

Evaluating impacts of Density Dependent processes on Northeast Atlantic mackerel via MSE simulations

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Version 1.0 (07 March 2023)

Version 1.1 (09 March 2023)

Version 1.2 (10 March 2023)

Version 1.3 (13 March 2023)

Version 1.4 (16 March 2023; fixed error in reference point table)

Version 1.5 (17 March 2023; fixed error in figure 15; added two scenarios)

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Executive summary

The current management of fish stocks is based on achieving the fishing mortality (F_{MSY}) that achieves the maximum sustainable yield (MSY). Estimation of MSY generally only includes the stock recruitment relationship when considering density dependent population regulation mechanisms. Density dependence, however, may also operate in processes such as growth, sexual maturity, and natural mortality. A main aim of this study was to condition Operating Models (OMs) on alternative hypotheses about density dependence for use in Management Strategy Evaluation (MSE). The objective is to evaluate the robustness of the assessments conducted to support the ICES advice framework. To do this OMs were developed that include density dependence in growth, maturity, natural mortality, individually and combined. These OMs were then used to evaluate the consequences of not including density dependence management advice.

The Operating Models were

- Base Case, with varying M-at-age
- Density dependence in mass-at-age,
- Density dependence in mass, maturity-at-age,
- Density dependence in mass, maturity and M-at-age,

The MSY reference points B_{MSY} and F_{MSY} are generally based on equilibrium assumptions, either from combining yield per recruit and spawner per recruit relationship (Sissenwine and Shepherd 1987) or by conducting long-term projections under constant fishing mortalities.

Initial evaluations were conducted based on life history theory, as used by the International Council for the Exploration of the Sea (ICES) to develop advice conducting MSE for data poor stocks (Fischer, DeOliveira, and Kell 2020). **Figure 10** shows the the equilibrium curves of catch v SSB assuming a) no density dependence, and density dependence in b) mass-at-age, c) mass & maturity-at-age, and d) mass, maturity and natural mortality-at-age. These allow the relationships between the MSY reference points and virgin biomass to be seen.

Each of the OMs were then projected for the values of F_{MSY} based on the four assumptions about density dependence. This allows a comparison between the yield that could potentially be achieved and that forgone by making an incorrect assumption about density dependence. The OMs were first projected, without process error in recruitment, from the end of the historical estimates for a range of fishing mortality (spanning 0 to F_{crash}) for 30 years into the future. The estimates in the final year of the projections were then be used to construct equilibrium curves (**Figure 15**). The points on the curve correspond to the projected outcomes for the values of F_{MSY} from each OM. This was run as a check, as the equilibrium and projections should agree, i.e. the points at MSY should be the same color as the curve.

The OMs were also projected for the estimates of different estimates F_{MSY} , with stochasticity in the recruitment deviates. This allows the impact of misspecification of density dependence to be evaluated, i.e. if F_{MSY} is underestimated then yield will be less than MSY, while if F_{MSY} is overestimated yield will be lost due to overfishing. Stochastic projections of the four Operating Models for the four estimates of F_{MSY} are shown in **Figures 16-19**. **Figures 20-22** summarizes the yields, SSBs and Fs obtained for each Operating Model under the correct and mis-specified form of density dependence.

Estimating density-dependence from observations was only possible for mass-at-age and maturity age. Density dependence in natural mortality can only be explored from theoretical considerations (because current assessment does not include age or time varying natural mortality).

Including density dependence has a major impact on reference points. Especially F_{MSY} is much higher when including DD. However, the expected yields in equilibrium conditions are expected to be very similar. The main difference is in the initial step from the current F_{MSY} to any new F_{MSY} that would include DD, as the higher F_{MSY} would be applied to a stock that is estimated without DD.

1 Introduction

The purpose of this work is to support the project “ F_{MSY} -project for six high profile fish stocks”. The project focuses on the current management approach for fish stocks based on single-species F_{MSY} Values where the only density-dependent process that is included is recruitment. The project includes three other density-dependent population dynamics: growth (mass-at-age), sexual maturity and natural mortality.

This report deals with the evaluation of density dependent processes for Northeast Atlantic mackerel using Management Strategy Evaluation (MSE). Steps in the analysis:

1. Conditioning and summaries based on the 2022 ICES assessment (section 2)
2. Estimating Density Dependent effects based on equilibrium analyses and explore DD before setting up the OMs (section 3)
3. Setting up the Operating Models (OM) (section 4)
4. Running MSE's (section 5)

Four alternatives OMs have been included in the analyses:

1. No density dependent processes
2. DD in growth
3. DD in growth and maturity
4. DD in growth, maturity and natural mortality

All MSE's have been developed within the FLR framework (<https://flr-project.org/>) and all the code is stored on github (<https://github.com/martinpastoors/ddmse>).

All data and results are available on a dedicated DropBox folder.

2 Conditioning and summaries based on the 2022 ICES assessment

All conditioning of the operating models and estimation of potential density dependent processes have been based on the ICES 2022 SAM assessment of Northeast Atlantic mackerel.

Mass-at-age

Trends in (stock) mass-at-age are shown in figure 1. Weight-at-age in the stock is calculated as the average of the weight-at-age in the three spawning components, weighted by the relative size of each component (as estimated in the egg surveys). The decreasing trend in weight-at-age observed since 2005 for fish of age 3 and older seems to have stopped in 2013 and values in the last 8 years show an increasing trend.

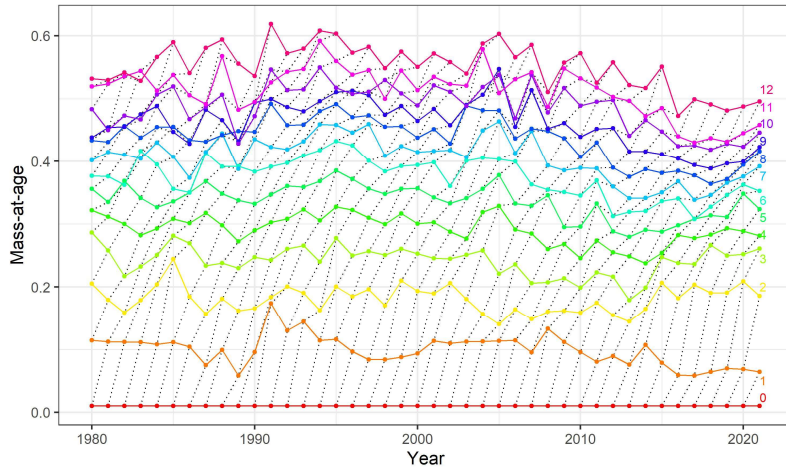


Figure 1: Northeast Atlantic mackerel. mass-at-age by year and cohort

Maturity-at-age

The annual maturity ogive for mackerel is calculated as the average of the maturity ogives of the three spawning components weighted by the relative size of each component calculated as described above for the stock weights. The ogives for the North Sea and Southern components are fixed over time. For the Western component the maturity ogive is updated every year, using maturity data from commercial catch samples from Germany, Ireland, the Netherlands and the UK collected during the first and second quarters. Most of the variability in maturity-at-age is on ages 2 and 3. Nearly all fish of age 4 and older are estimated to be mature.

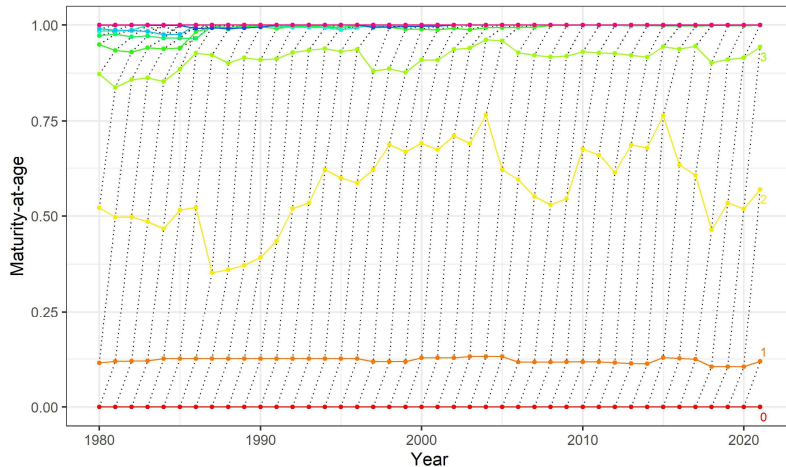


Figure 2: Northeast Atlantic mackerel. Maturity-at-age by year and cohort

Natural mortality-at-age

Natural mortality is assumed to be 0.15 for all age groups and constant over time. This value was calculated based on estimates of total mortality derived from tagging data combined with catch data (Hamre (1980); ICES (2022b); ICES (2022a)).

In order to assess the impacts of density dependent processes on natural mortality, additional assumptions need to be made about the distribution of natural mortality across ages. This will be done in section 3 of this report.

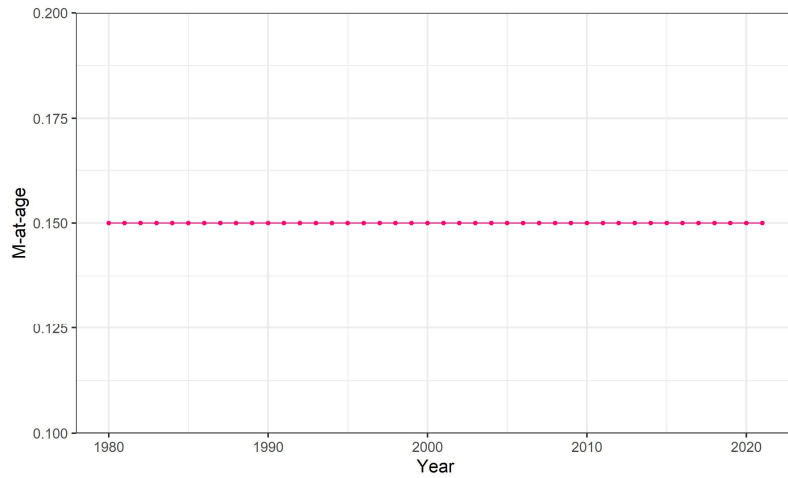


Figure 3: Northeast Atlantic mackerel. Natural mortality-at-age by year and cohort (all ages and years the same M)

Density dependence in mass-at-age vs. Total biomass

The distribution of mass-at-age is shown in the figure below (left) and the relationship between mass-at-age and total biomass of mackerel is shown to the right. Consistent negative slopes on the biomass-mass-at-age plots can be observed for ages 4 and beyond. The patterns for the younger ages are less clear. It should be remembered that the younger ages do not appear strongly in the catches.

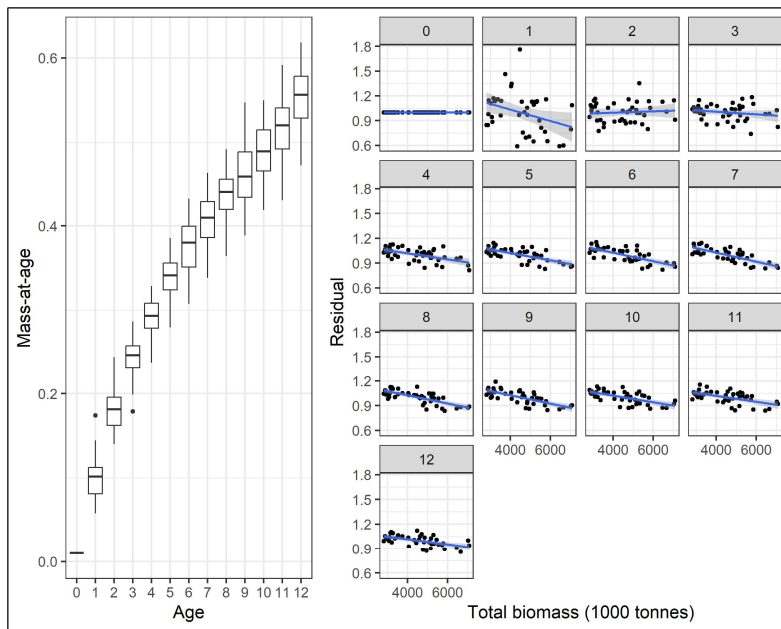


Figure 4: Northeast Atlantic mackerel. Density dependence and mass-at-age.

GAMM-at-age

A Generalized Additive Mixed Model (GAMM) was estimated to assess the relationship between mass-at-age and total biomass.

weights are predicted from two variables: a smoother of total biomass/mean(total biomass) and age. The resulting factor is shown below, indicating a nearly linear decline in mass-at-age as total biomass increases.

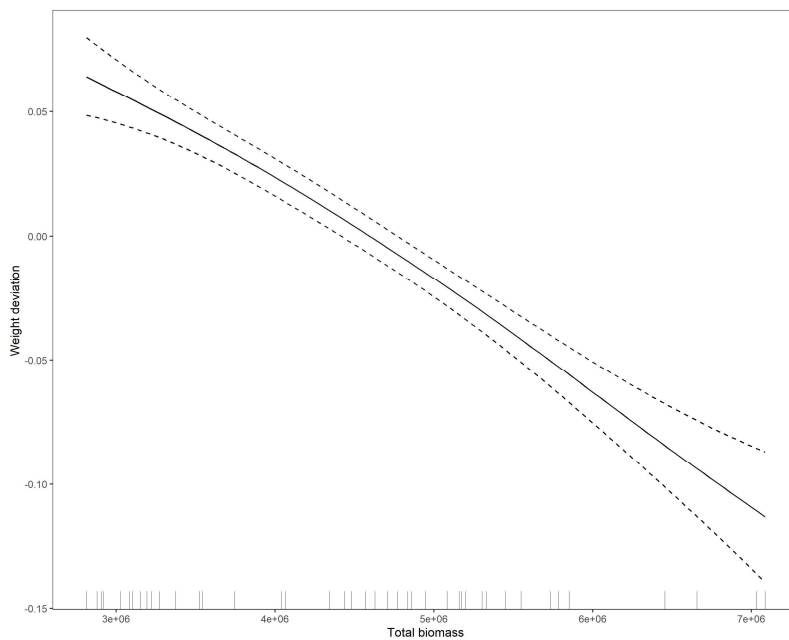


Figure 5: Northeast Atlantic mackerel. GAMM analysis of density dependence and mass-at-age.

A summary of the GAMM model is shown in the table below.

```

Family: gaussian
Link function: identity

Formula:
log(data) ~ s(tb/mean(tb), bs = "tp") + age

Parametric coefficients:
      Estimate Std. Error t value Pr(>|t|)
(Intercept) -2.34542    0.01539  -152.42 <2e-16 ***
age2         0.62723    0.02176   28.82 <2e-16 ***
age3         0.92079    0.02176   42.31 <2e-16 ***
age4         1.11028    0.02176   51.02 <2e-16 ***
age5         1.25334    0.02176   57.59 <2e-16 ***
age6         1.35980    0.02176   62.48 <2e-16 ***
age7         1.43847    0.02176   66.10 <2e-16 ***
age8         1.51318    0.02176   69.53 <2e-16 ***
age9         1.56657    0.02176   71.99 <2e-16 ***
age10        1.62197    0.02176   74.53 <2e-16 ***
age11        1.67507    0.02176   76.97 <2e-16 ***
age12        1.74790    0.02176   80.32 <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
      edf Ref.df    F p-value
s(tb) 1.719  1.719 74.47 <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq. (adj) = 0.96
Scale est. = 0.0099455 n = 504

```

Table 1: Northeast Atlantic mackerel. GAMM summary of density dependence and mass-at-age.

Linear model of density dependence in mass-at-age

The change in relative mass-at-age (i.e. observed - mean values) is plotted against total biomass, this allows the relationship between growth and total biomass to be compared across all ages. It is seen that there is a common negative relationship for all ages. A summary of the linear model is in the table below. The trend of growth with biomass is -0.18, this was then used to model mass-at-age as:

$$W_a = \overline{W}_a (B/B_{MSY})^{\beta_a}$$

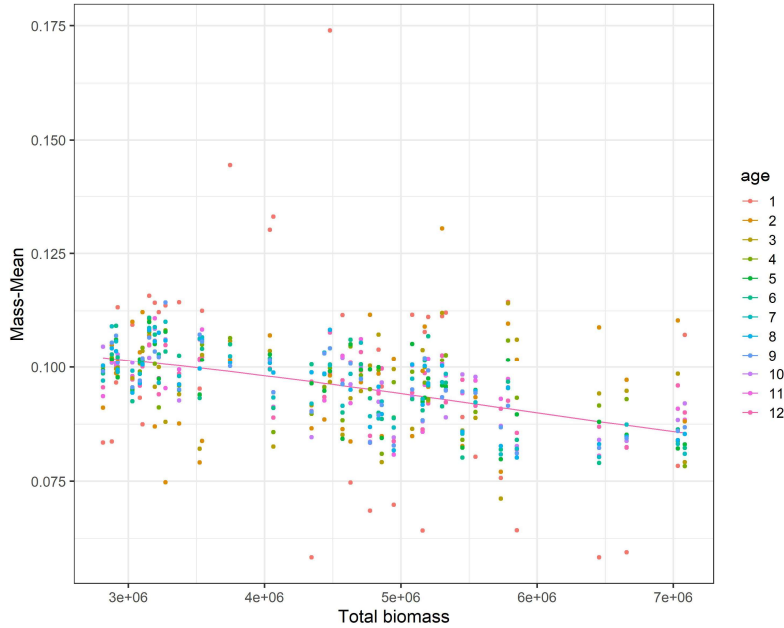


Figure 6: Northeast Atlantic mackerel. LM analysis of density dependence and mass-at-age.

```
Call:
lm(formula = hat ~ tb, data = transform(wt2, tb = tb/mean(tb)))

Residuals:
    Min       1Q   Median       3Q      Max
-1.2440 -0.1782  0.1609  0.3450  0.5153

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept) -0.92491    0.08527  -10.847  <2e-16 ***
tb          -0.18429    0.08244   -2.235  0.0258 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.4892 on 502 degrees of freedom
Multiple R-squared:  0.009857, Adjusted R-squared:  0.007884
F-statistic: 4.997 on 1 and 502 DF, p-value: 0.02583
```

Table 2: Northeast Atlantic mackerel. LM summary of density dependence and mass-at-age.

Density-dependence analysis of maturity-at-age

The distribution of maturity-at-age is shown in the figure below (left) and the relationship between maturity-at-age and total biomass of mackerel is shown to the right. Negative slopes on the biomass-maturity-at-age plots can be observed for ages 2 and 3, which are the most relevant ages for maturity as all fish of age 4 and above are mature.

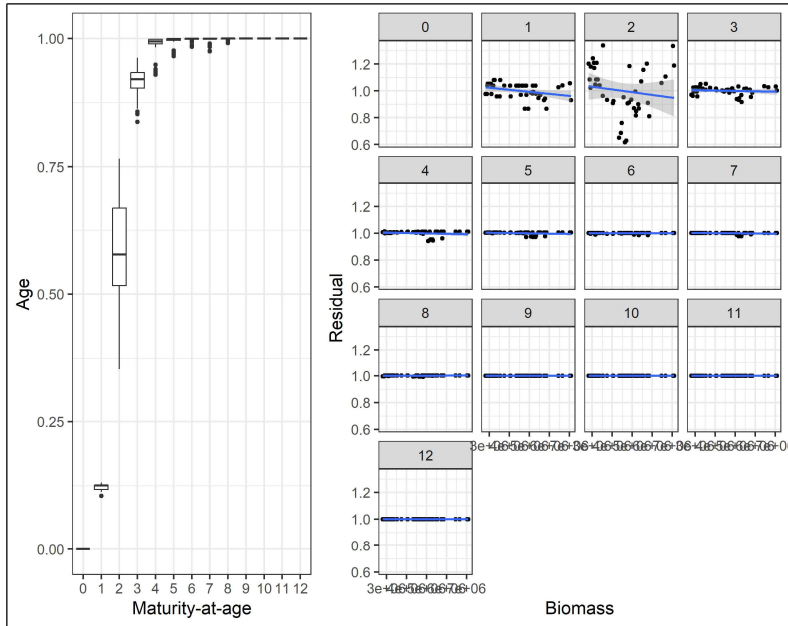


Figure 7: Northeast Atlantic mackerel. Analysis of density dependence and maturity-at-age.

Estimated maturity at weight

A maturity at weight ogive was generated from this formula:

$$f(x) = \frac{1}{1 + e^{-k(x-x_0)}}$$

This resulted in the parameters $k=28.1$ and $W_{50}=0.166$ which have been used in subsequent simulations.

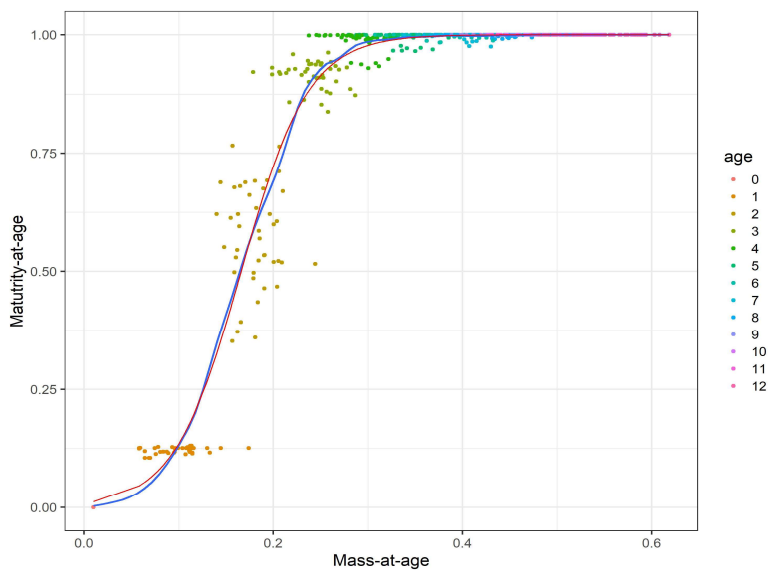


Figure 8: Northeast Atlantic mackerel. Estimated maturity ogive at weight

3 Estimating Density Dependent effects based on life-history parameters

Life history parameters are used to develop an example of modelling density dependence for mass, maturity and natural mortality-at-age. The parameters are first used to construct an ***FLBRP** object representing the equilibrium, and are then coerced into an **FLStock** to model the time series dynamics.

3.1 Mass-at-age

Mass-at-age (W_a) is modeled as

$$W_a = \overline{W}_a (B/B_{MSY})^{\beta a}$$

Where \overline{W}_a and β are estimated from a regression of mass-at-age (W_a) on total biomass (B_a), based on empirical data. W_a is constrained so that sizes do not become unfeasible large or small.

3.2 Maturity-at-weight

Maturity is then modeled as a logistic function of mass-at-age i.e.

$$O(W_a) = 1/(1 + e^{k(W_a - W_{50})})$$

3.3 Natural mortality

Natural mortality is assumed to vary at unit length (L_1).

Empirical and theoretical studies (Lorenzen (2000)) have shown that natural mortality (M) decrease with fish length, but increase with the von Bertalanffy parameters of curvature k and asymptotic length L_∞ . Therefore, M can be derived from life history parameters, e.g. $M = 1.5kL_\infty/L$ (Pope et al. (2021)) or $M=1.5k$ Jensen (1985). Lorenzen (2008) Lorenzen, Camp, and Garlock (2022) showed that natural mortality rates vary with body size and age, often by orders of magnitude over the life cycle and support the existence of an allometric relationship between M and body mass (W) at-age of the form:

$$M = M_u W^d$$

Where M_u is M at unit weight, and d is the allometric exponent from empirical relationships shown to range from -0.3 to -0.37. d is approximately equal to -1/3, which implies that M is inversely proportional to body length, since mass is approximately proportional to the third power of length. This is consistent with (Gislason et al. 2008), who proposed a relationship for natural mortality based on length

$$M = \alpha k (L_\infty \chi) L \beta$$

The plot below shows the equilibrium values by age for simulations initiated with different levels of biomass relative to B_{MSY} . The red line indicates the values from the current assessment (for natural mortality that varies by mass and hence age).

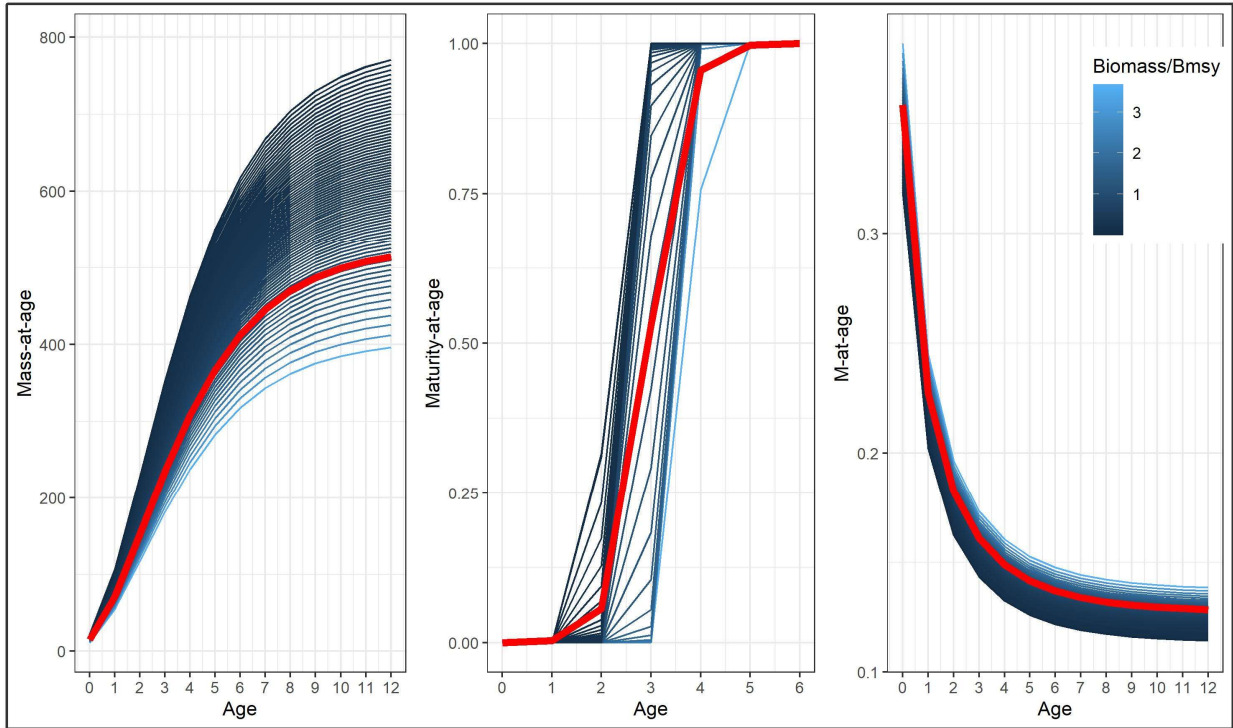


Figure 9: Simulation of density dependence in mass-at-age, maturity-at-age and Natural mortality-at-age for different levels of biomass relative to B_{MSY} . Red line is without density dependence.

From the theoretical life-history parameters and simulations, we can compare the equilibrium total biomass and yield from an assessment without density dependence, and then adding, step-by-step, the density dependent processes for mass-at-age, maturity-at-age and natural mortality-at-age. Comparison of equilibrium yield plots for simulation with and without density-dependent processes indicates that the expected values for B_{MSY} tend to become lower when density dependence is included and that MSY becomes somewhat higher.

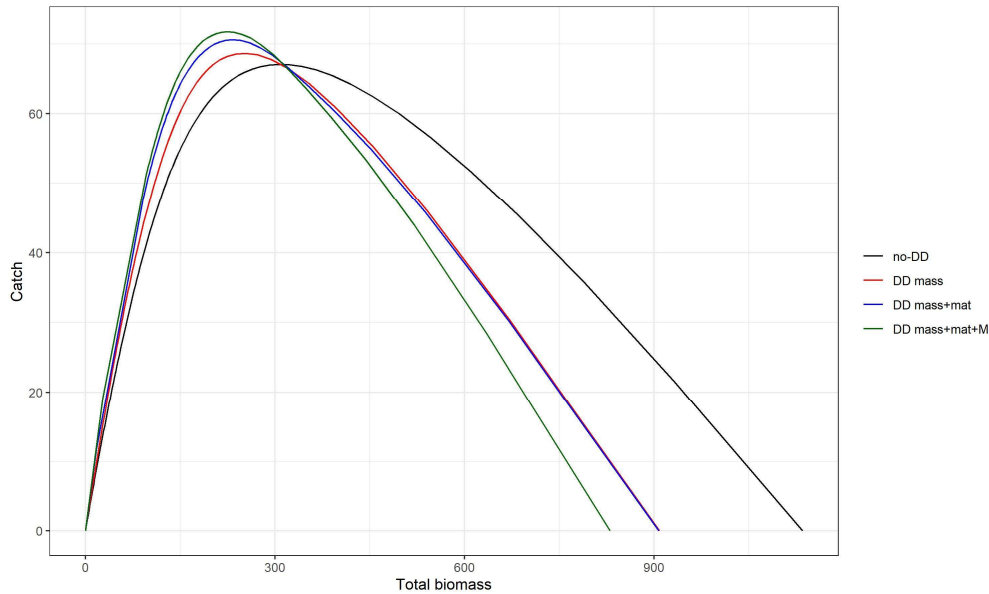


Figure 10: Simulation of density dependence in M -at-age for different levels of biomass relative to B_{MSY}

4 Setting up the Operating Models (OM)

Stock assessments

The operating models for this study are derived from the 2022 stock assessment. SAM is a statistical catch-at-age model that estimates error in the catch-at-age. In the case of mackerel, the assessment gives a higher weight to the recruitment index than to the catch data for ages 0 and 1. This means that the estimates of recruitment in the assessment can be very different from the actual number of fish that are recruited to the fishery. To ensure the MSE projections and the historical estimates are comparable, a Virtual Population Analysis (VPA) was conducted on the whole catch matrix and the survivors in the most recent year and oldest age. In the next step, we applied a natural mortality-at-age vector derived from the Lorenzen approach which would mimic the VPA assessment with fixed M -at-age. The figure below compares the SAM assessment with the VPA and the VPAM assessment. A main difference is in the recruitment estimates. Using age-varying M tends to flatten the recruitment pattern. The vpaM model was used as the base case to be compared against the density-dependent simulations.

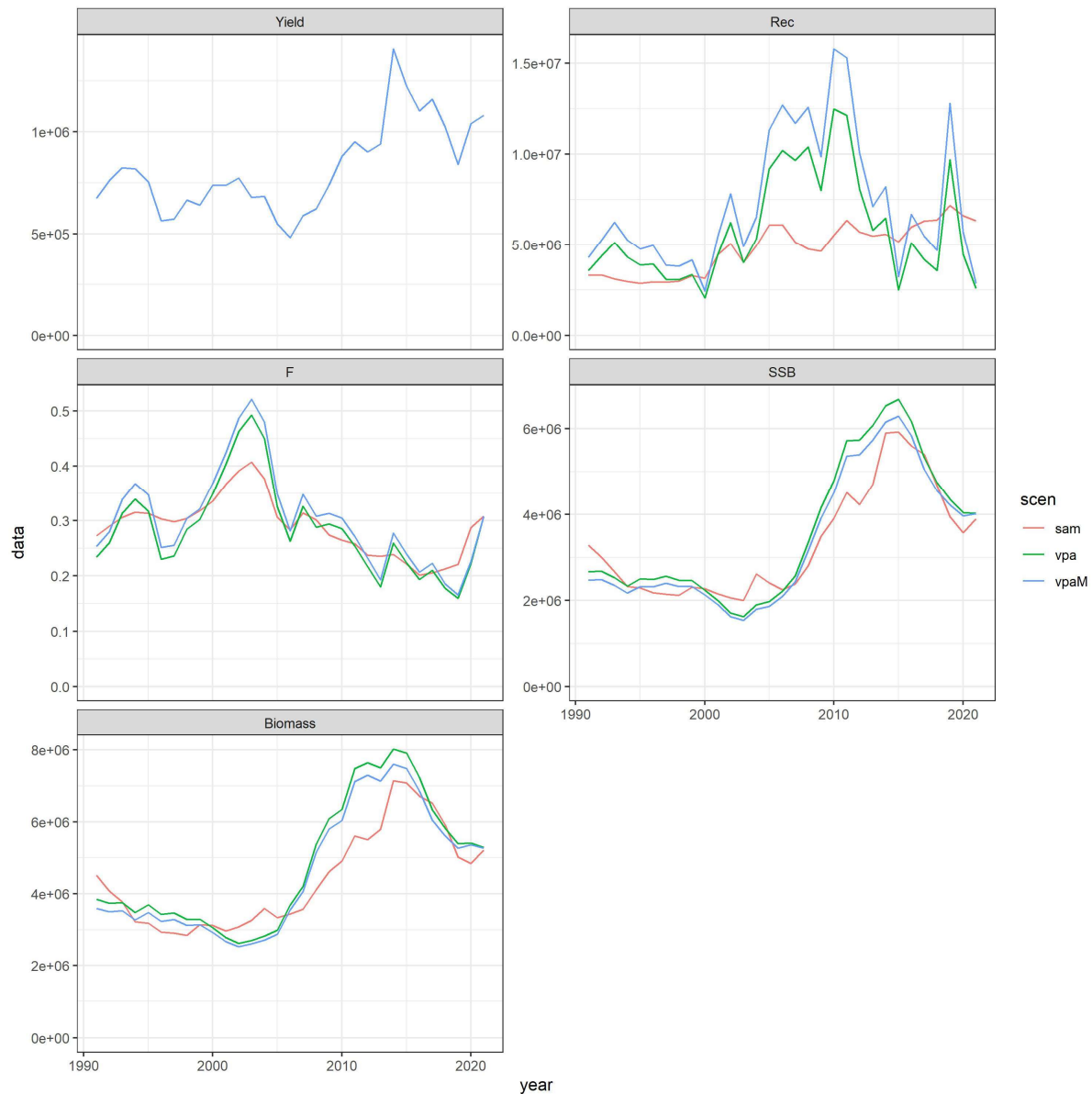


Figure 11: Comparison of different assessments. VPA-M is used as the base case going forward

Density dependence in mass-at-age

When applying density dependent processes to mass-at-age (i.e. lower mass-at-age for higher biomass), B_{MSY} is expected to be somewhat lower. The expected increase in MSY is small.

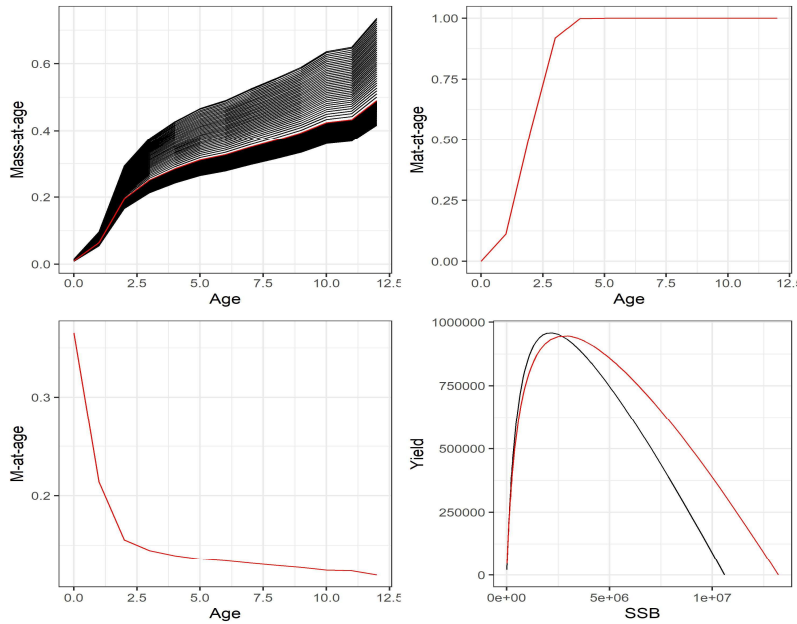


Figure 12: Simulation of density dependence in Mass-at-age. Red lines are the non-density dependent values.

Density dependence in mass-at-age and maturity-at-age

When applying density dependent processes to both mass-at-age and maturity-at-age, B_{MSY} is expected to be lower again and MSY is expected to increase.

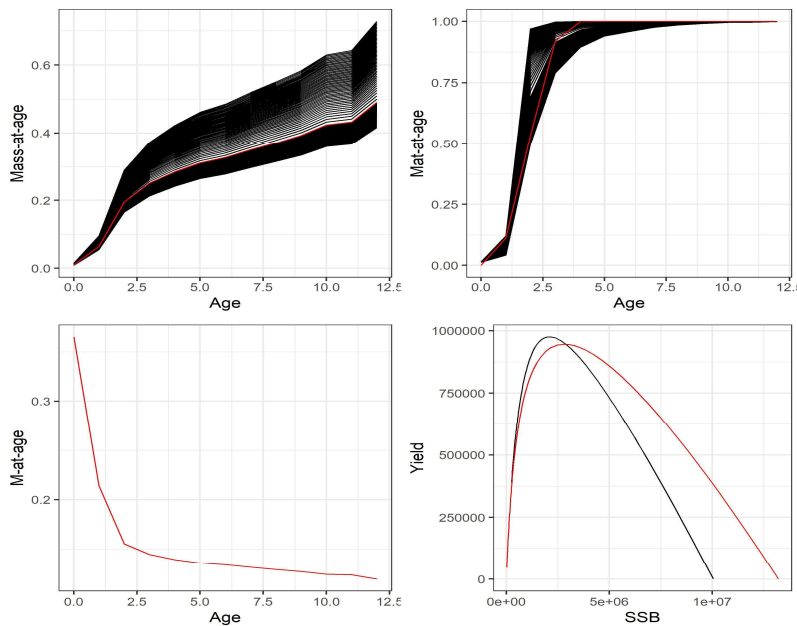


Figure 13: Simulation of density dependence in Mass-at-age and Maturity-at-age. Red lines are the non-density dependent values.

Density dependence in mass-at-age, maturity-at-age and M-at-age

When applying density dependent processes to all three variables, B_{MSY} is expected to be lower again and MSY is expected to increase a bit more.

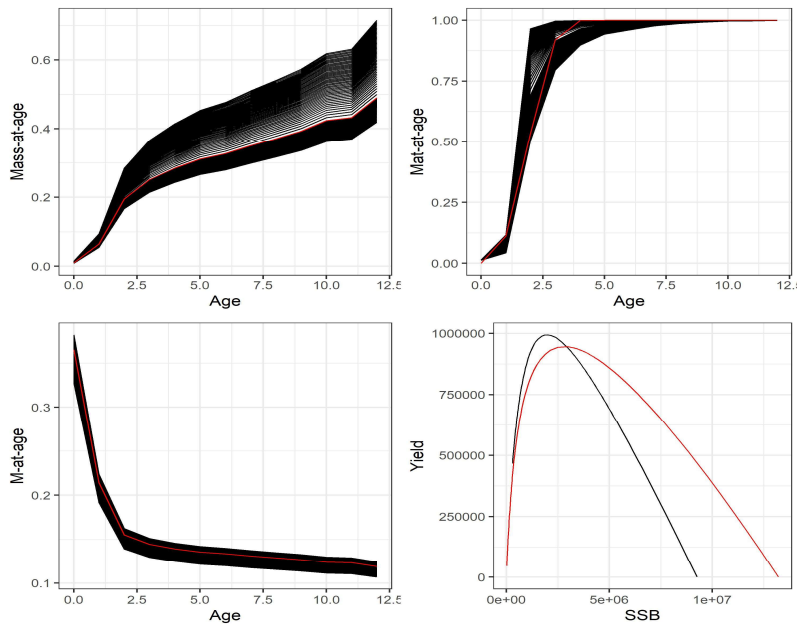


Figure 14: Simulation of density dependence in Mass-at-age, maturity-at-age and M-at-age. Red lines are the non-density dependent values.

Comparison of equilibrium curves for density dependence analyses: biomass against yield and F

The comparison of the equilibrium curves, indicate that B_{MSY} is expected to decrease by 30%, F_{MSY} is expected to increase by 113% and catch (MSY) is expected to increase by 5%. So while, inclusion of density-dependent processes, has a substantial impact on biological reference points, the resulting change in equilibrium catch is expected to be small.

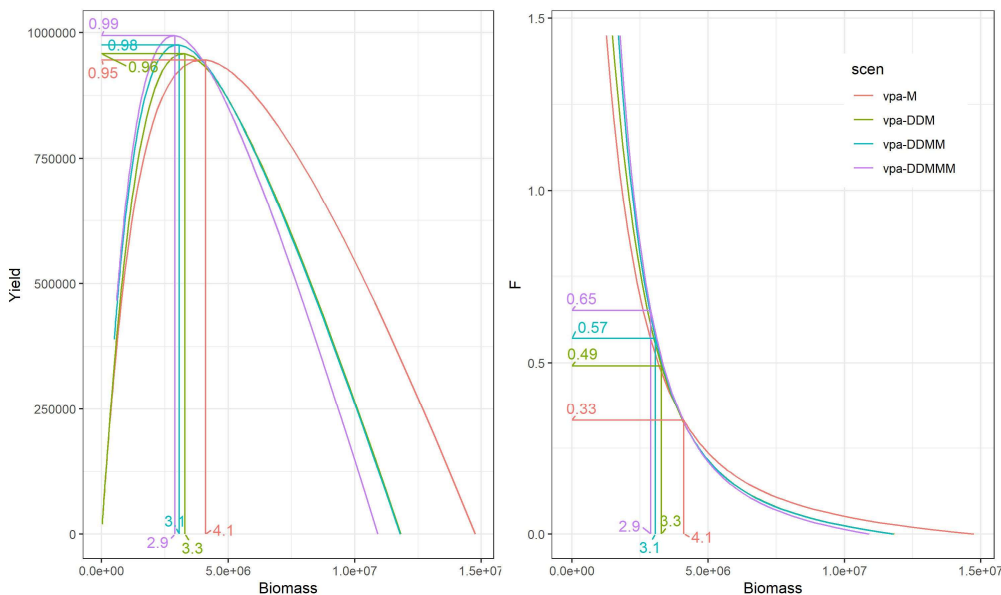


Figure 15: Equilibrium curves for density dependence analyses: biomass against yield and biomass against F

5 Forward projections without feedback

Forward projections were run in two modes. Firstly in deterministic mode and secondly in probabilistic mode. We used the F_{MSY} to project forward from 2020 until 2050.

Reference points estimated for the different scenarios are in the table below.

scen	Bmsy	SSBmsy	MSY	Fmsy	Virgin	B0
Base	4,106,412	2,946,492	945,792	0.3315	13,218,658	14,757,139
DD Mass	3,098,045	2,012,831	985,096	0.5711	10,581,603	11,812,772
DD Mass, Mat	2,762,563	1,872,714	1,006,383	0.7308	10,039,198	11,780,746
DD Mass, Mat, M	2,660,300	1,781,911	1,028,576	0.8107	9,251,026	10,895,522

Table 3: Northeast Atlantic mackerel. Reference points for the different scenarios

We used both the F_{MSY} that is applicable to the density dependent scenario, but also evaluated what would happen if the 'wrong F_{MSY} ' would be used with a particular scenario.

The plot below shows the deterministic runs with the appropriate F_{MSY} value being used to project forward. F_{MSY} is highest when density dependence is taken into account for all three processes. Nevertheless, expected catches are somewhat lower when density dependence is taken into account.

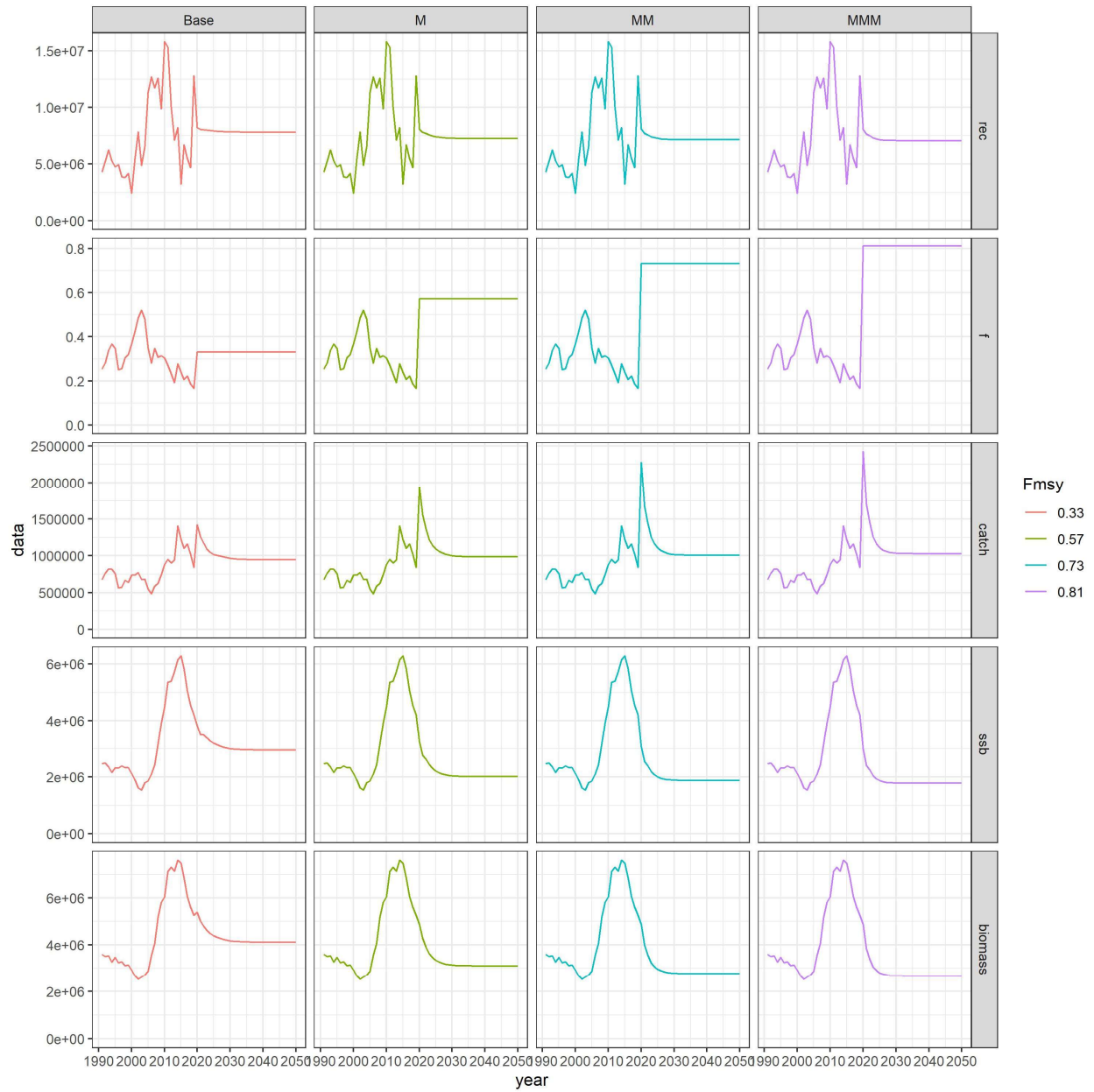


Figure 16: Deterministic projections at F_{MSY} for different scenarios

Deterministic projections at F_{MSY} for different scenarios: trends in weight, maturity and M-at-age

How can we understand the results of the deterministic runs? Below is a plot of the trends in stock mass-at-age, maturity-at-age and natural mortality-at-age, for the most relevant ages (1-6) and for the four different scenarios (Base, DDM, DDMM and DDMMM). The density dependent effect of maturity is strongest when both stock weight and maturity are density dependent. When natural mortality is also density dependent, this affects the stock size and hence also the density dependence for stock weight and maturity, leading to a smaller density dependent effects for those variables.

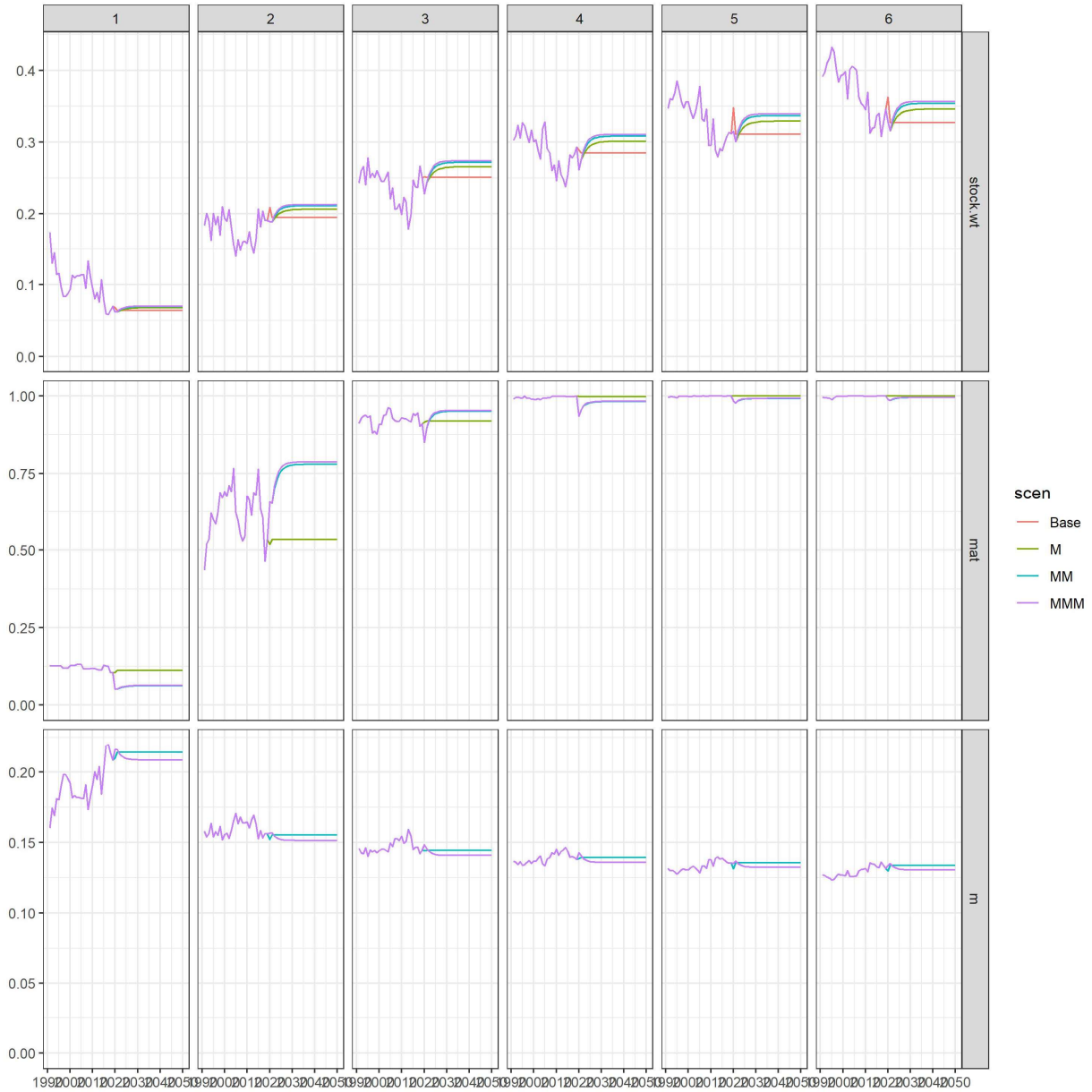


Figure 17: Deterministic projections at F_{MSY} for different scenarios: trends in weight, maturity and M-at-age

Stochastic projections at F_{MSY} for different scenarios

Using stochastic projections by including random processes for recruitment deviations and the F_{MSY} values that are consistent with the different scenarios, leads to the overview below. SSB and total biomass are highest in the case of no density dependence. Catches are different in the first years of 'switching' to the new reference points, but afterwards, the catches for the different scenarios are highly comparable.

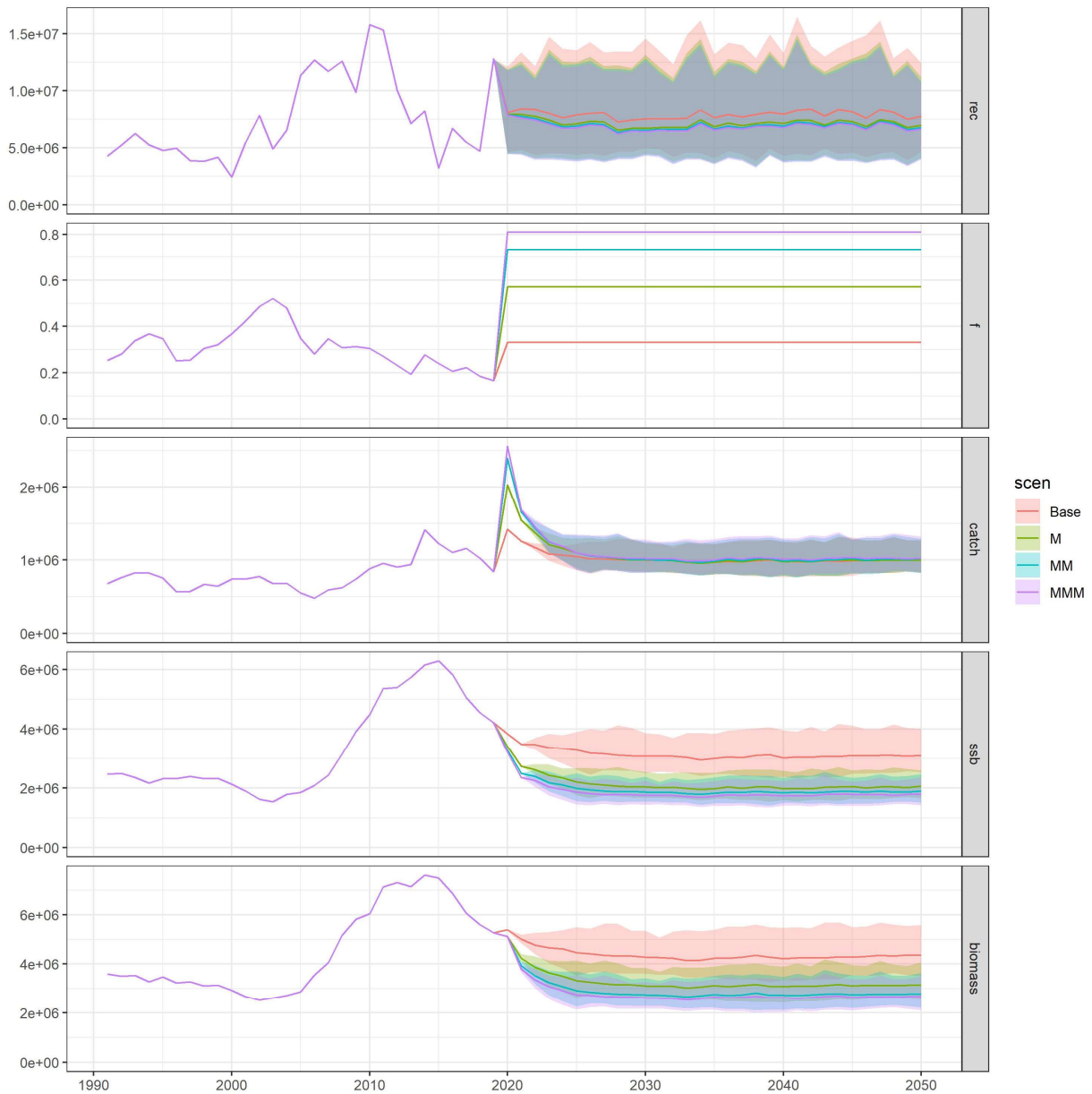


Figure 18: Stochastic projections at F_{MSY} for different scenarios

Histograms of probability distributions in 2050 for different scenarios

The histograms of the probability distributions in 2050 for different scenarios, again demonstrate the expected larger stock size without taking density dependence into account, and only marginal differences in catch.

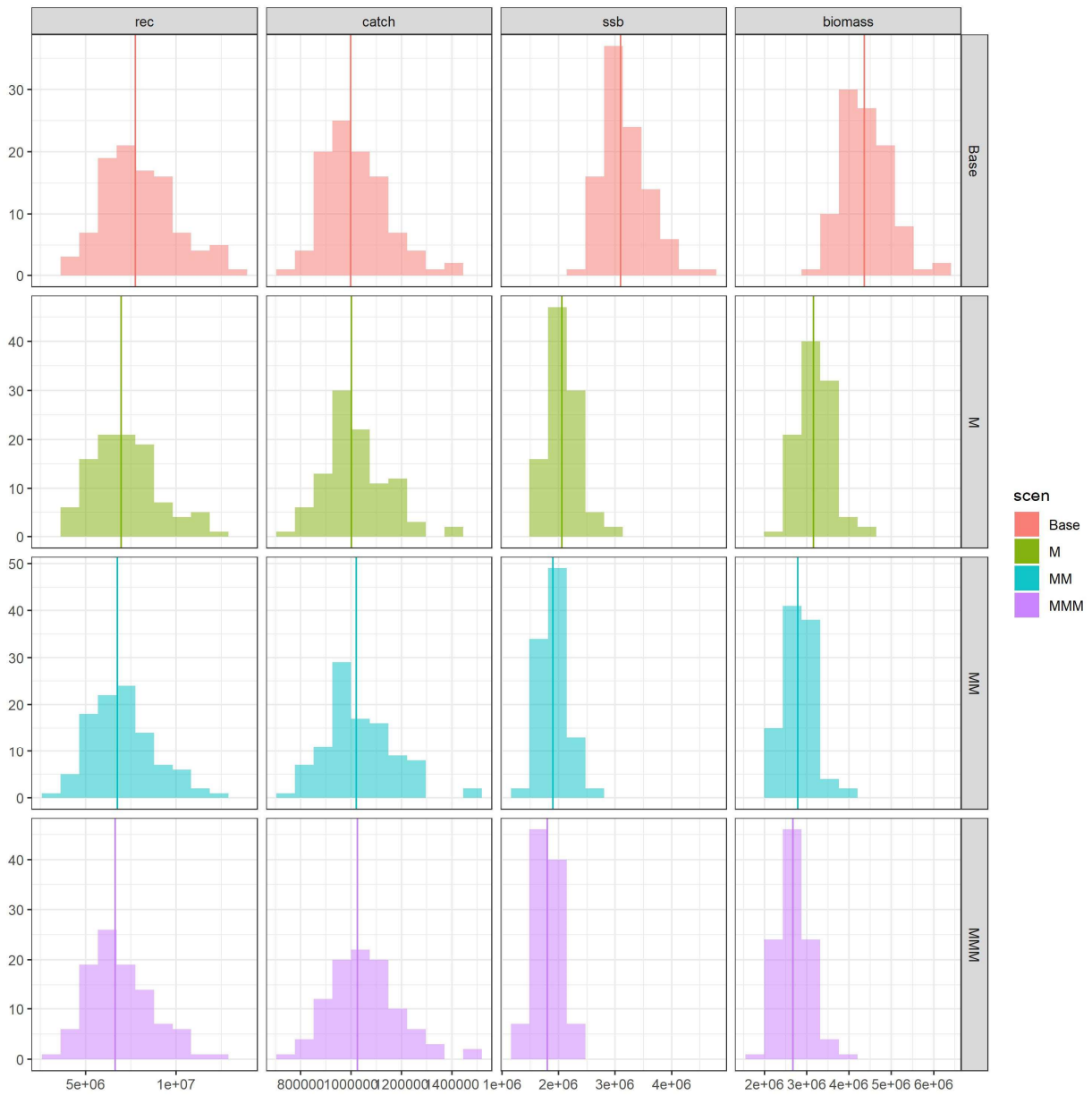


Figure 19: Histograms of probability distributions in 2050 for different scenarios

Stochastic projections at all F_{MSY} 's from all scenarios

For the stochastic projections at all F_{MSY} 's, we added two F scenarios: one with $F=0.1$ and one with $F=1.5$.

Misspecification of F_{msy} , i.e. using an F_{msy} from one scenario and applying it to a different scenario has only limited impacts on the overall outcomes in terms of recruitment, biomass or yield. In the plot below, the scenarios for density dependence are shown in the columns and the F 's are shown as the colours. For example, a valid combination is the Base case with the yellow-brownish curve ($F_{msy}=0.33$) or the M (mass) scenario with the green curve. The misspecification of F_{msy} does not result in noticeable differences in catch although they do have important difference for biomass. Application of a low $F (=0.1)$ is expected to lead to lower catches in all scenarios.

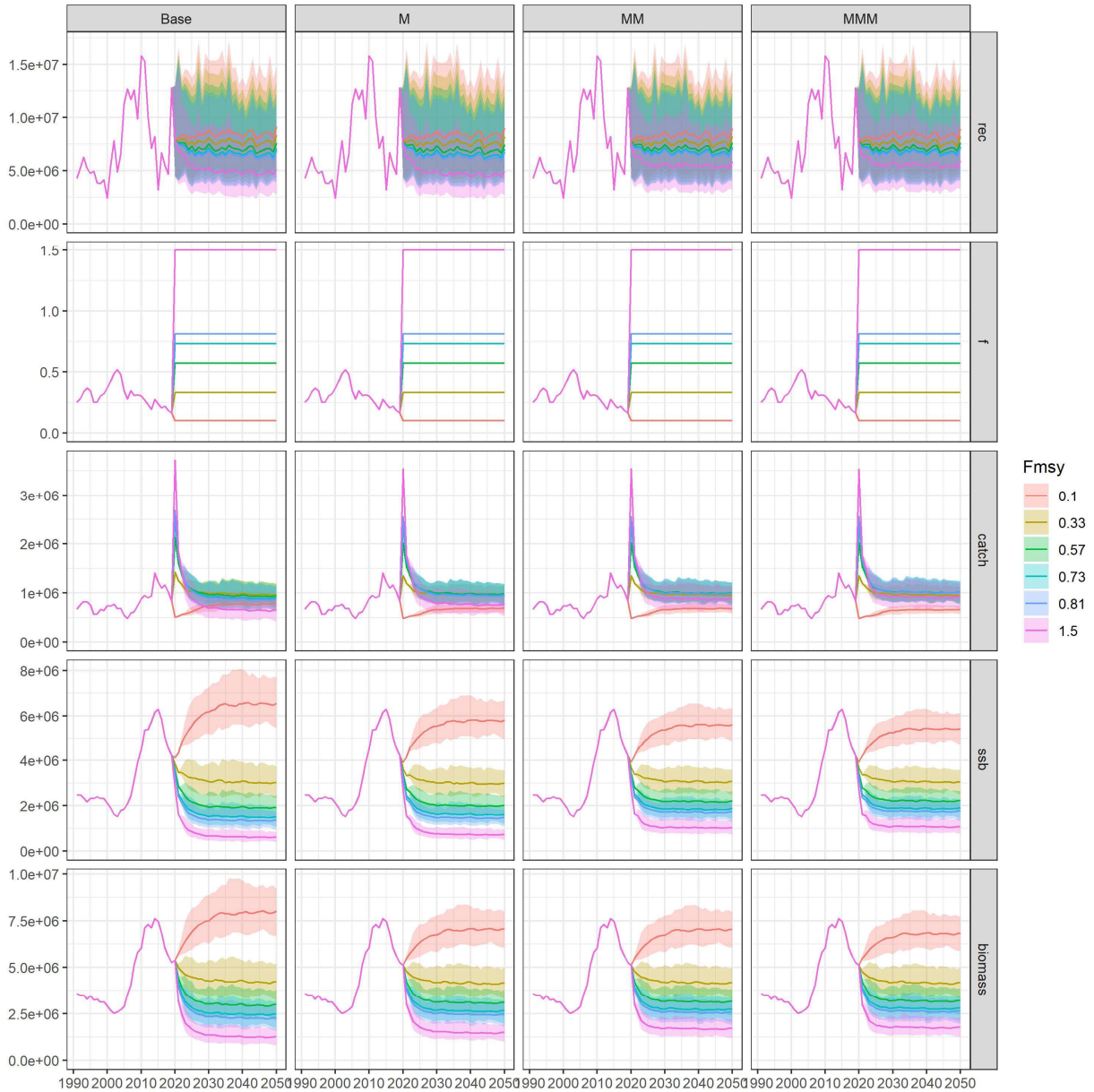


Figure 20: Stochastic projections at all F_{MSY} 's from all scenarios

For the four F_{MSY} -scenarios and the two additional F scenarios, we plotted the Kobe phase plot for 2050 with the associated density functions for B/B_{MSY} and $Catch/MSY$. The results confirm the results that equilibrium catch is not really affected by the DD assumptions of the F_{MSY} applied, but that biomass is sensitive to the assumptions.

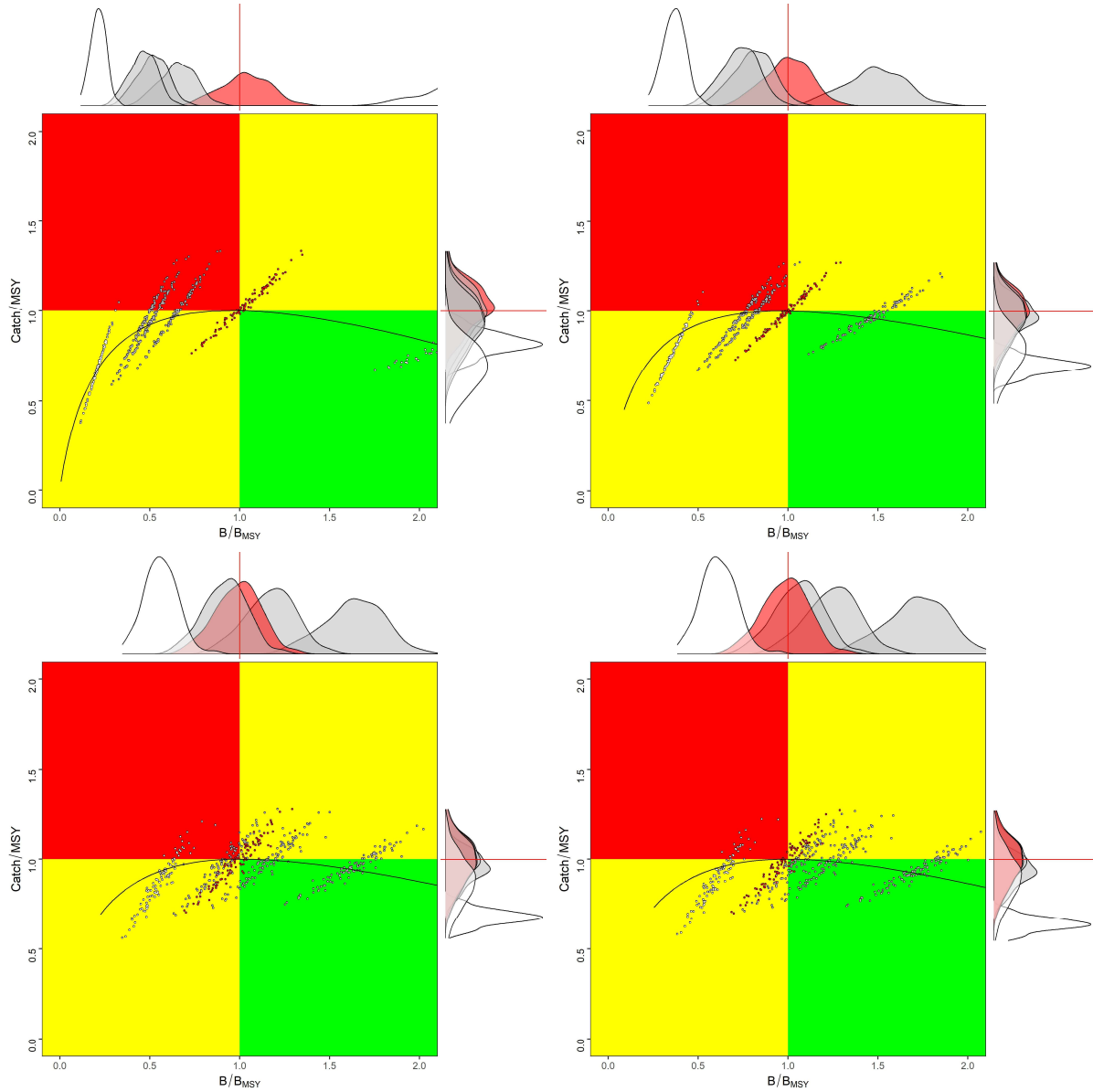


Figure 21: Kobe plot for 2050 for base case (no DD) for all F_{MSY} 's (red is from the right scenario). Topleft: base, topright: M, bottomleft: MM, bottomright: MMM . White densities refer to the low and high F scenarios

We then plotted the Kobe phase plot for 2050 with the associated density functions for F/F_{MSY} and $Catch/MSY$. Because there is no uncertainty included in the fishing mortality during the simulations, the marginal distributions of F do not exist in this plot.

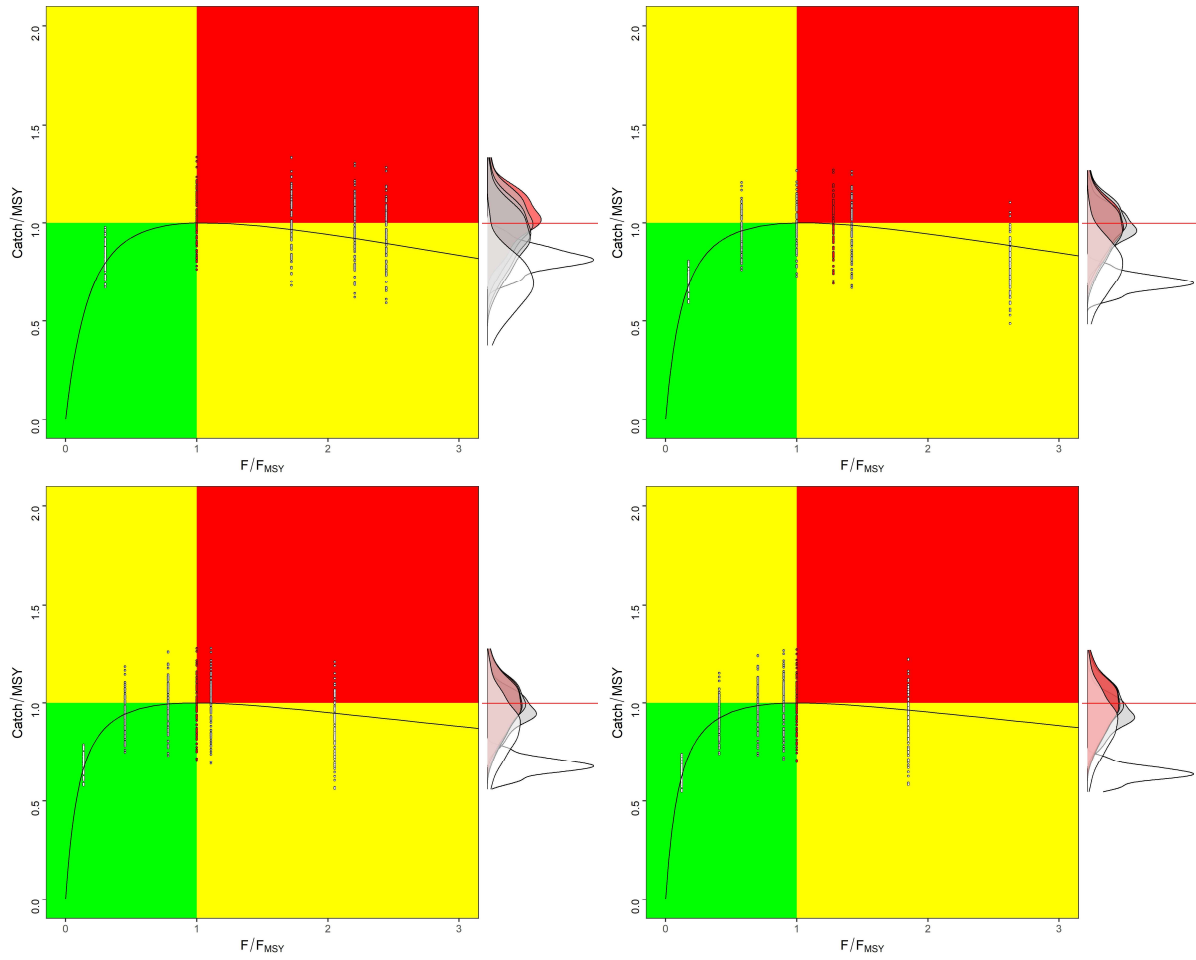


Figure 22: F Kobe plot for 2050 for base case (no DD) for all F_{MSY} 's (red is from the right scenario). Topleft: base, topright: M, bottomleft: MM, bottomright: MMM . White densities refer to the low and high F scenarios

Finally, as a check, we assessed the outcomes of the equilibrium curves from simulating over a wide F range, with the equilibrium values (points) in 2050 from the forward projections at different values of F_{MSY} (colors). The points fall on the equilibrium curve, thereby confirming the consistency between the two approaches.

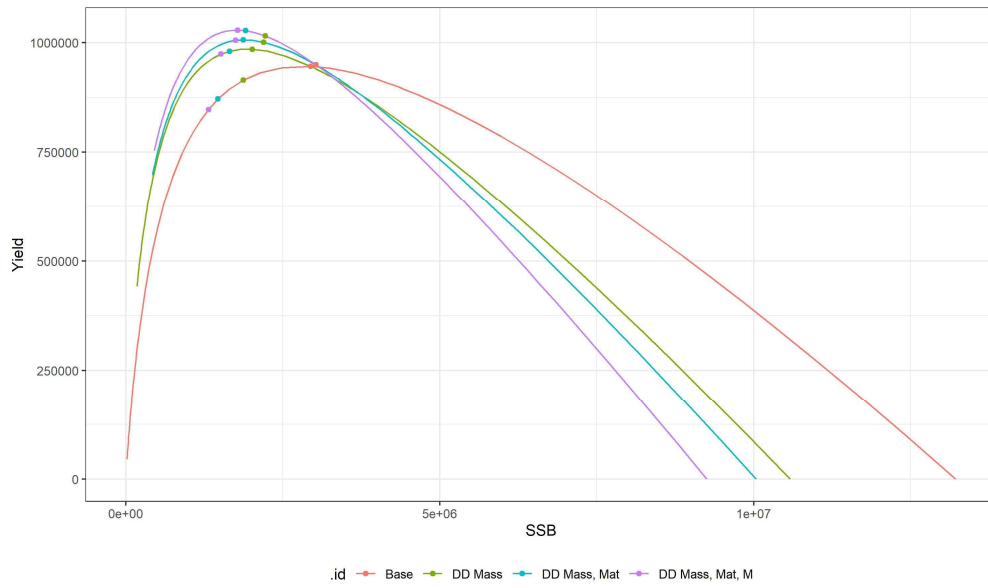


Figure 23: Check of equilibrium curves against end points of simulated time series at F_{MSY} 's from all scenarios

6 Discussion and conclusions

The current management of fish stocks is based on achieving a fishing mortality (F_{MSY}) that is expected to achieve the maximum sustainable yield (MSY). Estimation of MSY generally only includes the stock recruitment relationship when considering density dependent population regulation mechanisms. Density dependence, however, may also operate in processes such as growth, sexual maturity, and natural mortality. A main aim of this study was to condition Operating Models (OMs) on alternative hypotheses about density dependence for use in Management Strategy Evaluation (MSE). The objective is to evaluate the robustness of the assessments conducted to support the ICES advice framework. To do this, OMs were developed that include density dependence in growth, maturity, natural mortality, individually and combined. These OMs were then used to evaluate the consequences of including or not including density dependence in management advice.

Initial explorations of density dependent effect were conducted based on life history theory, as used by the International Council for the Exploration of the Sea (ICES) to develop advice conducting MSE for data poor stocks (Fischer, DeOliveira, and Kell 2020). **Figure 10** shows the the equilibrium curves of catch v SSB assuming a) no density dependence, and density dependence in b) mass-at-age, c) mass & maturity-at-age, and d) mass, maturity and natural mortality-at-age. These allow the relationships between the MSY reference points and virgin biomass to be seen.

Estimating density-dependence from observations was only possible for mass-at-age and maturity-at-age. Density dependence in natural mortality can only be explored from theoretical considerations (because current assessment does not include age or time varying natural mortality).

In the next step, we applied a natural mortality-at-age vector based on (Lorenzen 2000) which would mimic the VPA assessment with fixed M-at-age. The figure below compares the SAM assessment with the VPA and the VPAM assessment. A main difference is in the recruitment estimates. Using age-varying M tends to flatten the recruitment pattern. The vpaM model was used as the base case to be compared against the density-dependent simulations.

Next, the operating models were constructed. This was done in a number of steps.

1. The ICES (SAM) assessment was taken from the ICES WGWIDE files (2022). SAM is a statistical catch-at-age model that estimates error in the catch-at-age. In the case of Northeast Atlantic mackerel, the assessment gives a higher weight to the recruitment index than to the catch data for ages 0 and 1. This means that the estimates of recruitment in the assessment can be very different from the actual number of fish that are recruited to the fishery.
2. Next, a VPA model model was estimated. This was done to ensure the MSE projections and the historical estimates are comparable. The Virtual Population Analysis (VPA) was conducted on the whole catch matrix and the survivors in the most recent year and oldest age.
3. The third step was to convert the VPA model with fixed natural mortality at age and by year into an age-varying natural mortality vector. We applied a natural mortality-at-age vector derived from the Lorenzen approach (Lorenzen (2000)) which would mimic the VPA assessment with fixed M-at-age. This assessment was then treated as the base case against which the density dependent operating models were compared.
4. The density-dependent scenarios were constructed cumulative. First by adding density dependence in mass-at-age (M), then in mass and maturity-at-age (MM) and then in mass, maturity and M-at-age (MMM),

Therefore, the four Operating Models were

- VPA Base Case, with varying M-at-age
- Density dependence in mass-at-age,
- Density dependence in mass, maturity-at-age,
- Density dependence in mass, maturity and M-at-age,

The MSY reference points B_{MSY} and F_{MSY} were calculated based on equilibrium assumptions, either from combining yield per recruit and spawner per recruit relationship (Sissenwine and Shepherd 1987) or by conducting long-term projections under constant fishing mortalities.

Each of the four OMs were then projected for the values of F_{MSY} based on the four assumptions about density dependence. This allows a comparison between the yield that could potentially be achieved and that forgone by making an incorrect assumption about density dependence.

The OMs were first projected, without process error in recruitment, from the end of the historical estimates for a range of fishing mortality (spanning 0 to F_{cra}) for 30 years into the future. The estimates in the final year of the projections were then be used to construct equilibrium curves (**Figure 15**). The points on the curve correspond to the projected outcomes for the values of F_{MSY} from each OM. This was run as a check, as the equilibrium and projections should agree, i.e. the points at MSY should be the same color as the curve.

The OMs were also projected for the estimates of different estimates F_{MSY} , with stochasticity in the recruitment deviates. This allows the impact of misspecification of density dependence to be evaluated, i.e. if F_{MSY} is underestimated then yield will be less than MSY, while if F_{MSY} is overestimated yield will be lost due to overfishing. Stochastic projections of the four Operating Models for the four estimates of F_{MSY} are shown in **Figures 16-19**

Figure 20 summarizes the yields and SSBs obtained for each Operating Model under the correct and misspecified form of density dependence and the associated reference points, **Figure 21** shows the Kobe plots of the final 2050 distributions of biomass and yield and **Figure 22** the Kobe plots for F and yield.

Estimating density-dependence from observations was only possible for mass-at-age and maturity age. Therefore, density dependence in natural mortality can only be explored from theoretical considerations, because current assessment does not include age or time varying natural mortality. M is likely to vary by age and time in relation to processes such as density dependence. While the recent expansion in distribution area and change in weight-at-age could be associated with changes in natural mortality. Therefore in the OMs we modeled M as a function of mass-at-age.

The impact of including density dependence was primarily on the biological reference points. Especially F_{MSY} is much higher when including density dependence. However, the expected yields in equilibrium conditions are very similar. The main difference is in the initial step from the current F_{MSY} to any new F_{MSY} that would include DD, as the higher F_{MSY} would be applied to a stock that is estimated without DD.

Since the early 1980s, natural mortality (M) for mackerel has been fixed within the assessment model at 0.15, for all ages and all assessment years. This value was calculated based on estimates of total mortality derived from tagging data combined with catch data (Hamre 1980). M must, however, vary both by age and over time due to changes in abundance of predators, feeding conditions, disease etc. (Siegfried and Sansó 2009). Particularly any changes in mackerel distribution and growth will affect natural mortality.

Given the uncertainty in the assessment and the estimation of density dependence, it is likely that the Pretty Good Yield approach would ensure sustainable exploitation. Also, because we did not yet consider stochastic variability in future developments in mass, maturity and natural mortality which are likely to obscure the impacts of density dependence. Variations in these processes due to changes in climate and range expansion are also likely to occur.

It is suggested that empirical harvest control rules that respond to changes in productivity could be evaluated in contrast to the highly complex harvest rules based on SAM stock assessment models.

The quality of this analyses lives up to the quality standards that are required by ICES and so can potentially be used when providing advice to fisheries managers. The software is publicly available via Github (<https://github.com/mar-tinpastors/ddmse>). All data is derived from WGwide 2022 ICES (2022b).

7 Funding

This work was funded under a consultancy agreement between the University of Copenhagen and Martin Pastoors F&F as part of the project “117957 Fmsy-project for six high profile fish stocks”. The current work focused on North-east Atlantic mackerel and was carried out in the months of January-March 2023. A similar project was carried out for Blue whiting by Sea++. Both projects were carried in close coordination between Sea++ and Martin Pastoors F&F.

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