}{\alpha} \quad \text{Eq.8}$$

3

which can be substituted back into the BH model to determine equilibrium recruitment (R^*):

$$R^* = \frac{\alpha SSB^*}{1 + \frac{\alpha SSB^*}{R_0}} \quad \text{Eq.9}$$

6

The equilibrium catch (C^*) is simply the product of R^* and YPR_F :

9

$$C^* = R^* \cdot YPR_F \quad \text{Eq.10}$$

12 We estimated F_{msy} by calculating C^* for each value of F , and selecting the value where C^* was maximised.

15 Reference Points

18 Reference points from the SPR and YPR analyses were found using a grid search across the set of F (Table 1). F_{refs} estimated from the YPR were F_{max} which is the fishing mortality resulting in the maximum YPR and $F_{0.1}$ which is the fishing mortality where the slope of the YPR curve is 10% that of the slope at the origin. From the SPR an estimate of F_{spr40} representing the fishing mortality at which the SPR is reduced to 40% of the SPR estimated for unfished ($F=0$) population.

24 Using the production model F_{msy} and F_{col} (F that could cause stock collapse) were estimated through a grid search to find the fishing mortality rate that produces maximum sustainable yield (F_{msy}) and the fishing mortality rate that drives the population to extinction, respectively. Specifically, F_{col} was estimated by finding the value of F where the BH parameter α , the slope at the origin, equals $1/SPR_F$. The profile likelihood for F_{msy} was found by mapping the profile likelihood for α to F_{msy} using the production model.

30 An alternative reference point that has been used when SRRs are not well defined was suggested by Sissenwine and Shepard (1987; but see Legault and Brooks 2013). This reference point finds the F that produces a replacement line with a slope that equals the average survival ratio. They suggested it could be estimated from the median survival ratio in which case it is often referred to as F_{med} (Quinn and Deriso 1999) and is the level of fishing mortality where recruitment has been more than sufficient to balance losses to fishing mortality in 50% of the observed years (Jacobsen 1993). We found F_{med} , using an objective function to 1) minimize the absolute difference in the number of observations above and below the replacement line and 2) minimize the sum of squared differences.

39

Decision Theoretic Approaches to Reference Points

42 The profile likelihoods and likelihood surfaces for the BH at any of the time periods suggested that although MLE parameter estimates for α and R_a could be obtained, the parameters were not always well defined (see Results). Previous work by Clark (1991) suggested that if reasonable ranges of α are known a production-based reference F can be estimated without any knowledge of

45

the true SR through maximising the minimum yield across the set of α 's. A meta-analysis of Atlantic cod populations provided distributions of α and $\alpha K (\equiv R_a)$ (Myers et al. 2001) which could be used to inform such an analysis. However, the levels of estimated production for this population of cod preclude this as a viable option as even during the highest biomass and recruitment period (1978-1992) the production is well below the meta-analytic distributions (see Results).

The profile likelihoods for the full time series of SR show that R_a is not precisely estimated (see Results). Consequently, the data do not preclude the possibility that the population could be larger than the MLE. Larger population sizes would lead to larger yields from the fishery, and given the uncertainty in the parameter estimates, a reference point based on the maximum likelihood estimates for the parameters may not be appropriate if it reduced the probability of obtaining larger catches. Similarly, for the two shortened time series α was not well defined (see Results), suggesting that the population's ability to rebound at low population sizes was not well defined under truncated data series.

To address these issues, a set of plausible SR parameters can be viewed as alternative hypotheses about the productivity of the population, and an F_{ref} can be defined as the fishing mortality rate that maximises the expectation of the equilibrium catch over this set of alternative hypotheses (Iannelli and Heifetz 1995), this reference point is denoted $F_{max.E(C)}$.

Estimating $F_{max.E(C)}$ requires the determination of a parameter space, Ω , for the two dimensions representing α and R_a . We used $\alpha = \frac{1}{SPR_{F=0}}$ as the lower limit for α for each time

period. This lower limit was chosen as α levels below this limit, would not maintain a viable population since reproduction would not offset natural mortality. Although, the productivity of Georges Bank cod is suggested to be lower than that provided by the meta-analysis of Myers et al. 2001 (see Results), we did not want to preclude the potential for higher growth, as such, we set the upper bound for α at the upper 99% percentile of the random effects distribution. Similarly we used the 1st and 99th percentiles of the random effects distribution of R_a for the bounds. Sensitivity analysis suggests that the choice of range for both α and R_a had very minimal impact on $F_{max.E(C)}$ (results not shown). Using the maturity schedules and natural mortality defined in Table 1, the expectation of the equilibrium catch can be estimated as:

$$E(C^*(F)) = \iint C^*(F, \alpha, R_a) p(\alpha, R_a) dR_a d\alpha \quad \text{Eq.11}$$

where $C^*(F, \alpha, R_a)$ is the equilibrium catch as a function of the fishing mortality rate, the maximum reproductive rate and the asymptotic recruitment level, and $p(\alpha, R_a)$ is the probability density evaluated at α and R_a . We calculated $p(\alpha, R_a)$ using the likelihood surface for each time block as:

$$p(\alpha, R_a) = \left\{ \begin{array}{ll} \frac{L(\mathbf{R} | \mathbf{S}, \alpha, R_a)}{\iint_{\Omega} L(\mathbf{R} | \mathbf{S}, \alpha, R_0) d\alpha dR_a}, & \alpha, R_a \in \Omega \\ 0 & \text{otherwise} \end{array} \right\} \quad \text{Eq.12}$$

$F_{maxE(C)}$ is then the F that maximises the expectation of the catch is then:

$$F_{\max .E(C)} = \operatorname{argmax}_F E(C * (F)) .$$

Using $F_{maxE(C)}$, an estimate of the percent SPR_{F0} was made to display the equivalent $F_{spr\%}$ given the proposed F_{ref} .

RESULTS

Following the previous work in Wang and O'Brien (2013) we performed *SPR* and *YPR* analyses to estimate several F_{refs} for the early (1978-1992), late (1994-2010) and full time series of data. The early time block represented a period with assumed lower natural mortality on the older ages, older age at maturity and the population had a larger weight at age (Table 1). The same population and fishery information was used for the late and full time series and will therefore be considered together. Across each of $F_{0.1}$, F_{max} and F_{spr40} reference points increased by between 175 and 210% from the early to the late period as a result of the increasing natural mortality (Table 2; Figure 2,3). F_{med} did not follow this pattern as the reference point was higher for the early period at, 0.427, compared to the late time period of 0.05 or the full time period of 0.11 (Table 2).

The density independent, Beverton-Holt and Ricker parametric stock recruitment relationships for George's Bank cod were comparable with delta AICc's <3 and all showed a characteristic linear increase across the range of data (Figure 4). Neither the Ricker nor the Beverton-Holt model displayed compensatory recruitment decreases over the observed range of data. Compensatory decreases in recruitment rates with increasing spawner abundance were achieved with the non-parametric models (Figure 4). The use of a loess smoother (span=0.52) followed the data trajectory, but did suggest the potential for multiple equilibria and the upper confidence bounds from wild bootstrap did not follow the same asymptotic relationship and was therefore not explored further (Figure 5). The shape constrained additive model (SCAM) did force compensation and asymptotic recruitment, however this lead to significant patterning in the recruitment residuals, such that spawning stock biomasses above 30 kt all had positive residuals (Figure 5). For the remainder of the analyses the BH stock recruitment relationship was used as it was not rejected as a suitable model for describing the SR and it was considered the best fit SR model for many previously examined cod stocks (Myers et al. 2001).

Comparing the BH parameters with those obtained from meta-analysis (Myers et al. 2001) suggested that George's Bank cod are maintained at a lower carrying capacity, and have a lower maximum reproductive rate than the combined information across populations (Figure 6). Moreover, SRR data suggests that the biomass of spawners produced per spawner have only rarely been observed to be above the meta-analytic BH relationship (Figure 6).

The likelihood profiles for the BH parameters across the full time series suggested that α could be defined, as there was evidence of both upper and lower limits of the likelihood ratio based confidence bounds (Figure 7). The asymptotic recruitment (R_a) was ramped with evidence of a lower bound but not a reasonable estimate of the upper bounds. Mapping the profile likelihood for α to F_{msy} through the production model suggested that the MLE for F_{msy} was 0.079 with likelihood ratio 95% confidence bounds of (0 and 0.17 - Figure 7, Table 2). In contrast, both the early and late time series blocks were ramped for α , and the late time period was also ramped for R_a (Figure 8, 9). The likelihood ratio 95% confidence lower bounds were 0.16 for the early time block and 0.12 for the late time block, suggesting that the confidence bounds for α were not significantly different than that for the full time series (Figure 7-9). From these two time blocks MLE estimates of F_{msy} were estimated to be 0.33 and 0.42 respectively (Table 2), however the likelihood profiles suggest that

the upper limits for these estimates are not defined and do not preclude the possibility that α and F_{msy} could be larger than the MLE (Figure 8, 9).

F_{col} was estimated for the full time series to be 0.172 which is below the current F_{msy} proxy at 0.18 (Table 2). The estimates of F_{col} for the early and late time series were high at levels >1.6 for both (Table 2). There would also be considerable uncertainty in the shortened time series for F_{col} as the α parameter is not well defined for either time period.

Exploring the set of parameter space of α and R_a under a decision theoretic framework yielded estimates of $F_{maxE(C)}$ of 0.281, 0.097 and 0.097 for the early, late and full time series of data respectively (Figure 10, 11). For both the early and late time series the estimate of F_{msy} was larger than the estimate of $F_{maxE(C)}$ which was likely due to the greater uncertainty in the α BH parameter for these time periods. Conversely, α was better defined for the full time series, which yielded a marginally higher estimate of $F_{maxE(C)}$. Converting the full time series $F_{maxE(C)}$ to the equivalent currently used F_{msy} proxy would result in $F_{spr80\%}$.

DISCUSSION

Although the biomass and recruitment data suggests that George's Bank cod have undergone productivity changes, attempting to model the SRR data as two separate time periods did not improve the ability to predict production. As such, the full time series of data should be considered for defining F reference points. Moreover, when defining precautionary reference points it is often suggested to use the full time series of data to ensure the full breadth of observed productivity is included.

Applying a decision theoretic approach to defining the F reference point, $F_{maxE(C)}$, allowed for the incorporation of uncertainty in stock recruitment relationship through the integration of the likelihood surface and production models. Previous simulation studies have suggested that $F_{maxE(C)}$ exhibited less variability and substantially reduced the risk of overexploiting populations when compared to fishing near F_{msy} (Gibson and Myers 2004). An F_{ref} based on the estimate of $F_{maxE(C)}$ of 0.097 (~ 0.1) is therefore proposed as the fisheries reference point for Eastern George's Bank cod stock.

The estimate of F_{med} of 0.11 for the full time series of data was very similar to the $F_{maxE(C)}$. Recent work by Legault and Brooks (2013) has shown that F_{med} may not be a useful proxy for F_{msy} or $F_{spr\%}$ as it does not necessarily describe any biological or productivity feature of the stock. In instances, such as this example for the George's Bank cod, when there is a fairly long time series of spawning stock biomass estimates, and the hypothesis of a density independent SR cannot be rejected, the median replacement line or F_{med} may be considered a robust slope of the origin model and may be meaningful as a fishing mortality reference point. However a full simulation analysis of this suggestion is warranted.

The increase in natural mortality between early and late periods resulted in an increase in YPR and SPR F reference points. This pattern has been shown elsewhere and is due to the decrease in overall YPR and SPR as individuals are removed from the fishable or spawning population at a much faster rate (Legault and Palmer 2013). The higher F_{refs} from this type of analysis do not lend themselves appropriate to a precautionary fishery strategy, unless the population has entered a new equilibrium state and there is no expectation of the fish returning to their natural productivity levels. There is no evidence to suggest EGB cod cannot increase their productivity levels in the future.

Under the BH stock recruitment relationship and the recently updated SPR analysis, the fishing mortality rate that would cause stock collapse (F_{col}) was estimated to be 0.17, which is below the

3 current F_{msy} proxy at 0.18. Although, there remains variability around this estimate of F_{col} , the spawning stock biomass of EGB cod stock appears to be variable and declining from 2009-2012 even as estimated fishing mortalities were at or below 0.18 (Wang and O'Brien 2013). This supports the suggestion that the reevaluation and lowering of the F_{ref} was warranted.

6 Based on the time series of data available, the EGB cod population is not as productive as many of the North Atlantic cod stocks. Specifically, during periods when the spawning stock biomass levels are similar to those of other stocks, the resultant recruitment appears to be lower, which was the
9 situation even during periods of highest spawner biomass (Myers et al. 2001). Several explanations for this pattern may include higher mortality on the pre-recruiting animals, higher interspecific competition (e.g. Collie et al. 2009) or perhaps lower reproductive capacity. The
12 discussion on this topic is beyond the realm of the current working paper.

15 In summary, because attempts to model the SR in ways that reflect apparent productivity changes did not improve the ability to predict productivity, the full time series of data should be considered for defining F_{refs} . We propose $F_{maxE(C)}$, which was 0.097 (~0.1), as a suitable F_{ref} for Eastern
18 Georges Bank cod that better reflects M changes in the VPA.8 model, and minimises variability overexploitation risk relative to F_{msy} .

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TABLES

3 Table 1: Age specific information used for yield and spawner per recruit analysis.

Measure		Full Time Series / Late Time Series- 1994-2010	Early Time Series – 1978- 1992
Age		1 : 10+	1: 10+
Weight at age	Fishery	0.37, 1.16, 1.93, 2.81, 3.80, 4.88, 6.10, 7.41, 8.85, 11.65	0.68, 1.15, 1.89, 2.93, 4.2, 5.72, 7.39, 8.96, 10.49, 15.23
	Population	0.07, 0.63, 1.37, 2.19, 3.14, 4.39, 5.39, 7.40, 8.74, 11.65	0.88, 1.51, 2.36, 3.63, 5.02, 6.59, 8.33, 9.74, 11.37, 14.74
Maturity at age		0,0,1,1,1,1,1,1,1,1	0.13, 0.57, 0.92, 1, 1, 1, 1, 1, 1, 1
Partial Recruitment		0.01, 0.1, 0.6, 1, 1, 1, 1, 1, 1, 1	0.0001, 0.19, 0.66, 1, 1, 1, 1, 1, 1, 1
Mortality at age		0.2, 0.2, 0.2, 0.2, 0.2, 0.8, 0.8, 0.8, 0.8, 0.8,	0.2, 0.2, 0.2, 0.2, 0.2, 0.2, 0.2, 0.2, 0.2, 0.2,
Fishing mortality		0.001,0.002,....1.999, 2	0.001,0.002,....1.999, 2

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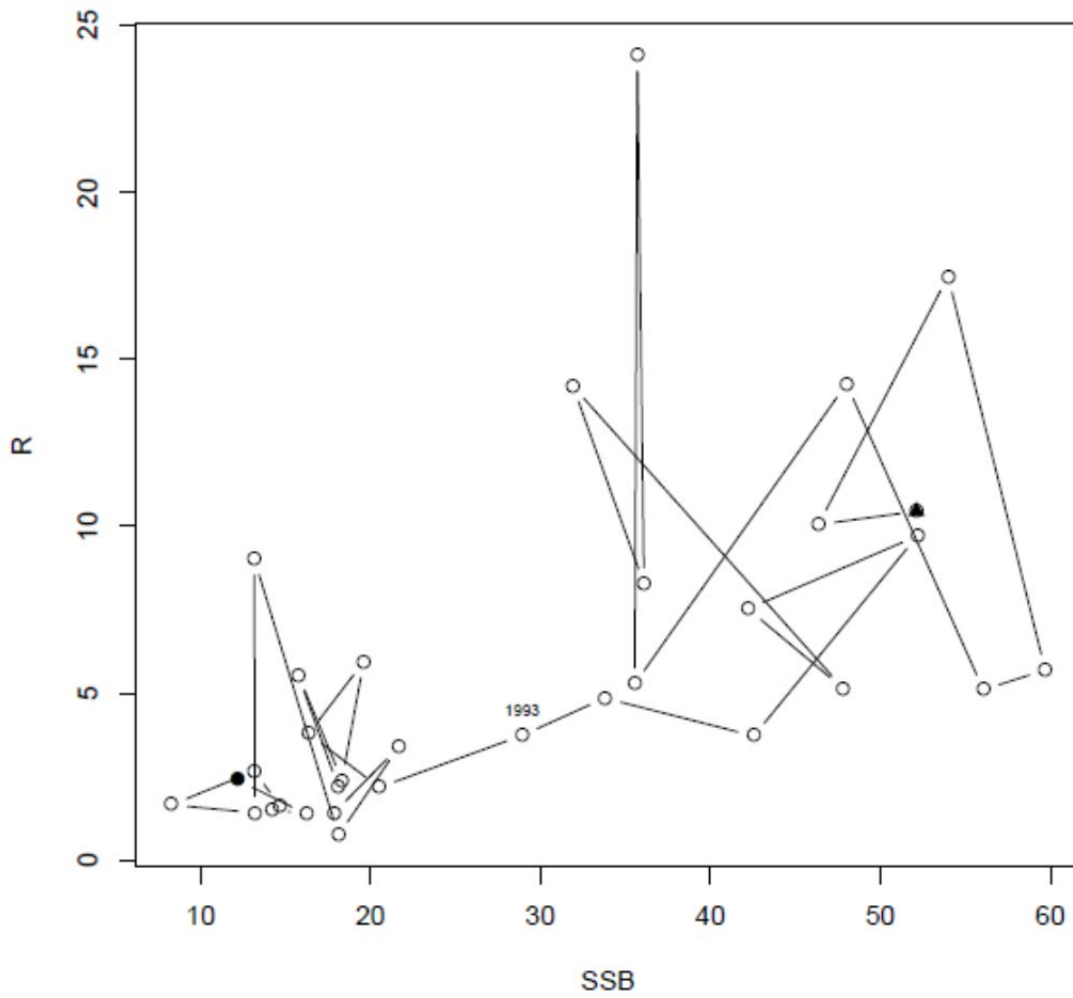
12 Table 2: MLE parameter estimates for the Beverton-Holt (BH) stock recruitment relationship with α
 15 representing the slope at the origin and R_a the asymptotic recruitment level. Fishing mortality reference points
 estimated under several methods are shown for three different time blocks.

Theoretical Basis	MLE Parameter Estimate / Reference Point	Full Time Series (1978-2010)	Early Time Series (1978-1992)	Late Time Series (1994-2010)
BH	A	0.203	2.9E7	0.78
	R_a	5.9E8	8.43	2.97
Yield per Recruit	$F_{0.1}$	0.461*	0.168	0.461*
	F_{max}	0.916*	0.33	0.916*
Spawner per Recruit	$F_{40\%}$	0.518*	0.167	0.518*
	SPR_{F0}	7.20	26.2	7.2
	F_{med}	0.11	0.427	0.05
Production Model	F_{col}	0.173	>2	1.61
	F_{msy}	0.079	0.33	0.424
Decision Theoretic	$F_{max.E(C)}$	0.097	0.281	0.097

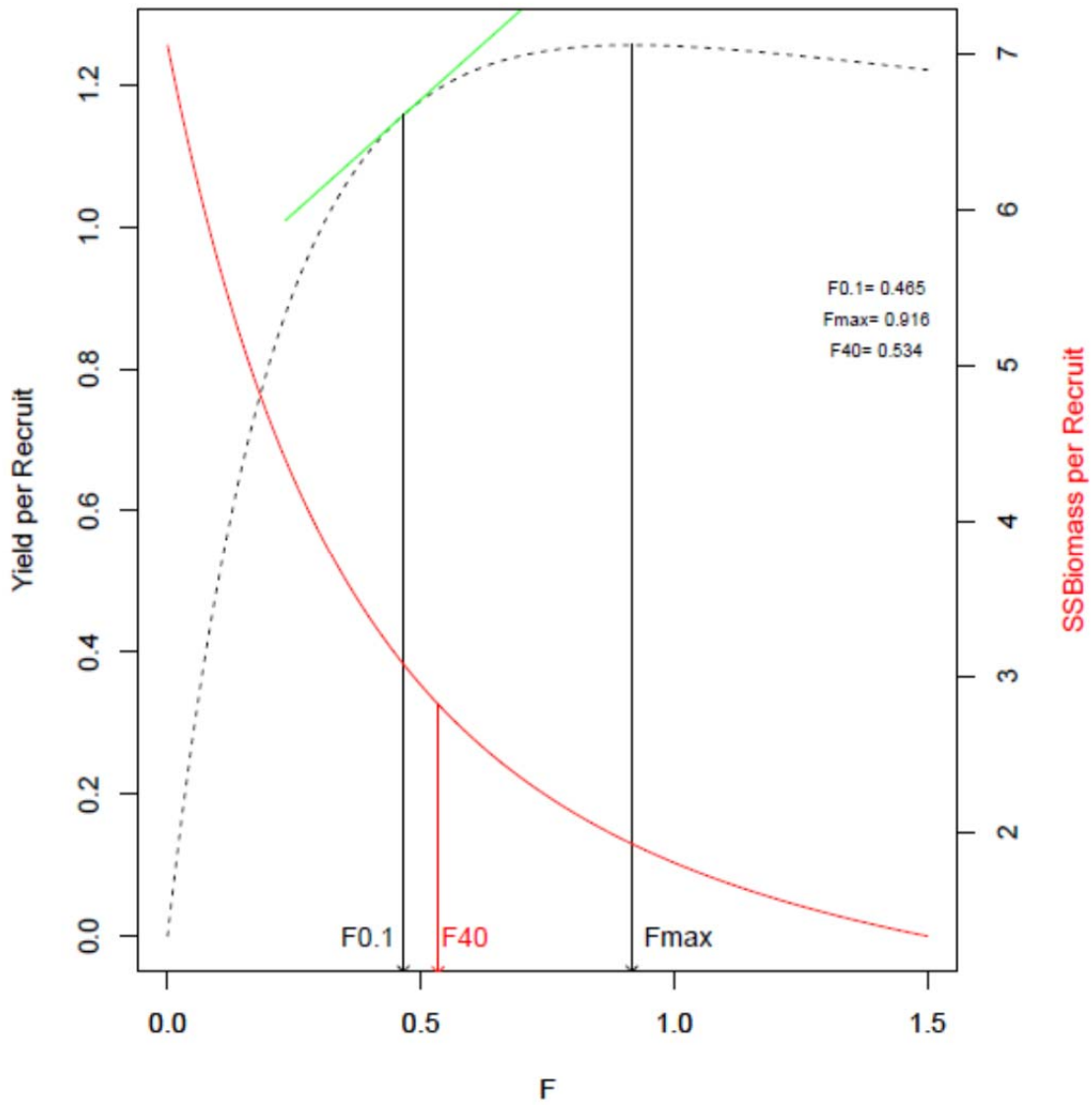
*Reference points are based on the same life history parameters in both periods and are therefore the same.

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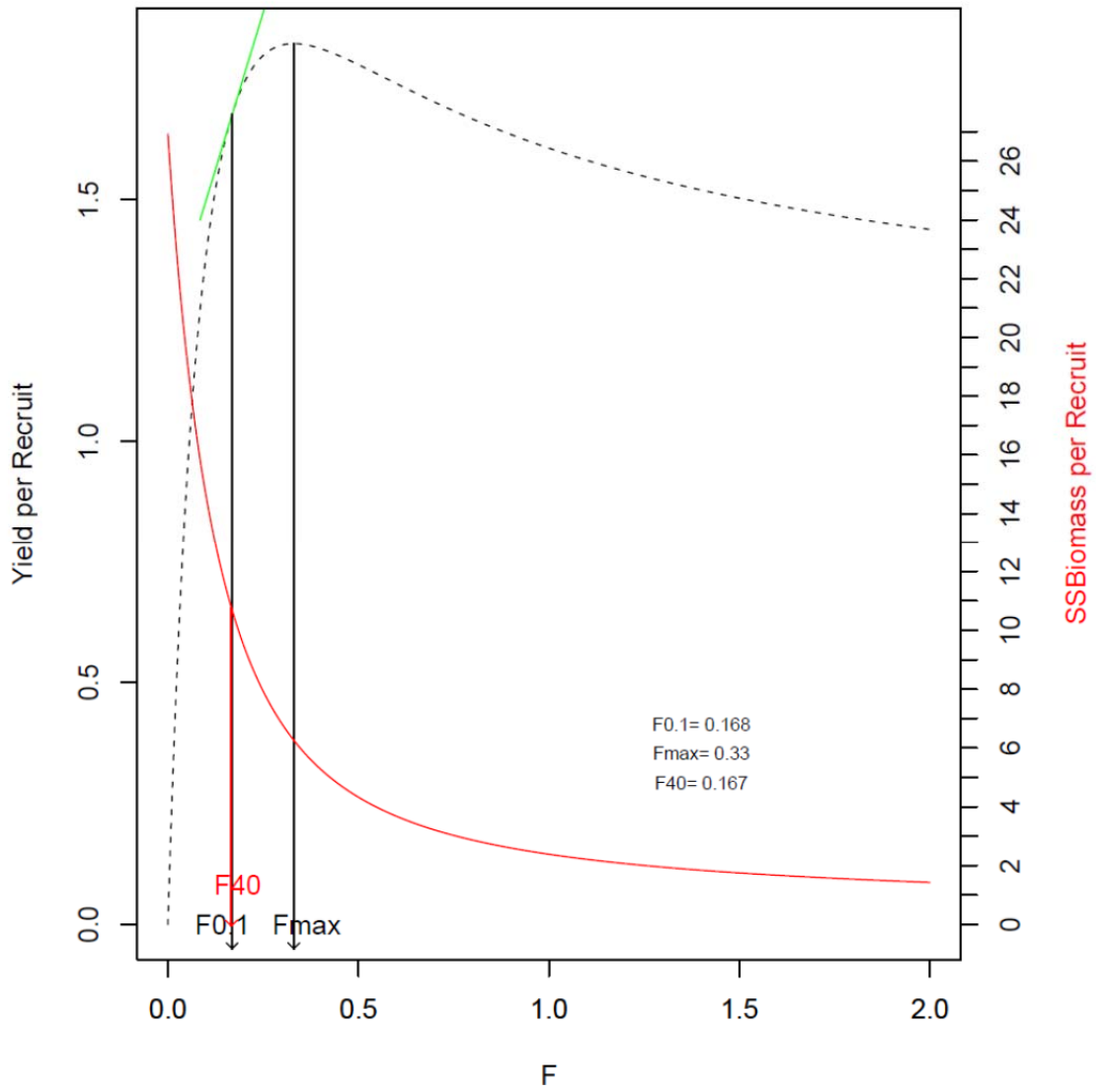
FIGURES



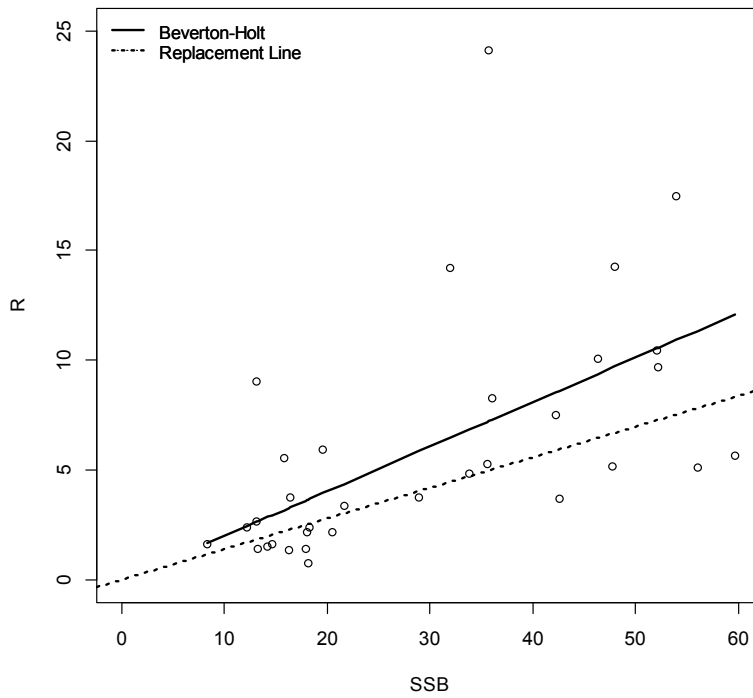
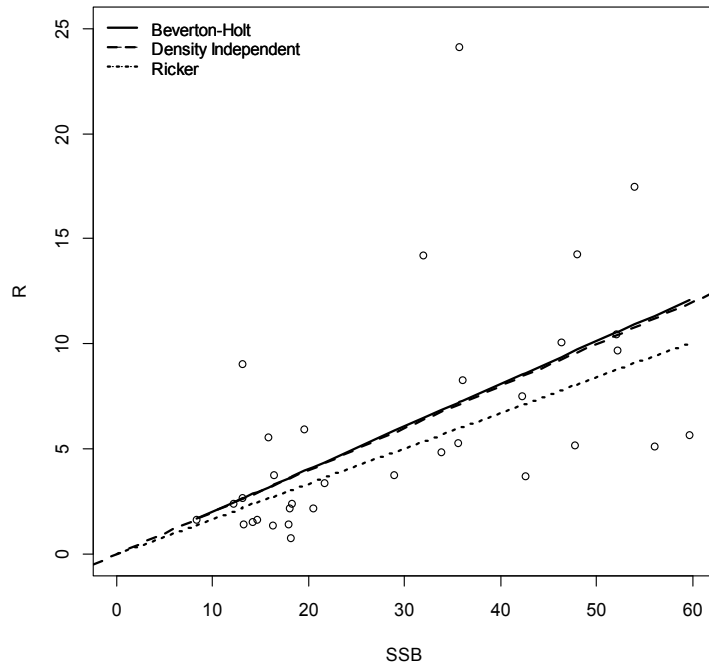
3 Figure 1: Trajectory of spawner biomass (kt) and recruit (millions of fish) data. Time series begins in 1978 (denoted by a filled triangle) and continues to 2010 (denoted by a filled circle).



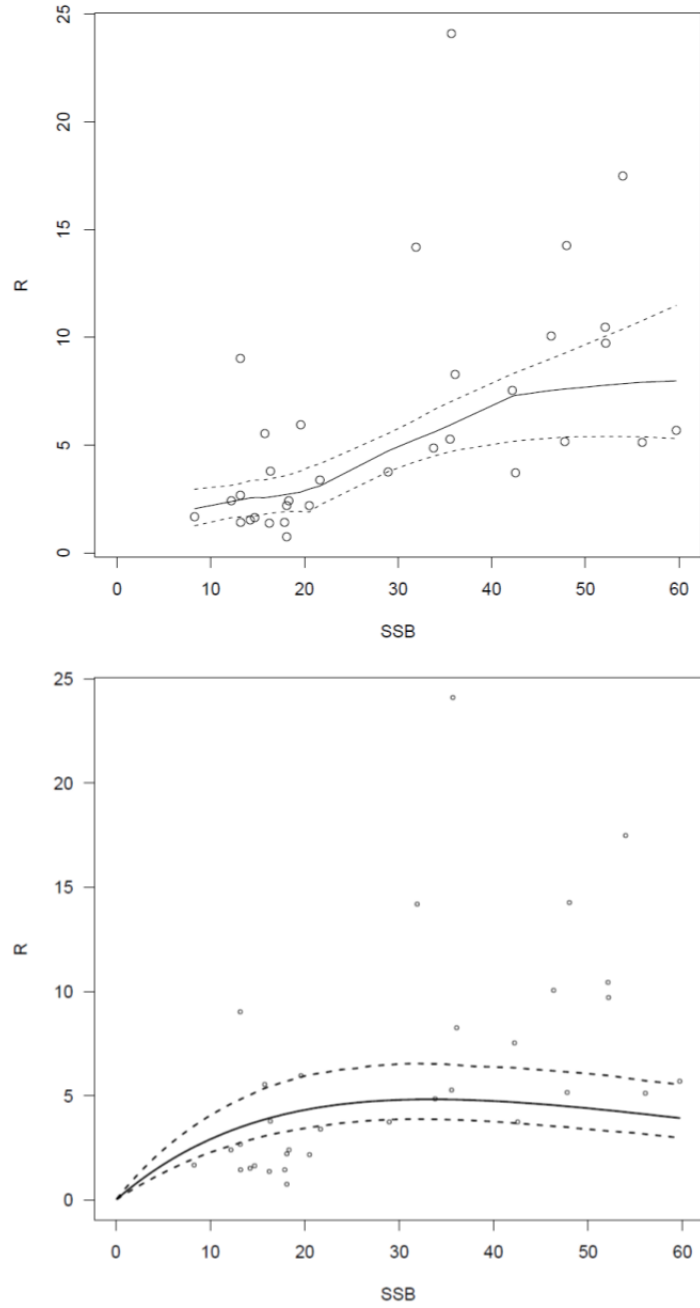
3 Figure 2: Yield (black line) and spawning stock biomass (red line) per recruit curves for Georges Bank cod. Fishing mortality reference based on these two equilibrium models are shown. Results are for the full time series of data



3 Figure 3: Yield (black line) and spawning stock biomass (red line) per recruit curves for George's Bank cod during 1978-1992. Fishing mortality reference based on these two equilibrium models are shown.



3 Figure 4: Stock recruitment relationships for George's Bank Cod. (Upper) Beverton-Holt (solid),
 6 Ricker (dotted) and density independent (dashed) relationships. (Lower) Beverton-Holt SR (solid)
 with replacement line F_{rep} (dotted) at $1/SPR_{F0}$.



3 Figure 5: Stock recruitment relationships for George's Bank Cod. (Upper) Loess SRR with a span of 0.52 and wild bootstrapped confidence intervals. (Lower) Shape constrained additive model (SCAM) with 95% confidence intervals.

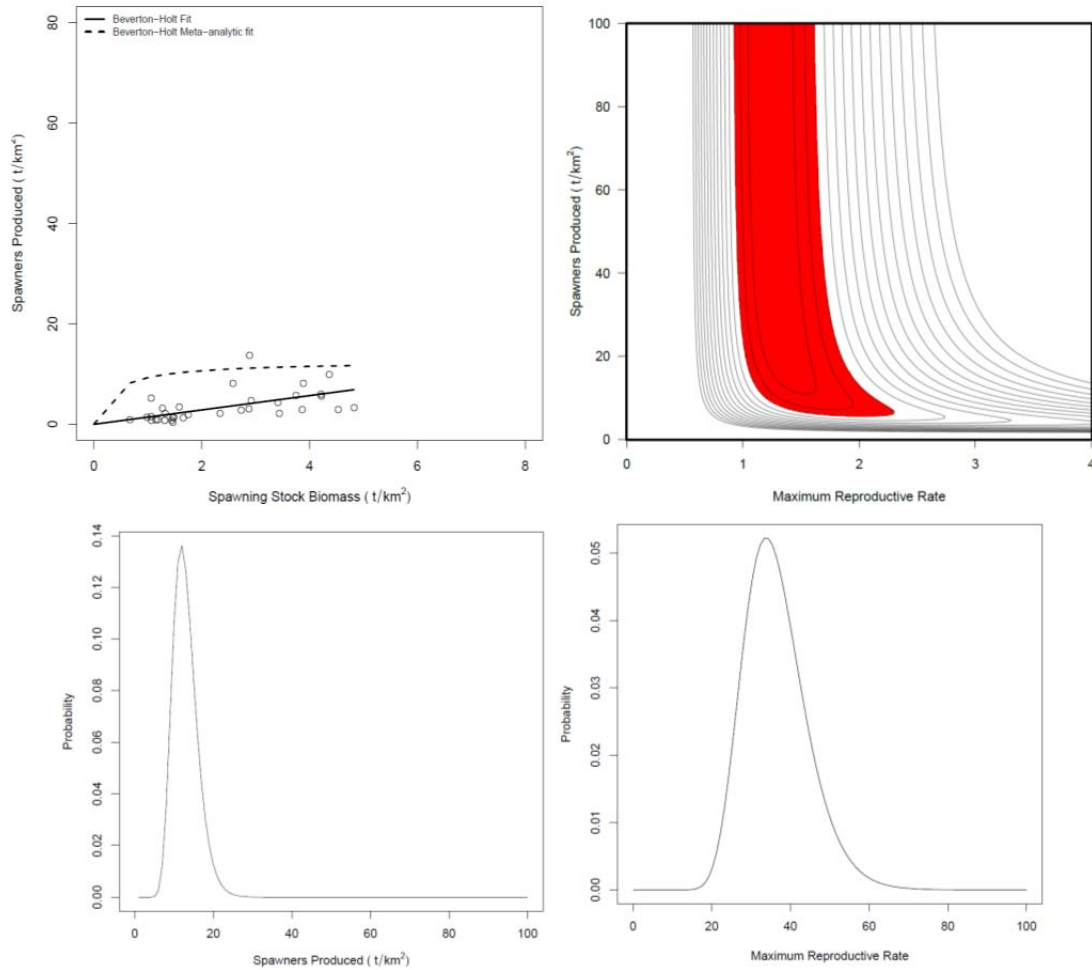


Figure 6: Comparison of current George's Bank stock recruitment data with meta-population stock and recruitment parameters of Myers et al. (2001). (Top left) Stock and recruitment relationship (where recruitment is weight of spawners produced) scaled to tons per square kilometer as per Figure 3 in Myers et al (2001). (Top right) Joint log-likelihood plot with for maximum reproductive rate (α) and asymptotic biomass of spawners produced. (Bottom left) Meta-analytic mixed-effects probability distributions for maximum reproductive rate (α) and asymptotic spawner production (Myers et al. 2001 Table 2). Note the different ranges for scale in the top right and bottom panels.

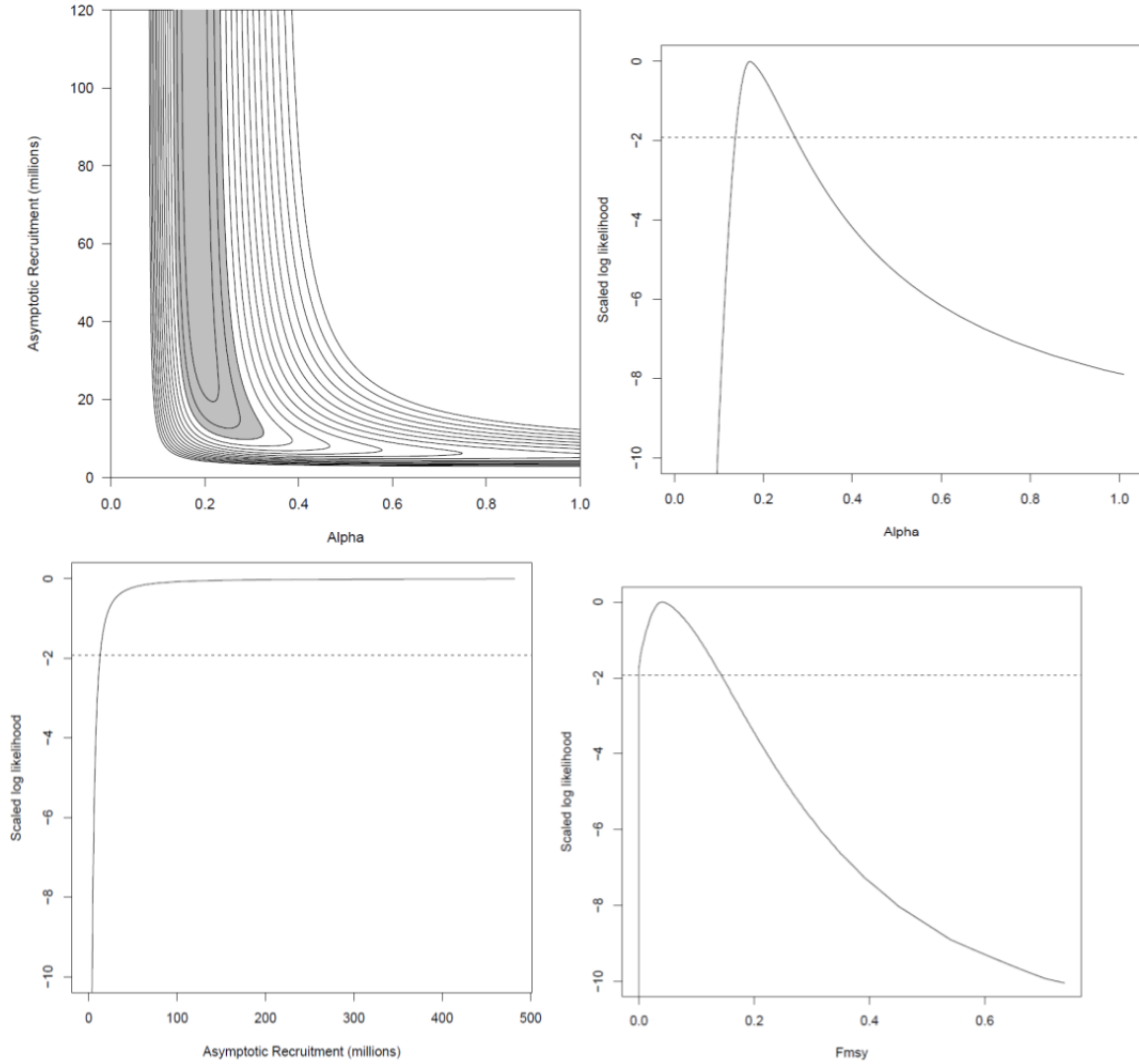


Figure 7: Log-likelihood profiles for the Beverton-Holt stock recruitment relationship for the full time series. (Top left) Joint log likelihood surface for the slope at the origin (α) and the asymptotic recruitment. (Top right) Profile log-likelihoods for α and (Bottom left) asymptotic recruitment. (Bottom right) Profile log-likelihood for F_{msy} obtained from the profile log-likelihood for the α parameter. Log-likelihoods were standardized to a maximum of zero by subtracting the maximum log-likelihood value. The intersection of the dashed-line and the log-likelihood profile shows the likelihood ratio based 95% confidence intervals for each parameter.

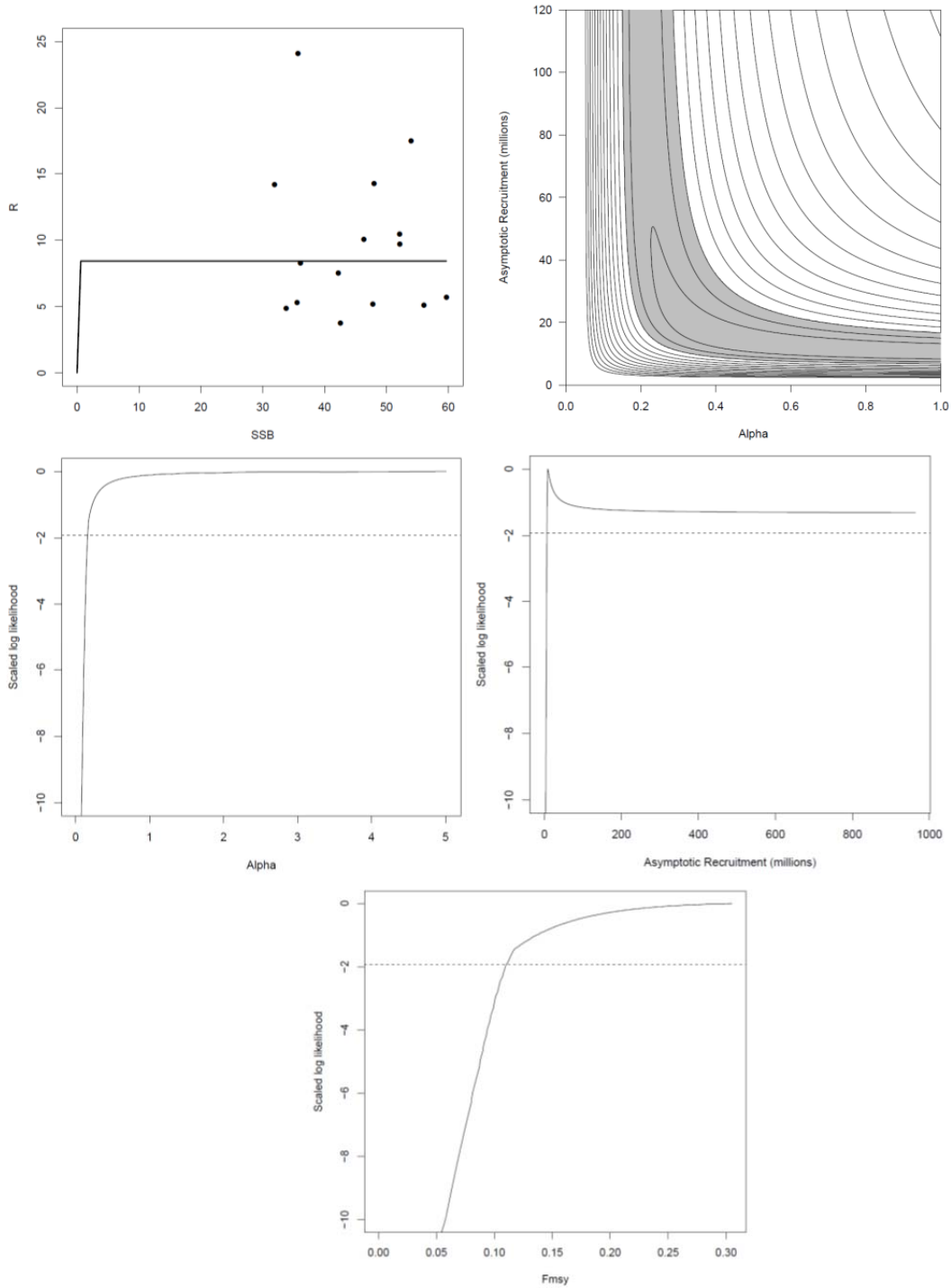


Figure 8: Log-likelihood profiles for the Beverton-Holt stock recruitment relationship (upper left) for the time period of 1978-1992. (Top) Joint log likelihood surface for the slope at the origin (α) and the asymptotic recruitment. (Middle) Profile log-likelihoods for α (left) and asymptotic recruitment (right). (Bottom) Profile log-likelihood for F_{msy} obtained from the profile log-likelihood for the α parameter. Log-likelihoods were standardized to a maximum of zero by subtracting the maximum log-likelihood value. The intersection of the dashed-line and the log-likelihood profile represents the likelihood ratio 95% confidence intervals for each parameter.

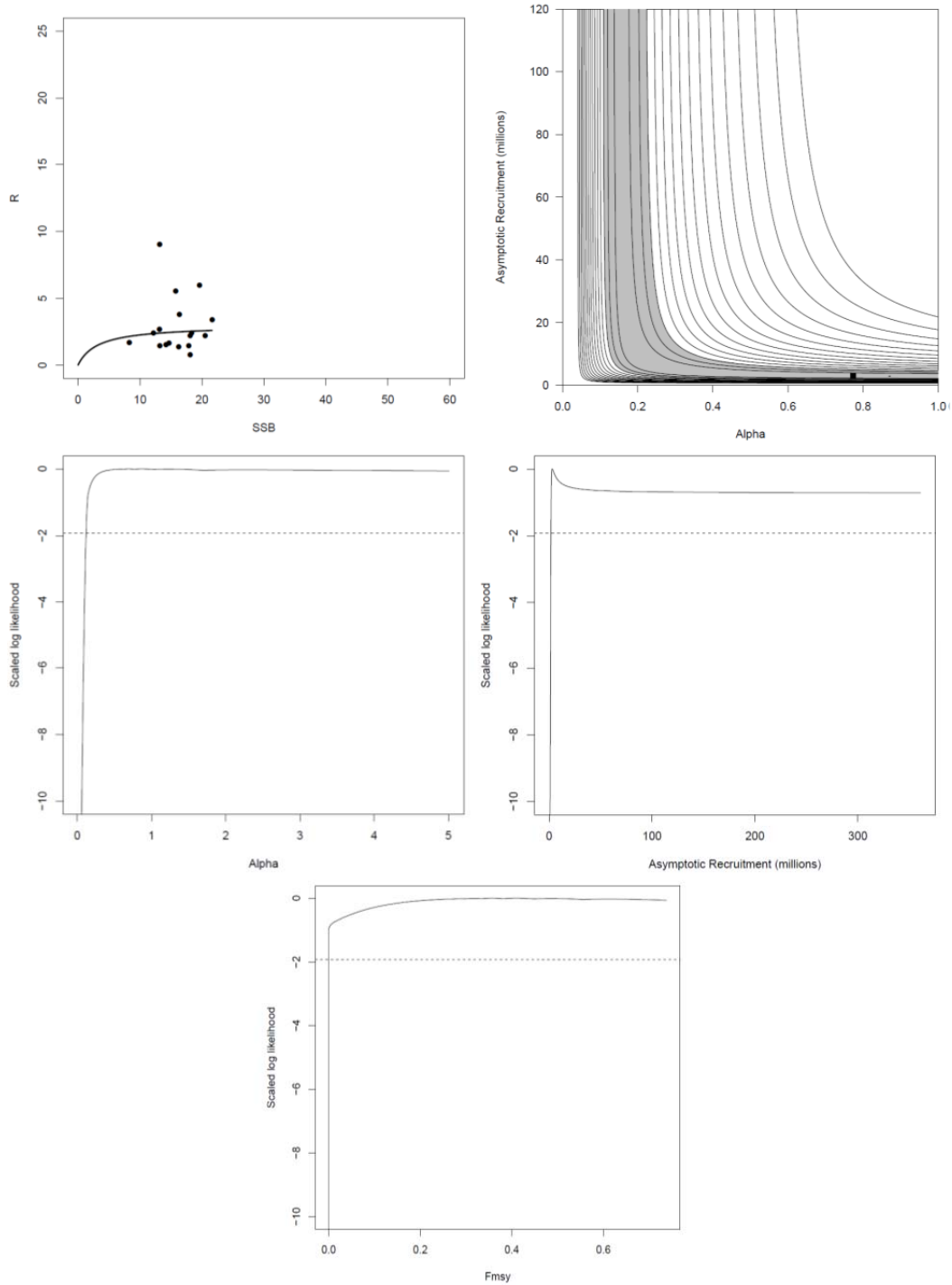


Figure 9: Log-likelihood profiles for the Beverton-Holt stock recruitment relationship (upper left) for the time period of 1994-2010. (Top) Joint log likelihood surface for the slope at the origin (alpha) and the asymptotic recruitment. (Middle) Profile log-likelihoods for alpha (left) and asymptotic recruitment (right). (Bottom) Profile log-likelihood for F_{msy} obtained from the profile log-likelihood for the alpha parameter. Log-likelihoods were standardized to a maximum of zero by subtracting the maximum log-likelihood value. The intersection of the dashed-line and the log-likelihood profile represents the likelihood ratio 95% confidence intervals for each parameter.

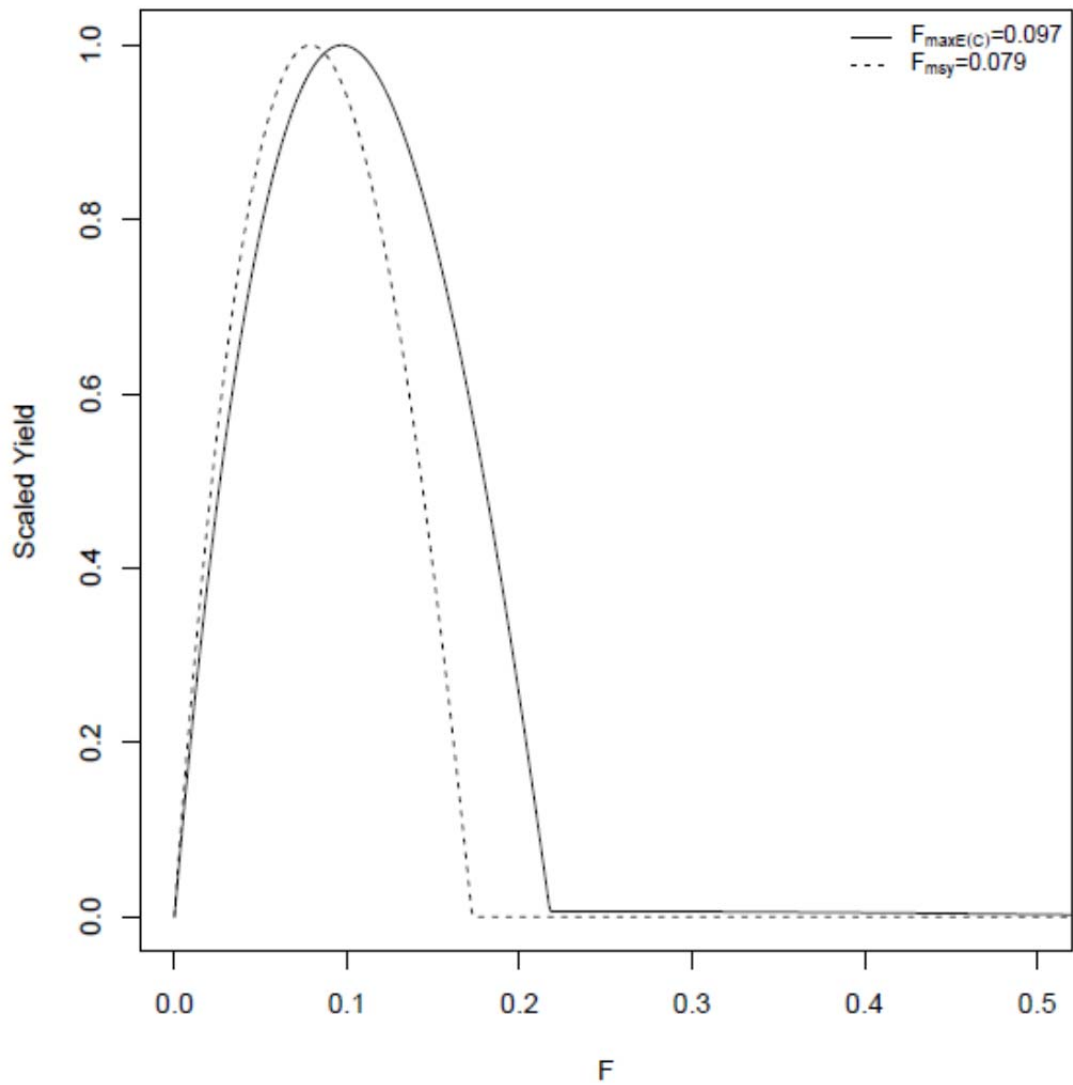


Figure 10: Relationships between equilibrium yield and F following the decision theoretic (solid line) and production model (dashed line) for the full time series of stock recruitment data using the recent life history data for the spawner and yield per recruit analysis. Reference points of $F_{\max E(C)}$ and F_{msy} represent the maximum equilibrium yield for each.

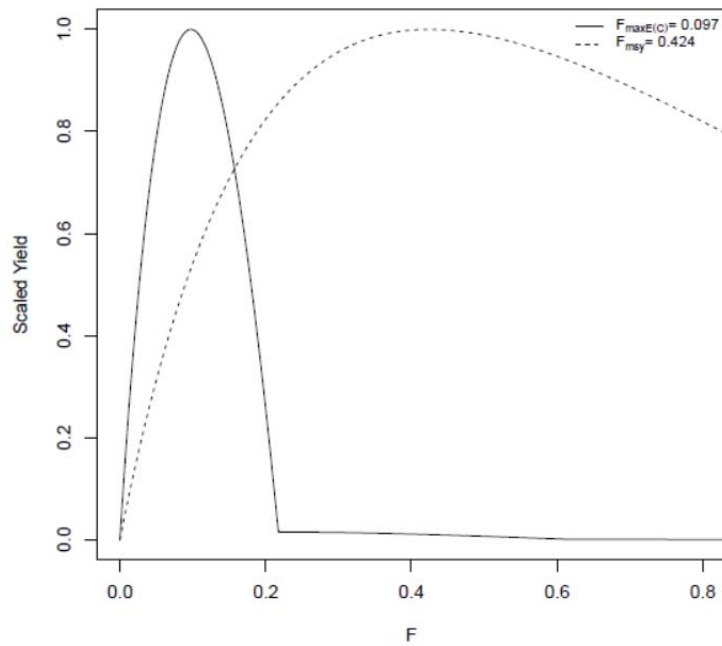
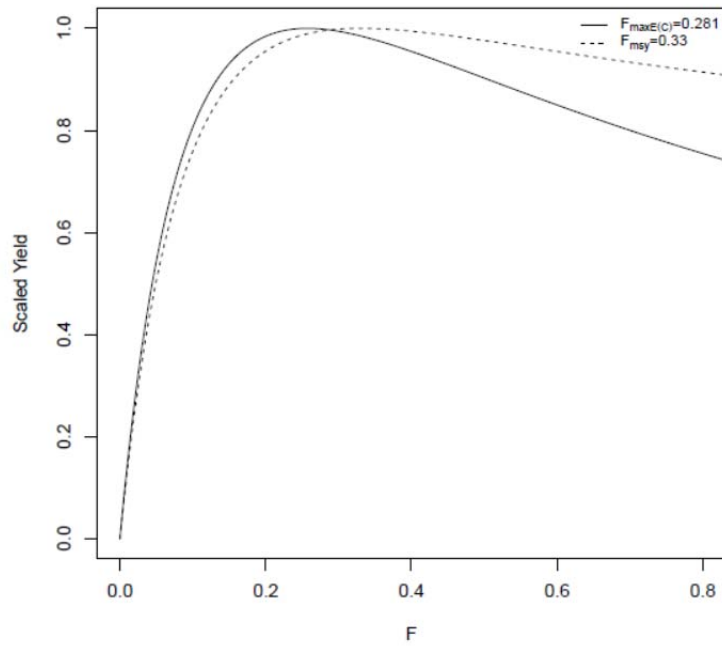


Figure 11: Relationships between equilibrium yield and F following the decision theoretic (solid line) and MLE (dashed line) production models for the 1978-1992 (upper) and 1994-2010 (lower) series of stock recruitment data using the time period specific life history data for the spawner and yield per recruit analysis. Reference points of $F_{maxE(C)}$ and F_{msy} represent the F at maximum yield for each curve.