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Extending the Northern Cod (*Gadus morhua*) Assessment Model - Part II: Quantifying the Impact of Capelin and Seals

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Understanding the dynamics of marine ecosystems is crucial for effective fisheries management. The dynamics of Northern cod *(Gadus morhua)* are influenced by various ecological factors, including the availability of key prey species like Capelin *(Mallotus villosus)* and consumption by predators such as seals. Previous research has explored the impact of Capelin availability and Harp Seal *(Pagophilus groenlandicus)* predation on Northern cod mortality; however, specific age-related effects and the combined influence of these factors on natural mortality rates remain less understood. Here we show that Capelin abundance significantly affects the rates of natural mortality experienced by Northern cod, especially the older age groups. Additionally, our study indicates that Harp Seals have an impact on cod, particularly younger age groups. This study contributes to existing knowledge by uncovering nuanced age-related influences of Capelin and Harp Seals on cod mortality. Integrating these factors into predictive models enhances our ability to forecast changes in cod populations and underscores the importance of considering multi-faceted ecological interactions in fisheries management. Overall, this research represents an effort to move away from a purely descriptive assessment and towards a more mechanistic explanation of changes in Northern cod productivity. The overarching goal is to support an ecosystem approach to managing this important stock.

1. INTRODUCTION

Single species stock assessment models offer detailed perspective on long term dynamics of fishing pressure on a stock. In many assessment models the natural mortality (M) is assumed to be a constant value. In state-space models, process error and variance processes such as random walk and autoregressive processes on M offer insight on underlying unknown changes in stock dynamics and rarely are models able to estimate baseline M levels. The xteNCAM (extended Northern Cod Assessment Model) model for Northern cod *(Gadus morhua)*, described in Regular et al. (2025) incorporates multiple sources of data, including many years of tagging data and is able to estimate baseline levels of M. This paper is an extension of this model to explore the impacts of prey (Capelin) and predator (Harp Seal) population on this underlying processes affecting the stock. We model both the prey and predatory dynamics as explanatory variables for the natural mortality process.

Capelin (*Mallotus villosus*) have long been known to be an important food source for Northern cod (Templeman 1965), and a growing number of studies have demonstrated links between Capelin biomass and cod productivity (e.g., Krohn et al. 1997, Rose and O’Driscoll 2002, Buren et al. 2014, Koen-Alonso et al. 2021). Further, strong correlation was observed between Capelin availability, an indicator of Northern cod’s starvation rates based on body condition data, and the natural mortality rates estimated in the NCAM model (Regular et al. 2022). These links, along with the fact that the Capelin collapse preceded the collapse of cod, indicate that prey availability may have contributed, in part, to the collapse of cod. Moreover, cod have yet to rebound to levels last observed in the 1980s, and this may be related to the persistent low-productivity state of Capelin. Here, we aim to explore these ideas further by integrating the availability of Capelin into the assessment model. Given previous findings, we expect rates of mortality to increase as the relative abundance of Capelin decreases. Overall we aim to gain a more precise and mechanistic explanation of the changes in productivity of Northern cod.

For as long as Capelin have been known to be an important prey source for Northern cod, the Harp Seal (*Pagophilus groenlandicus*) has been flagged as a concerning source of natural mortality for cod. After undergoing an significant increase since the early-1970s, the seal population in the 2J3KL region peaked during the mid-1990s. This was followed by a subsequent decline, although the population remains higher than it was prior to the late-1980s (Tinker et al. 2023). Given this trend in the population there is a hypothesis proposing that seals might have a substantial impact on the recovery of Northern cod population. However, Buren et al. 2014 suggests that seals do not play a pivotal role in Northern cod recovery, emphasizing instead a bottom-up ecological dynamics, where the abundance of Capelin along with fisheries is key factor governing the dynamics of the cod populations. This contrasts with research in the northern Gulf of St. Lawrence (NGSL) where, underlined that in warmer conditions, achieving even a partial recovery for cod population might require substantial reductions in both fishing activity and Harp Seal predation (Bousquet et al. 2014). It is not yet clear whether the difference in inferences across these regions are related to modeling differences or actual ecological effects. We therefore revisit the quantification of the impact of seals on Northern cod to try and refine our understanding of the impact of this predator on the stock. Given previous findings on the age structure of cod consumed by Harp Seals (Stansbury et al. 1998), we do not expect the abundance of seals to explain changes in the mature component of the stock, but they may help explain some of the variation in the juvenile component of the population.

2. METHODS

Below we describe methods we utilize to try and quantify the impact of Capelin and seals on Northern cod using a state-space, age-structured assessment model. All models presented in this research document utilize the extended version of the Northern cod assessment model, generally referred to as xteNCAM, described in Regular et al. 2025. Specifically, we utilize three formulations of xteNCAM, all of which integrate juvenile survey data and apply a Beverton-Holt stock-recruit (S-R) relationship, but apply different assumptions to the estimation of baseline rates of natural mortality:

1. model **M11** estimates constant baseline rates of natural mortality,
2. model **M12** estimates and allometric effect, and
3. model **M13** estimates shifts in the baseline rates (M-shift2).

The constant approach (model **M11**) can be looked at as a NULL hypothesis where baseline rates are assumed constant across years and ages, the allometric approach (model **M12**) accounts for the possibility that mortality decreases as body size increases (Lorenzen 2022), and the shifting mortality option (model **M13**) attempts to capture substantive shifts in baseline levels of natural mortality (*sensu* the M-shift input used in the current assessment; Brattey et al. 2018). Both prey and predators likely affect change in the rates of mortality experienced by Northern cod and we aim to determine whether Capelin availability and seal abundance capture some of these changes. For reference, trends in cod, Capelin, and seals are shown in Figure 1. Like Part I (Regular et al. 2025), we will use model diagnostics and Akaike Information Criterion (AIC) to gauge whether the estimation of Capelin and/or seal effects provide a better explanation of the data than models **M11-M13**. Brief descriptions of the models presented here are included in Table 5.1.

2.1. MODELLING CAPELIN INTERACTION

Previous research demonstrated general correspondence between the availability of Capelin, an index of starvation rates of Northern cod estimated using body condition data, and rates of natural mortality estimated by NCAM (Regular et al. 2022). These results are highly suggestive of a mechanistic link between Capelin availability and rates of natural mortality experienced by Northern cod. To move beyond post-hoc analyses and further test these potential links, we integrated Capelin data into xteNCAM to utilize it as a predictor of the rates of natural mortality for Northern cod. Specifically, we used the ratio of Capelin/cod biomass as a covariate (*sensu* Regular et al. 2022) since rates of starvation are expected to be exacerbated when there are insufficient Capelin to support the cod biomass currently in the system. The process equation for natural mortality was modified as follows:

$$M_{a,y} = m_{a,y} \cdot \left(\frac{\hat{I}_{y}^{(B_{\text{cap}})}}{\hat{I}_{y-1}^{(B_{\text{cod}})}} \right)^{\beta_a^{(\text{cap})}} \cdot \exp(\delta_{a,y}), \qquad \mathbf{(2.1)}$$

where $\beta_a^{(\text{cap})}$ represents the effect of the log ratio of Capelin to cod biomass indices ($\hat{I}_{y}^{(B_{\text{cap}})}/\hat{I}_{y-1}^{(B_{\text{cod}})}$), $m_{a,y}$ are baseline rates, and $\delta_{a,y}$ are the process deviations (i.e., changes not explained by baseline rates or the Capelin effect). The baseline rates are either estimated using a constant parameter (model **M11**), an allometric equation (model **M12**), or a parameter for the pre-collapse, collapse, and post-collapse periods (model ; see Regular et al. [2025] for more details). Two options are presented with regards to the implementation of the $\beta_a^{(\text{cap})}$ effect. The first assumes that the effect is consistent across age. The second estimates parameters in age blocks (2–3, 4–8, 9+); given previous results, the effect is predicted to increase with age (Regular et al. 2022). In both cases, $\beta^{(\text{cap})}$ is assumed to be 0 for ages 0 and 1 since Capelin are not thought to be an important component of their diet.

The ratio used in Equation 2.1 requires an index of Capelin and cod biomass. For Capelin, we used the spring acoustic survey index of Capelin biomass as it is the best available data we have for the Capelin stock in 2J3KL (DFO 2022). For cod, we first tried to utilize internal estimates of cod biomass; however, this approach failed to converge, likely due to the circular nature of the formulation whereby rates of natural mortality, the response, were affecting estimates of cod biomass, which were in-turn affecting the ratio of Capelin to cod, the covariate. A simplified approach was therefore applied where we utilized the biomass index from the Fisheries and Oceans Canada (DFO) fall 2J3KL research vessel (RV) survey. Since the RV survey is conducted in the fall, it is likely a better indicator of the cod population that will be in the system consuming Capelin through the winter and spring of the following calendar year. The RV survey index of cod was therefore lagged by one year to better indicate the biomass of cod relative to the biomass of Capelin in a given year. Though the simplified approach was utilized, the use of internal estimates of cod biomass, perhaps aggregated into specific age groups, should be revisited as it is not yet clear why it was causing convergence issues. There may be a solution to this problem and it would be better to implement an internal approach.

Both the Capelin and cod indices are imperfect and have associated estimates of observation error for each annual index. We therefore utilize a random walk to account for this uncertainty, which is the same approach used in the Woods Hole Assessment Model (WHAM) for integrating environmental covariates (Stock and Miller 2021). We model the random walk process for the Capelin and cod biomass indices (Figure 1) as follows:

$$\log(\hat{I}_y) \sim N(\log(\hat{I}_{y-1}), \sigma_{\hat{I}}), \qquad \mathbf{(2.2)}$$

where $\hat{I}_y$ is either the predicted Capelin or cod biomass index and $\sigma_{\hat{I}}$ represents the variance of the process. Finally the observations are assumed to be lognormally distributed:

$$log(I_y) \sim N(log(\hat{I}_y), \sigma_{Iy}) \qquad \mathbf{(2.3)}$$

where I_y is the observed Capelin or cod biomass index, and σ_{Iy} are annual estimates of observation error of the log index (~ coefficient of variation); these values were supplied. Not only does this random walk approach account for uncertainty associated with the indices, but it also provides a formal mechanism through which missing years can be estimated (e.g., the 2020 Capelin index). That said, we did not attempt to use this model to extrapolate cod and Capelin levels back to 1954 as the non-stationary random walk process would provide highly uncertain estimates. The Capelin/cod ratio was therefore limited to all years following 1983, after the RV survey and acoustics surveys began.

2.2. MODELLING SEAL INTERACTION

2.2.1. Data

In addition to the dataset used in the xteNCAM model, as described in Regular et al. (2025), we have incorporated time series data on seal abundance, seal biomass (Figure 1), and the consumption of cod by seals. Seal biomass was determined by the product of seal abundance and the average weight of seals. It was assumed that the average weight of seals was 80 kg before 1996 and 72 kg thereafter (Stenson, unpublished data). The calculation of seal consumption of cod was based on a fixed percentage, a coarse approximation of 3.2%, of the total seal consumption (Stenson 2013).

We have used data from otolith samples retrieved from seal stomachs and the age-length key obtained from the RV survey to estimate the age-specific proportion of cod within the seal diet (Figure 2).This analysis utilizes a collection of over 5,000 cod otoliths from seal stomachs collected between 1982–2019. Most of the otoliths were collected from the Northwest Atlantic Fisheries Organization (NAFO) Division (Div.) 3K. We have used an empirical relationship to convert the otolith length to fish length. Not all lengths of cod were consistently obtained from seal stomachs each year and applying an observed Age-Length Key (ALK) would result in missing age-composition data for years with fewer samples in any age. To obtain a full age-composition information each year, we therefore employed the "modeled ALK" (Ogle 2018). This involved fitting a multinomial logistic regression model on fish age predicted by length data obtained from the DFO fall RV survey. Through this approach, probabilities for each category of the dependent variable (age) were estimated based on the values of the independent variable (length). Further, since majority of seal stomachs were collected during Jan.-Feb., and assuming minimal growth during the winter months (Robert Gregory, pers comm.), we used the ALK from the respective previous year fall RV survey to calculate the age structure.

2.2.2. Model

We have explored the influence of seals within the current xteNCAM modeling framework using two different approaches:

1. the seal-consumption approach, and;
2. the seal-covariate approach.

2.2.2.1. The seal-consumption approach

Seal predation-induced mortality (M^{seal}) has been incorporated into the total mortality rate (Z) of cod in the xteNCAM model; Consequently, Z has partitioned into three distinct components (1) fishing mortality rate (F), (2) M^{seal}, and (3) natural mortality rate (M) (excluding seal) with process error (δ) as shown in Equation 2.4:

$$Z_{a,y} = F_{a,y} + M^{\text{seal}}_{a,y} + M_{a,y} \cdot \exp(\delta_{a,y}), \quad a = 0, \dots, A;\ y = 1954, \dots, Y, \qquad \mathbf{(2.4)}$$

The modelling structures of $F_{a,y}$ and $M_{a,y}$ are unchanged from xteNCAM model (Regular et al. 2025).

We assume the logarithm of M^{seal} in Equation 2.4 has a fixed-effect baseline mean $log(\mu_{\text{seal}})$ and random deviations $\Delta_{a,y}$, which follows a multivariate normal distribution (MVN) with mean 0 and separable covariance matrix Σ_{seal} as in Equation 2.5:

$$log\left(M^{seal}_{a,y}\right) = log\left(\mu^{\text{seal}}\right) + \triangle_{a,y}; \quad \triangle_{a,y} \sim MVN\left(0, \Sigma^{\text{seal}}\right), \quad a = 0, \dots 7; y \geq 1982 \qquad \mathbf{(2.5)}$$

In the equation presented above, the age range extends from 0 to 7, aligning with the highest reported age of cod found in the seal diet, which is 7 years. As a result, we assume that seals have either no or minimal impact on cod aged 8 and older. We model $\Delta_{a,y}$ as a two-dimension autoregressive (2D AR(1)) process with autocorrelation over age and year. The 2D AR(1) structure offers flexibility, demanding only a few parameters while enabling smooth deviation over time and across age. It indicates that data points from nearby years and age categories display stronger correlations than those separated by greater distances (Kumar et al. 2020). The correlation and covariance between any two elements in Σ^{seal} are defined as shown in Equation 2.6:

$$Cov\left(\Delta_{a,y}, \Delta_{a-i,y-j}\right) = \frac{\sigma_\Delta^2 \phi_A^{|i|} \phi_Y^{|j|}}{(1 - \phi_A^2)(1 - \phi_Y^2)}; \quad Corr\left(\Delta_{a,y}, \Delta_{a-i,y-j}\right) = \phi_A^{|i|} \phi_Y^{|j|}, \qquad \mathbf{(2.6)}$$

where, ϕ_A and ϕ_Y are autocorrelation coefficients for age and year respectively, and σ_{Δ}^2 is a common variance in Σ^{seal}.

However, before 1982, due to the unavailability of cod otolith data, we lack age-specific dietary information of seal. Consequently, instead of 2D AR(1) structure for $\Delta_{a,y}$, we implement an AR(1) structure over year, where all ages share a common effect within a given year Equation 2.7:

$$log\left(M_{a,y}^{\text{seal}}\right) = \log\left(\mu^{\text{seal}}\right) + \triangle_y, \quad \triangle_y \sim AR(1), \quad \text{if } y < 1982 \qquad (\mathbf{2.7})$$

An average size-selective shape was attempted in earlier iterations, however, convergence issues precluded the estimation of age-specific mean effect, μ_a^{seal}. Since Harp Seals are expected to exert a greater average effect on the youngest ages, alternative ways to estimate an allometric effect should be considered in the future.

2.2.2.2. Observation model for the consumption approach

To aid in the optimization of parameters related to estimation of $M_{a,y}^{\text{seal}}$ in Equation 2.4, we incorporate observation models. These models fit the proportion of cod ages in the seal diet using continuation ratio logits (CRLs) and the extent of total seal consumption of cod Q_y through censored landings. The data for seal consumption Q_y is obtained after performing several steps which include estimating seal population, the energetic needs of this population, and the proportion of energetic needs satisfied by cod consumption based on analysis of otoliths in seal. Therefore, there is considerable uncertainty the calculation of Q_y. We use the approach of censored likelihood (Equation 2.8) in fitting Q_y to allow the incorporation of lower LB_y and upper UB_y bounds on Q_y. The censored-likelihood l is defined as:

$$l\left(Q_y|\theta\right) = \sum_{y=1954}^{Y} log \left\{ \Phi_N \left[\frac{\log\left(\frac{UB_y}{\hat{Q}_y}\right)}{\sigma_Q} \right] - \Phi_N \left[\frac{\log\left(\frac{LB_y}{\hat{Q}_y}\right)}{\sigma_Q} \right] \right\},\ 1954 \leq y \leq Y \qquad (\mathbf{2.8})$$

where, ΦN is the cumulative distribution function (CDF) for a standard normal random variable,σ_Q is fixed at 0.5, and $\hat{Q}$ is the the predicted total consumption as shown in the Equation 2.9:

$$\hat{Q}_y = \sum_a \hat{Q}_{a,y} = \sum_a \frac{N_{a,y}(1 - e^{-Z_{a,y}}) M_{a,y}^{\text{seal}} W_{a,y}}{Z_{a,y}} \qquad (\mathbf{2.9})$$

where, $W_{a,y}$ is the weight-at-age of cod. We use autumn weight because the majority of seal consumption takes place during the autumn and early winter months.

Instead of fitting seal consumption-at-age, we fit CRLs. In this approach, we are able to directly use the proportion in numbers of cod-at-age $P_{a,y}$ in seal stomachs (derived from ageing of cod otoliths in seal stomachs). The proportions are converted to CRLs. To calculate CRLs, first proportions-at-age are converted to conditional probabilities $\pi_{a,y}$ (Equation 2.10); the $\pi_{a,y}$ are logit transformed to obtain CRLs $X_{a,y}$ (Equation 2.11). CRLs fit from year$\geq$ 1982,which corresponds to the year when otolith data became available.

$$\pi_{a,y} = Prob(age = a|age \geq a) = \frac{\hat{P}_{a,y}}{\sum_a^7 \hat{P}_{a,y}}; \quad a = 0, \dots, 7-1; \quad y = 1982, \dots, Y \qquad (\mathbf{2.10})$$

$$X_{a,y} \sim N\left(\log\left(\frac{\pi_{a,y}}{1-\pi_{a,y}}\right), \sigma_3\right); \quad a = 0,\ldots,7-1; \quad y = 1982,\ldots,Y \qquad (\mathbf{2.11})$$

where σ_3 is the variance parameter that accounts for sampling and aging error.

2.2.2.3. The seal-covariate approach

The implementation of “seal-covariate approach” is similar to the implementation of Capelin interaction in xteNCAM model. In this approach, we incorporated the ratio of estimated seal biomass $\hat{I}^{(B_{\text{seal}})}$ to the estimated total abundance index of cod $\hat{I}^{(N_{\text{cod}})}$ from the RV fall survey as a covariate, in addition to accounting for process error (δ), for the estimation of M (Equation 2.12). The effect or coefficient associated with the covariate ($\beta_a^{(\text{seal})}$) was estimated for specific age groups, which were combined into age categories such as 0–3 and 4–8, thereby sharing a common estimate for β_a^{seal} within each of these defined groups. Note that the effect was assumed to be zero for ages 9+ as such cod are rarely observed in the diet of seals. The seal biomass estimates are for the population prior to pupping in early winter. However, seal migration to the stock area happens in late fall to early winter which is also the time when consumption effect is expected to be the highest (Stenson 2013). Hence one-year-ahead estimates for seal biomass are used for the calculation of the covariate effect. That is, the seal population indexed in the winter of year $y+1$ are present in the fall of year y, affecting the survival of cod indexed in the fall of year y. These survey data were therefore used to predict M in year y as follows:

$$M_{a,y} = m_{ay} \cdot \left(\frac{\hat{I}_{y+1}^{(B_{\text{seal}})}}{\hat{I}_{y}^{(N_{\text{cod}})}}\right)^{\beta_a^{(\text{seal})}} \cdot \exp(\delta_{a,y}), \qquad (\mathbf{2.12})$$

Since RV fall survey index of cod ($I_y^{(N_{\text{cod}})}$) is available only from 1983, the log of seal over cod ratio is set to zero prior to 1983; essentially, the covariate is contributing to estimates of $M$from 1983 onward.

As with the modelling of Capelin interaction, random walk processes were fitted for both seal biomass $\hat{I}_y^{(B_{\text{seal}})}$ and cod abundance indices $\hat{I}_y^{(N_{\text{cod}})}$:

$$\log\left(\hat{I}_y^{(B_{\text{seal}}} \text{ or } \hat{I}_y^{(N_{\text{cod}})}\right) \sim N\left(\log(\hat{I}_{y-1}),\ \sigma_{\hat{I}^{(B_{\text{seal}})}} \text{ or } \sigma_{\hat{I}^{(N_{\text{cod}})}}\right) \qquad (\mathbf{2.13})$$

We assumed that observations are lognormally distributed as:

$$\log\left(I_y^{(B_{\text{seal}}} \text{ or } I_y^{(N_{\text{cod}})}\right) \sim N\left(\log(\hat{I}_y),\ \sigma_{I^{(B_{\text{seal}})}} \text{ or } \sigma_{Iy^{(N_{\text{cod}})}}\right) \qquad (\mathbf{2.14})$$

The coefficient of variation (CV) for the observation model in Equation 2.14 pertaining to seals ($\sigma_{I^{(B_{\text{seal}})}}$) is set at a constant value of 0.11, which corresponds to the CV of seal abundance estimated in 2019 (Tinker et al. 2023); while the annual CVs for the observation model related to cod ($\sigma_{Iy^{(N_{\text{cod}})}}$) are obtained from standard stratified analyses of the RV survey.

3. RESULTS

3.1. GENERAL OBSERVATIONS

Similar to Part I (Regular et al. 2025), trends in estimates of spawning stock biomass (SSB), average F and M (ages 5+) are broadly consistent across all models presented here, but there are some differences in estimates of recruitment (Figures 3–5). Likewise, estimates of M at age is consistent across models; however, there are signs that predictions of M using Capelin and seals explains some of the variation in the overall rates of M (Figures 6–8).

3.2. CAPELIN EFFECT

As expected, the ratio of Capelin to cod biomass had a negative effect on rates of M. When the beta are coupled for all ages 2 and above, the estimates are significant indicating that the Capelin/cod ratio has explanatory power in describing M. When beta parameters are estimated by age groups, the estimates for the larger age groups are significant (Figures 9–11). Under the M-shift2 formulation, the beta estimates are slightly smaller; this is explained by the higher baseline M in the post collapse period when the per capita availability of Capelin for cod is lower.

On comparing the M-at-age in the baseline M models versus the models with Capelin as a covariate, we see that the overall trends in M are very similar across all ages. Incorporation of Capelin effect explains some of the variations in M during the collapse, the peak in M in around 2010, and the increase in the recent years (Figures 6–8). All the models including Capelin covariate effect have lower AICs than the corresponding baseline M models with larger gains when a single beta parameter is estimated (Tables 2–4).

3.3. SEAL EFFECT

3.3.1. Seal consumption approach

The seal consumption of cod provided to the model as data was estimated as 3.2% of the total consumption estimated for seal. The wide bounds (0.5 to 1.5) provided to the censored likelihood fitting approach allowed the model to fit this data with considerable uncertainty. The predicted consumption suggests a decline in consumption by seal following the collapse in the mid-1990s where the estimated outputs fall below the bounds provided (Figure 12). There is another period in mid-2000s when the predictions fall slightly below the bounds provided. We also compare the predicted consumption against the constant 3.2% used for the estimation of consumption to explore how much the predicted values depart from the assumption of 3.2%. We find that these values mostly range between 2 to 5% throughout the time series, except in the post collapse period when the values dip below 1% of total consumption by the seal population (Figure 13). Considering large changes in cod biomass through the time series, this level of variability in not unexpected. It is possible that changes in consumption estimated by the model are driven by changes in levels of predation M estimated by the model.

A plot of M (Figure 14) showing the portion of mortality explained by consumption by seals versus other mortality show that seal mortality explains a large portion of M in mid-1990s to 2000s. Part of the reason for the process error decline and the explanation of the total mortality is the amount of flexibility allowed in the estimation of predicted consumption levels.

3.3.2. Seal covariate approach

Unlike the previous approach which used information from cod otoliths in seal stomachs, in this covariate approach, no additional information is available to the model about the impact of seal predation on different ages of cod. The impact is modelled by age-groups determined by the coupling of the beta parameter in the estimations. The beta parameter estimates were statistically significant for both age groups, with the effect being stronger for ages 0–3. These results indicate that as the seal biomass per unit of cod in the system increases, there is an effect on natural mortality for the younger ages of cod (Figures 9–11).

On comparing the M-at-age in the baseline M models versus the models with seal as a covariate, we see that the overall mortality patterns are similar for all age groups, except for age 0. For age 0 cod, there is no additional process error and the M estimates follow the temporal trend in the covariate (Figures 6–8). All the models including seal covariate effect have lower AICs than the corresponding baseline M models (Tables 2–4).

3.4. CAPELIN AND SEAL EFFECT

The comparison of AIC values among all approaches of baseline M and inclusion of effects showed lowest AIC values when both Capelin and seal effects were included. Beta estimates remain consistent between when seal or Capelin alone are included in the model (i.e., adding one covariate does not alter the beta estimations for the other covariate). Note that in the M-shift2 version, the beta estimates for all covariates (both Capelin and cod) are lower than under the other two baseline M approaches (Figure 11). Capelin and seal effects together explain a greater portion of the M estimates for the models (Figures 6–8), and together receive the lowest AIC scores (Tables 2–4).

4. DISCUSSION

4.1. CAPELIN EFFECT

As expected, the Capelin/cod has a significant effect on M for older-age cod (4+) but, contrary to expectations, evidence for our prediction that the effect increased with age group was equivocal. This may be related to the resolution of our data as noise from observations may be drowning out the signal. It may also be that the aggregate approach to the Capelin/cod ratio does not fully capture the effect of intra-specific competition, which may be stronger within size groups. Finally, it is possible that the effect is similar across all age groups. Whatever the case, our results show the value of using Capelin as a predictor of cod mortality as its inclusion explains some of the variation in M and, consequently, reduces AIC scores and estimates of process error variance. Though it has yet to be tested, this link with Capelin is expected to improve the forecasting skill of the model, particularly for cod ages 2+ (i.e., the component 'observed' by the RV survey).

Most previous studies on predator-prey links between cod and Capelin have indicated that Capelin availability affects changes in total cod biomass (e.g., Buren et al. 2014, Koen-Alonso et al. 2021) or that Capelin improves body growth and condition (e.g., Krohn et al. 1997, Rose and O'Driscoll 2002). The mechanism through which Capelin affects the productivity of the cod population has been unclear. Improvements in body growth and condition may bolster the production of recruits, and subsequently total biomass, or prey limitation may affect the mortality of adults through deteriorating body condition and, ultimately, starvation. Research presented in Regular et al. (2022) provides support for the latter hypothesis, as changes in a condition-based index of starvation-induced mortality appear to be associated with prey availability and rates of M estimated by NCAM. Analyses presented in this document provide further support for the hypothesis that Capelin availability affects cod mortality.

4.2. SEAL EFFECT

4.2.1. Seal consumption approach

This approach uses the most data available on the impact of seals on the cod population. One major assumption is that of the total consumption of fish by seals, cod constitutes 3.2% and this diet fraction does not change between years. Hence, we allowed a high level of flexibility in the prediction of consumption in the model. However, it is possible that this added flexibility is utilized by the model to explain some of the otherwise unexplained variance in the process error. The Newfoundland and Labrador Climate Index (NLCI) is suggested as an indicator of system productivity. A proxy index of M based on environmental conditions (EnvM) is derived as the exponentiation of the negative of the NLCI (Koen-Alonso, pers. comm.). Comparison of predicted trends with the NLCI show that there is some correlation between the predicted values of consumption and the EnvM (Figure 15). This leads to a speculation that perhaps the model flexibility, through wide bounds in the censored likelihood for total consumption, in the consumption approach could lead to trends that may or may not be entirely related to seal consumption of cod. Therefore, to effectively estimate the seal predation impact, there is need to explore the link with environmental variables in future modelling approaches, which have not been considered so far in the current analyses or in the biomass dynamics approaches (e.g., Buren et al. 2014, Koen-Alonso et al. 2021).

The otoliths collected from seal stomachs inform the proportions of different ages of cod consumed by seals and help partition the mortality between different age-groups of cod. In line with previous research (Stansbury et al. 1998), our analyses reiterate that seal predation is predominantly linked to younger cod. However, some of the variation observed between years in these proportions is an artifact of sampling area and time. In Div. 2J, sampling is predominantly in the fall, in 3K sampling is predominantly in early winter, however in some years there was relatively more sampling in late spring and summer. Further, because of additional data used to fit the different models, the AIC estimates from these models are not comparable with the models with baseline natural mortality, but the AIC values from these models are comparable between each other. Hence there are challenges associated with the assumptions and data constraints for this approach.

4.2.2. Seal covariate approach

As with the seal consumption approach, the exploration and quantification of the effect of seals was made possible by the extension of the model to include ages 0 and 1 through the inclusion of the Newman sound and the Fleming surveys. The significant estimates of beta indicate that pressure by seals per capita cod influenced M. In contrast to the consumption approach, where the model was provided a lot of flexibility in changing predicted consumption, such space was not provided in this approach. Yet, the model picks up this signal in the absence of any information on diet proportions. This leads to the reasoning that pressure, especially on young cod contributed to high levels of M in the early phase of cod recovery. Previous analyses have not identified predation as an important driver on cod (Buren et al. 2014); this is likely because these analyses were based on biomass dynamics models (wherein the contribution of younger ages) to the population biomass is small and is overshadowed by signals that impact the biomass available to the RV survey. In the base NCAM model (Regular et al. 2025), the proportion of fish age 2 and younger is less than 10% in the total population biomass; this shows the difficulty in identifying the effects on juvenile cod using biomass dynamics models. The collapse observed in the NL ecosystem was experienced not only by cod but also by other groundfish and forage species. In the aftermath of the collapse, measures were taken to reduce fishing pressure. However, it is possible that per capita predation increased as it impacted a smaller population compared to pre-collapse levels. This spike may be present for multiple species since the collapse was not isolated to cod (i.e., most prey species of seals collapsed in the early-1990s). It required time and likely favorable environmental conditions for species like cod, Capelin, and others to recover, during which time they may have experienced higher than average rates of predation induced natural mortality.

One aspect of the seal covariate approach that requires further consideration is the assumption that seals will continue to target cod even at low abundance. Such a depensatory effect may not be ecologically realistic as generalists predators like seals are expected to switch to other, more abundant, species (i.e., a type III functional response; Middlemas et al. 2006, Smout et al. 2014). In this context, although (Buren et al. 2014), rejected the link to Harp Seal predation, they found evidence of depensatory dynamics in cod. At the same time, it is not necessary that depensatory predation on juveniles should translate into stock level depensatory dynamics in response to predation. Further, when cod collapsed in the 1990s, many other species (including Capelin which are an important prey for seals) collapsed in the system and although seals are generalists, the availability of alternate prey were limited. Lastly, Capelin are an important prey for cod and for seals, and a shared foraging arena of cod, Capelin, and seals can be speculated. Given the complexity of the interactions between these species, other structural assumptions should be tested.

4.3. CAPELIN AND SEAL EFFECT

The combined use of Capelin and seals as predictors of M resulted in the best explanation of the data, capturing trends in the M for the juvenile and mature components of the population. This formulation did, however, have an impact on the stock-recruitment relationship and resulted in the highest estimates of α across all models. The specific cause of this difference requires further investigation.

5. CONCLUSION

In all approaches explored, the overall trends in natural mortality are similar, especially for the mature and exploitable population of cod. Hence the spawning stock biomass estimated from close to 20 different formulations of including Capelin and seals in the modelling are very similar. The highest gains in AIC were obtained from modelling both the Capelin and seal effects, with levels of seal per capita cod showing significant effects on younger cod, especially ages 0 to 3 and low levels of Capelin per capita cod showing significant effects on mortality of cod ages 3 and higher. Under the seal consumption approach and under Lorenzen formulation of M, the estimates of recruitment are higher than in the baseline models. Such an allometric effect and demographics are expected under ecological theory (Lorenzen 2022). The additional recruitment is depleted by the higher levels of natural mortality on younger ages in these models and by around age 5, the trends in all the models are very similar. The exploration of Capelin and seal effects contributes to an understanding of the M that was previously modeled exclusively as process error. These efforts represent a step away from a description of past changes towards an explanation of past changes. In doing so, we aim to aid the development of an ecosystem approach to managing Northern cod.

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7. TABLES

Table 1: Labels and descriptions of model formulations testing a range of assumptions regarding baseline levels of natural mortality, M, in combination with Capelin and/or seal effects.

Model	**Baseline M**	**Capelin effect**	**Seal effect**
M11	Constant	NA	NA
M12	Allometric	NA	NA
M13	M-shift2	NA	NA
M14	Constant	Constant covariate	NA
M15	Allometric	Constant covariate	NA
M16	M-shift2	Constant covariate	NA
M17	Constant	Age-based covariate	NA
M18	Allometric	Age-based covariate	NA
M19	M-shift2	Age-based covariate	NA
M20	Constant	NA	Age-based covariate
M21	Allometric	NA	Age-based covariate
M22	M-shift2	NA	Age-based covariate
M23	Constant	NA	Consumption
M24	Allometric	NA	Consumption
M25*	M-shift2	NA	Consumption
M26	Constant	Constant covariate	Age-based covariate
M27	Allometric	Constant covariate	Age-based covariate
M28	M-shift2	Constant covariate	Age-based covariate
M29	Constant	Constant covariate	Consumption
M30*	Allometric	Constant covariate	Consumption
M31	M-shift2	Constant covariate	Consumption

*model did not converge

*Table 2: Comparison of the number of parameters, k, log-likelihood, $ln(L)$, Akaike information criterion, AIC (top table), and select parameter estimates (bottom table; RV is research vessel, SN is sentinel, S-R is stock-recruitment, and NB is negative binomial) for models assuming constant baseline rates of M (**M11**, **M14**, **M17**, **M23**, **M20**, and **M26**). AIC and $ln(L)$ values are not shown for models using the seal consumption approach as they are not comparable.*

Model	**Baseline M**	**Capelin effect**	**Seal effect**	k	$ln(L)$	AIC	ΔAIC
M26	Constant	Constant covariate	Age-based covariate	205	17,938.36	36,286.71	0.000
M20	Constant	NA	Age-based covariate	204	17,946.14	36,300.29	13.575
M17	Constant	Age-based covariate	NA	205	17,950.09	36,310.17	23.461
M14	Constant	Constant covariate	NA	203	17,952.65	36,311.30	24.584

Model	**Baseline M**	**Capelin effect**	**Seal effect**	k	$ln(L)$	AIC	ΔAIC
M11	Constant	NA	NA	202	17,957.47	36,318.95	32.235
M23	Constant	NA	Consumption	208	NA	NA	NA

Quantity	**Symbol**	**M11**	**M14**	**M17**	**M23**	**M20**	**M26**
RV survey observation error	σ_{RV}	0.431	0.430	0.424	0.447	0.413	0.412
SN survey observation error (age 3)	σ_{SN_a}	0.668	0.670	0.673	0.656	0.663	0.663
SN survey observation error (ages 4-14)	-	0.128	0.131	0.138	0.138	0.128	0.130
Age correlation in SN q	$\varphi_{\text{SN}_q,\text{age}}$	0.868	0.867	0.872	0.867	0.871	0.870
Year correlation in SN q	$\varphi_{\text{SN}_q,\text{year}}$	0.886	0.885	0.885	0.890	0.881	0.879
SN q variance parameter	σ_{SN_q}	0.830	0.828	0.829	0.828	0.838	0.835
Age composition error (ages 0–2)	σ_{P_a}	1.831	1.845	1.835	1.799	1.849	1.864
Age composition error (ages 3–4)	-	0.844	0.848	0.854	0.886	0.850	0.857
Age composition error (ages 5–14)	-	0.306	0.307	0.303	0.307	0.302	0.302
Age correlation in process errors	$\varphi_{\delta,\text{age}}$	0.862	0.810	0.873	0.871	0.863	0.773
Year correlation in process errors	$\varphi_{\delta,\text{year}}$	0.766	0.831	0.802	0.821	0.787	0.860
Process error variance	σ_δ	0.281	0.258	0.236	0.246	0.278	0.247
Age correlation in F	$\varphi_{F,\text{age}}$	0.908	0.909	0.909	0.909	0.916	0.917
Year correlation in F	$\varphi_{F,\text{year}}$	0.998	0.998	0.998	0.998	0.998	0.998
F variance parameter	σ_F	0.203	0.203	0.202	0.207	0.198	0.198
S-R relationship parameter	α_{SSB}	7.233	9.337	8.663	18.176	11.177	21.569
S-R relationship parameter	$\log(\beta_{\text{SSB}})$	-11.994	-11.781	-11.897	-11.840	-11.239	-10.573
Variance of log-recruitment	σ_r	0.271	0.259	0.268	0.182	0.294	0.284
Baseline level of natural mortality	m	0.239	0.283	0.278	0.281	0.193	0.224
Variance of tagging F deviations (pre 1997)	$\sigma_{f_{x,1}}$	0.942	0.941	0.940	0.942	0.938	0.937
Variance of tagging F deviations (post 1997)	$\sigma_{f_{x,2}}$	1.051	1.050	1.050	1.054	1.053	1.051
NB overdispersion parameter for pre 1997 tag experiments	κ_1	16.112	16.105	16.096	16.389	16.104	16.082
NB overdispersion parameter for post 1997 tag experiments	κ_2	8.081	8.108	8.121	7.932	8.033	8.054
Juvenile survey observation error	σ_{juv}	1.158	1.157	1.161	1.162	1.149	1.147

Table 3: Comparison of the number of parameters, k*, log-likelihood,* $ln(L)$*, Akaike information criterion,* AIC *(top table), and select parameter estimates (bottom table; RV is research vessel, SN is sentinel, S-R is stock-recruitment, and NB is negative binomial) for models assuming an allometric* M *effect (**M12**, **M15**, **M18**, **M24**, **M21**, and **M27**).* AIC *and* $ln(L)$ *values are not shown for models using the seal consumption approach as they are not comparable.*

Model	**Baseline** M	**Capelin effect**	**Seal effect**	k	$ln(L)$	AIC	ΔAIC
M27	Allometric	Constant covariate	Age-based covariate	206	17,938.03	36,288.05	0.000
M21	Allometric	NA	Age-based covariate	205	17,945.63	36,301.27	13.216
M15	Allometric	Constant covariate	NA	204	17,950.51	36,309.02	20.973
M18	Allometric	Age-based covariate	NA	206	17,948.72	36,309.44	21.387
M12	Allometric	NA	NA	203	17,955.75	36,317.50	29.452
M24	Allometric	NA	Consumption	209	NA	NA	NA

Quantity	**Symbol**	**M12**	**M15**	**M18**	**M24**	**M21**	**M27**
RV survey observation error	σ_{RV}	0.435	0.433	0.427	0.450	0.415	0.412
SN survey observation error (age 3)	σ_{SN_a}	0.669	0.670	0.673	0.654	0.663	0.663
SN survey observation error (ages 4–14)	-	0.130	0.133	0.138	0.140	0.128	0.130
Age correlation in SN q	$\varphi_{\text{SN}_q,\text{age}}$	0.868	0.867	0.871	0.867	0.871	0.869
Year correlation in SN q	$\varphi_{\text{SN}_q,\text{year}}$	0.886	0.885	0.885	0.890	0.882	0.879
SN q variance parameter	σ_{SN_q}	0.829	0.827	0.828	0.827	0.838	0.835
Age composition error (ages 0–2)	σ_{P_a}	1.826	1.841	1.832	1.794	1.851	1.866
Age composition error (ages 3–4)	-	0.851	0.856	0.859	0.881	0.852	0.859
Age composition error (ages 5–14)	-	0.306	0.307	0.304	0.306	0.302	0.302
Age correlation in process errors	$\varphi_{\delta,\text{age}}$	0.860	0.802	0.864	0.874	0.866	0.778
Year correlation in process errors	$\varphi_{\delta,\text{year}}$	0.772	0.839	0.813	0.840	0.799	0.869
Process error variance	σ_δ	0.267	0.244	0.230	0.226	0.273	0.243
Age correlation in F	$\varphi_{F,\text{age}}$	0.911	0.912	0.910	0.913	0.918	0.918
Year correlation in F	$\varphi_{F,\text{year}}$	0.998	0.998	0.998	0.998	0.998	0.998
F variance parameter	σ_F	0.202	0.201	0.201	0.205	0.197	0.197
S-R relationship parameter	α_{SSB}	12.484	20.932	14.978	27.991	15.551	30.457
S-R relationship parameter	$\log(\beta_{\text{SSB}})$	-11.971	-11.704	-11.859	-11.910	-11.005	-10.299
Variance of log-recruitment	σ_r	0.260	0.245	0.258	0.183	0.297	0.289
Baseline level of natural mortality	m	0.189	0.214	0.221	0.188	0.159	0.187
Variance of tagging F deviations (pre 1997)	$\sigma_{f_{x,1}}$	0.942	0.941	0.940	0.943	0.938	0.937

Quantity	Symbol	M12	M15	M18	M24	M21	M27
Variance of tagging F deviations (post 1997)	$\sigma_{f_{x,2}}$	1.052	1.050	1.050	1.055	1.054	1.052
NB overdispersion parameter for pre 1997 tag experiments	κ_1	16.157	16.159	16.140	16.384	16.135	16.107
NB overdispersion parameter for post 1997 tag experiments	κ_2	8.092	8.116	8.122	7.962	8.029	8.051
Juvenile survey observation error	σ_{juv}	1.156	1.152	1.158	1.183	1.148	1.145

*Table 4: Comparison of the number of parameters, k, log-likelihood, $ln(L)$, Akaike information criterion, AIC (top table), and select parameter estimates (bottom table; RV is research vessel, SN is sentinel, S-R is stock-recruitment, and NB is negative binomial) for models assuming shifts in baseline M (**M13**, **M16**, **M19**, **M22**, and **M28**). AIC and $ln(L)$ values are not shown for models using the seal consumption approach as they are not comparable.*

Model	Baseline M	Capelin effect	Seal effect	k	$ln(L)$	AIC	ΔAIC
M28	M-shift2	Constant covariate	Age-based covariate	207	17,928.06	36,270.11	0.000
M22	M-shift2	NA	Age-based covariate	206	17,932.00	36,276.00	5.891
M19	M-shift2	Age-based covariate	NA	207	17,932.75	36,279.50	9.392
M16	M-shift2	Constant covariate	NA	205	17,937.52	36,285.04	14.932
M13	M-shift2	NA	NA	204	17,939.66	36,287.32	17.207

Quantity	Symbol	M13	M16	M19	M22	M28
RV survey observation error	σ_{RV}	0.428	0.426	0.422	0.416	0.412
SN survey observation error (age 3)	σ_{SN_a}	0.663	0.665	0.667	0.663	0.664
SN survey observation error (ages 4–14)	-	0.120	0.122	0.130	0.123	0.125
Age correlation in SN q	$\varphi_{\mathrm{SN}_q,\mathrm{age}}$	0.865	0.865	0.870	0.868	0.868
Year correlation in SN q	$\varphi_{\mathrm{SN}_q,\mathrm{year}}$	0.886	0.886	0.886	0.883	0.881
SN q variance parameter	σ_{SN_q}	0.824	0.823	0.824	0.831	0.830
Age composition error (ages 0–2)	σ_{P_a}	1.818	1.823	1.818	1.833	1.842
Age composition error (ages 3–4)	-	0.851	0.854	0.860	0.851	0.858
Age composition error (ages 5–14)	-	0.306	0.306	0.301	0.302	0.302
Age correlation in process errors	$\varphi_{\delta,\mathrm{age}}$	0.689	0.672	0.715	0.720	0.671
Year correlation in process errors	$\varphi_{\delta,\mathrm{year}}$	0.641	0.672	0.630	0.703	0.727
Process error variance	σ_{δ}	0.305	0.291	0.268	0.292	0.273
Age correlation in F	$\varphi_{F,\mathrm{age}}$	0.907	0.907	0.910	0.914	0.914
Year correlation in F	$\varphi_{F,\mathrm{year}}$	0.998	0.998	0.998	0.998	0.998
F variance parameter	σ_F	0.203	0.203	0.201	0.199	0.199
S-R relationship parameter	α_{SSB}	9.986	11.584	10.698	11.978	18.459
S-R relationship parameter	$\log(\beta_{\mathrm{SSB}})$	-11.638	-11.550	-11.679	-11.281	-10.922

Quantity	Symbol	M13	M16	M19	M22	M28
Variance of log-recruitment	σ_r	0.236	0.224	0.229	0.256	0.242
Baseline level of natural mortality (1954–90)	m_y	0.168	0.188	0.190	0.154	0.186
Baseline level of natural mortality (1991–94)	-	1.175	1.127	1.250	0.935	0.840
Baseline level of natural mortality (1995–2020)	-	0.398	0.462	0.424	0.333	0.405
Variance of tagging F deviations (pre 1997)	$\sigma_{f_{x,1}}$	0.944	0.943	0.943	0.943	0.941
Variance of tagging F deviations (post 1997)	$\sigma_{f_{x,2}}$	1.050	1.049	1.049	1.053	1.051
NB overdispersion parameter for pre 1997 tag experiments	κ_1	16.032	16.027	15.991	16.006	16.001
NB overdispersion parameter for post 1997 tag experiments	κ_2	8.018	8.043	8.044	7.999	8.023
Juvenile survey observation error	σ_{juv}	1.177	1.175	1.187	1.175	1.168

*Table 5: Comparison of the number of parameters, k, log-likelihood, $ln(L)$, Akaike information criterion, AIC (top table), and select parameter estimates (bottom table; RV is research vessel, SN is sentinel, S-R is stock-recruitment, and NB is negative binomial) for models using the seal consumption approach (**M23**, **M24**, **M29**, and **M31**).*

Model	Baseline M	Capelin effect	Seal effect	k	$ln(L)$	AIC	ΔAIC
M31	M-shift2	Constant covariate	Consumption	211	18,392.28	37,206.56	0.000
M29	Constant	Constant covariate	Consumption	209	18,400.57	37,219.14	12.576
M24	Allometric	NA	Consumption	209	18,405.76	37,229.52	22.956
M23	Constant	NA	Consumption	208	18,409.08	37,234.17	27.610

Quantity	Symbol	M23	M24	M29	M31
Baseline level of natural mortality (1954–90)	m_y	NA	NA	NA	0.274
Baseline level of natural mortality (1991–94)	-	NA	NA	NA	0.999
Baseline level of natural mortality (1995–2020)	-	NA	NA	NA	0.331
Baseline level of natural mortality	m	0.281	0.188	0.305	NA
RV survey observation error	σ_{RV}	0.447	0.450	0.441	0.440
SN survey observation error (age 3)	σ_{SN_a}	0.656	0.654	0.657	0.660
SN survey observation error (ages 4–14)	-	0.138	0.140	0.139	0.139
Age correlation in SN q	$\varphi_{\mathrm{SN}_q,\mathrm{age}}$	0.867	0.867	0.867	0.866
Year correlation in SN q	$\varphi_{\mathrm{SN}_q,\mathrm{year}}$	0.890	0.890	0.887	0.889
SN q variance parameter	σ_{SN_q}	0.828	0.827	0.826	0.824
Age composition error (ages 0–2)	σ_{P_a}	1.799	1.794	1.810	1.799
Age composition error (ages 3–4)	-	0.886	0.881	0.888	0.894
Age composition error (ages 5–14)	-	0.307	0.306	0.308	0.308
Age correlation in process errors	$\varphi_{\delta,\mathrm{age}}$	0.871	0.874	0.737	0.640
Year correlation in process errors	$\varphi_{\delta,\mathrm{year}}$	0.821	0.840	0.882	0.842

Quantity	Symbol	M23	M24	M29	M31
Process error variance	σ_{δ}	0.246	0.226	0.223	0.234
Age correlation in F	$\varphi_{F,\text{age}}$	0.909	0.913	0.909	0.908
Year correlation in F	$\varphi_{F,\text{year}}$	0.998	0.998	0.998	0.998
F variance parameter	σ_{F}	0.207	0.205	0.206	0.206
S-R relationship parameter	α_{SSB}	18.176	27.991	20.325	22.382
S-R relationship parameter	$\log(\beta_{\text{SSB}})$	-11.840	-11.910	-11.765	-11.699
Variance of log-recruitment	σ_{r}	0.182	0.183	0.174	0.162
Variance of tagging F deviations (pre 1997)	$\sigma_{f_{x,1}}$	0.942	0.943	0.940	0.943
Variance of tagging F deviations (post 1997)	$\sigma_{f_{x,2}}$	1.054	1.055	1.052	1.051
NB overdispersion parameter for pre 1997 tag experiments	κ_{1}	16.389	16.384	16.345	16.299
NB overdispersion parameter for post 1997 tag experiments	κ_{2}	7.932	7.962	7.951	7.944
Juvenile survey observation error	σ_{juv}	1.162	1.183	1.184	1.183

*Table 6: Comparison of the number of parameters, k, log-likelihood, $ln(L)$, Akaike information criterion, AIC (top table), and select parameter estimates (bottom table; RV is research vessel, SN is sentinel, S-R is stock-recruitment, and NB is negative binomial) for models estimating a Capelin effect (**M11**, **M14**, **M17**, **M12**, **M15**, **M18**, **M13**, **M16**, and **M19**).*

Model	Baseline M	Capelin effect	Seal effect	k	$ln(L)$	AIC	ΔAIC
M19	M-shift2	Age-based covariate	NA	207	17,932.75	36,279.50	0.000
M16	M-shift2	Constant covariate	NA	205	17,937.52	36,285.04	5.540
M13	M-shift2	NA	NA	204	17,939.66	36,287.32	7.816
M15	Allometric	Constant covariate	NA	204	17,950.51	36,309.02	29.521
M18	Allometric	Age-based covariate	NA	206	17,948.72	36,309.44	29.935
M17	Constant	Age-based covariate	NA	205	17,950.09	36,310.17	30.673
M14	Constant	Constant covariate	NA	203	17,952.65	36,311.30	31.797
M12	Allometric	NA	NA	203	17,955.75	36,317.50	38.001
M11	Constant	NA	NA	202	17,957.47	36,318.95	39.448

Quantity	Symbol	M11	M14	M17	M12	M15	M18	M13	M16	M19
Baseline level of natural mortality (1954–90)	m_{y}	NA	NA	NA	NA	NA	NA	0.168	0.188	0.190
Baseline level of natural mortality (1991–94)	-	NA	NA	NA	NA	NA	NA	1.175	1.127	1.250
Baseline level of natural mortality (1995–2020)	-	NA	NA	NA	NA	NA	NA	0.398	0.462	0.424

Quantity	Symbol	M11	M14	M17	M12	M15	M18	M13	M16	M19
Baseline level of natural mortality	m	0.239	0.283	0.278	0.189	0.214	0.221	NA	NA	NA
RV survey observation error	σ_{RV}	0.431	0.430	0.424	0.435	0.433	0.427	0.428	0.426	0.422
SN survey observation error (age 3)	σ_{SN_a}	0.668	0.670	0.673	0.669	0.670	0.673	0.663	0.665	0.667
SN survey observation error (ages 4–14)	-	0.128	0.131	0.138	0.130	0.133	0.138	0.120	0.122	0.130
Age correlation in SN q	$\varphi_{\text{SN}_q,\text{age}}$	0.868	0.867	0.872	0.868	0.867	0.871	0.865	0.865	0.870
Year correlation in SN q	$\varphi_{\text{SN}_q,\text{year}}$	0.886	0.885	0.885	0.886	0.885	0.885	0.886	0.886	0.886
SN q variance parameter	σ_{SN_q}	0.830	0.828	0.829	0.829	0.827	0.828	0.824	0.823	0.824
Age composition error (ages 0–2)	σ_{P_a}	1.831	1.845	1.835	1.826	1.841	1.832	1.818	1.823	1.818
Age composition error (ages 3–4)	-	0.844	0.848	0.854	0.851	0.856	0.859	0.851	0.854	0.860
Age composition error (ages 5–14)	-	0.306	0.307	0.303	0.306	0.307	0.304	0.306	0.306	0.301
Age correlation in process errors	$\varphi_{\delta,\text{age}}$	0.862	0.810	0.873	0.860	0.802	0.864	0.689	0.672	0.715
Year correlation in process errors	$\varphi_{\delta,\text{year}}$	0.766	0.831	0.802	0.772	0.839	0.813	0.641	0.672	0.630
Process error variance	σ_{δ}	0.281	0.258	0.236	0.267	0.244	0.230	0.305	0.291	0.268
Age correlation in F	$\varphi_{F,\text{age}}$	0.908	0.909	0.909	0.911	0.912	0.910	0.907	0.907	0.910
Year correlation in F	$\varphi_{F,\text{year}}$	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998
F variance parameter	σ_F	0.203	0.203	0.202	0.202	0.201	0.201	0.203	0.203	0.201
S-R relationship parameter	α_{SSB}	7.233	9.337	8.663	12.484	20.932	14.978	9.986	11.584	10.698
S-R relationship parameter	$\log(\beta_{\text{SSB}})$	-11.994	-11.781	-11.897	-11.971	-11.704	-11.859	-11.638	-11.550	-11.679

Quantity	Symbol	M11	M14	M17	M12	M15	M18	M13	M16	M19
Variance of log-recruitment	σ_r	0.271	0.259	0.268	0.260	0.245	0.258	0.236	0.224	0.229
Variance of tagging F deviations (pre 1997)	$\sigma_{f_{x,1}}$	0.942	0.941	0.940	0.942	0.941	0.940	0.944	0.943	0.943
Variance of tagging F deviations (post 1997)	$\sigma_{f_{x,2}}$	1.051	1.050	1.050	1.052	1.050	1.050	1.050	1.049	1.049
NB overdispersion parameter for pre 1997 tag experiments	κ_1	16.112	16.105	16.096	16.157	16.159	16.140	16.032	16.027	15.991
NB overdispersion parameter for post 1997 tag experiments	κ_2	8.081	8.108	8.121	8.092	8.116	8.122	8.018	8.043	8.044
Juvenile survey observation error	σ_{juv}	1.158	1.157	1.161	1.156	1.152	1.158	1.177	1.175	1.187

8. FIGURES

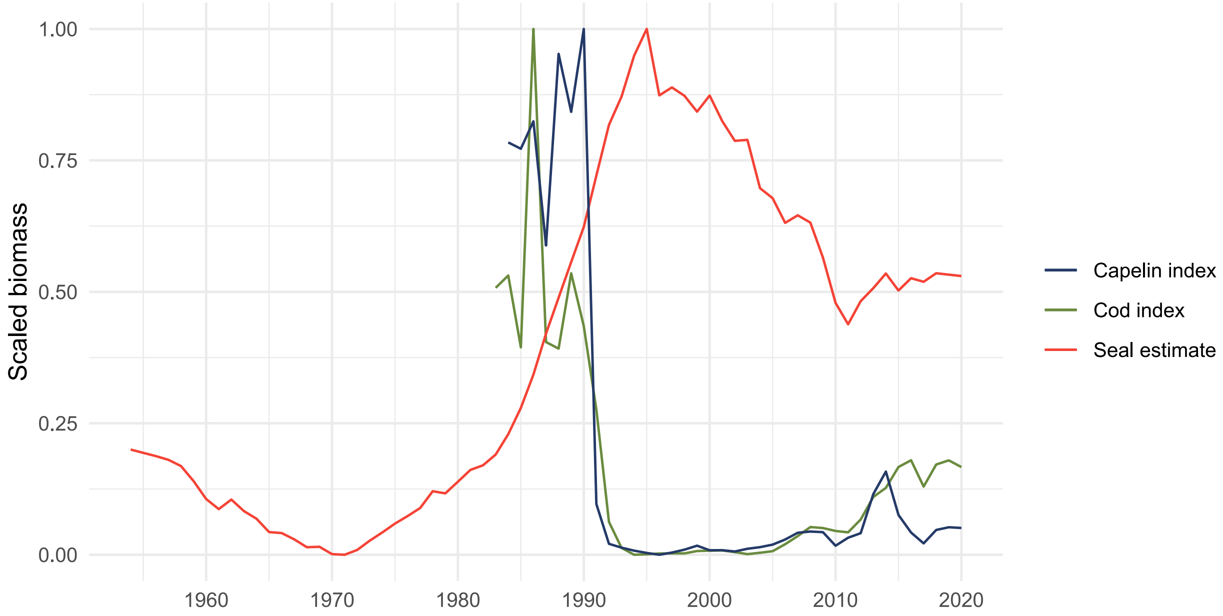

Figure 1: Index of Capelin biomass from an acoustic survey, index of cod biomass from a trawl survey, and estimate of seal biomass. Values are scaled to be between 0 and 1.

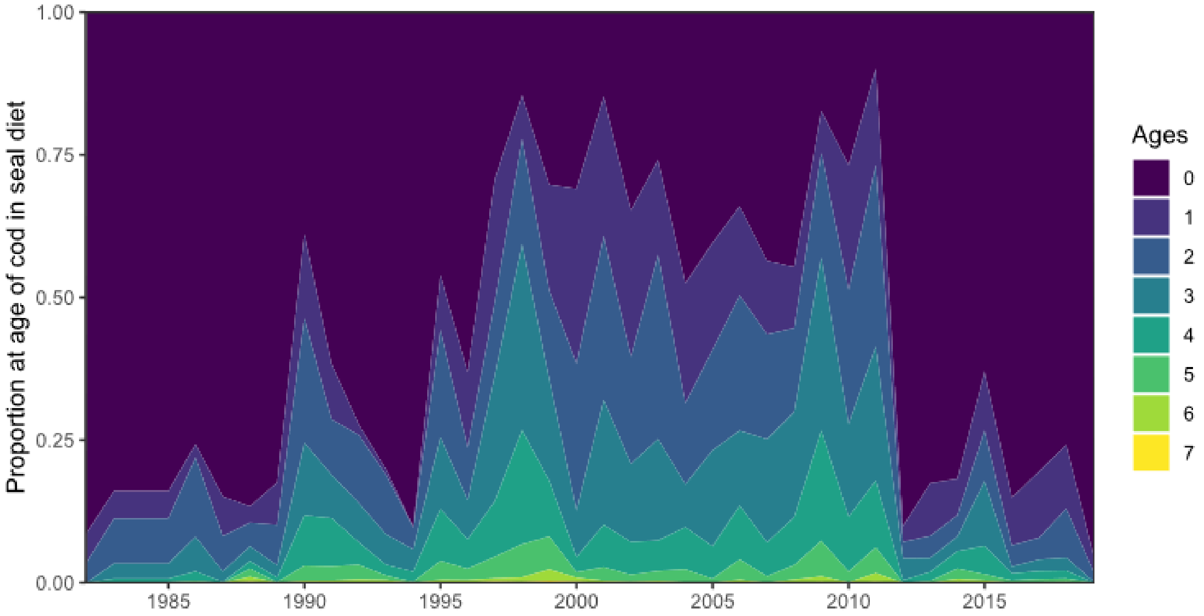

Figure 2: Proportion of cod by age estimated from seal stomach samples.

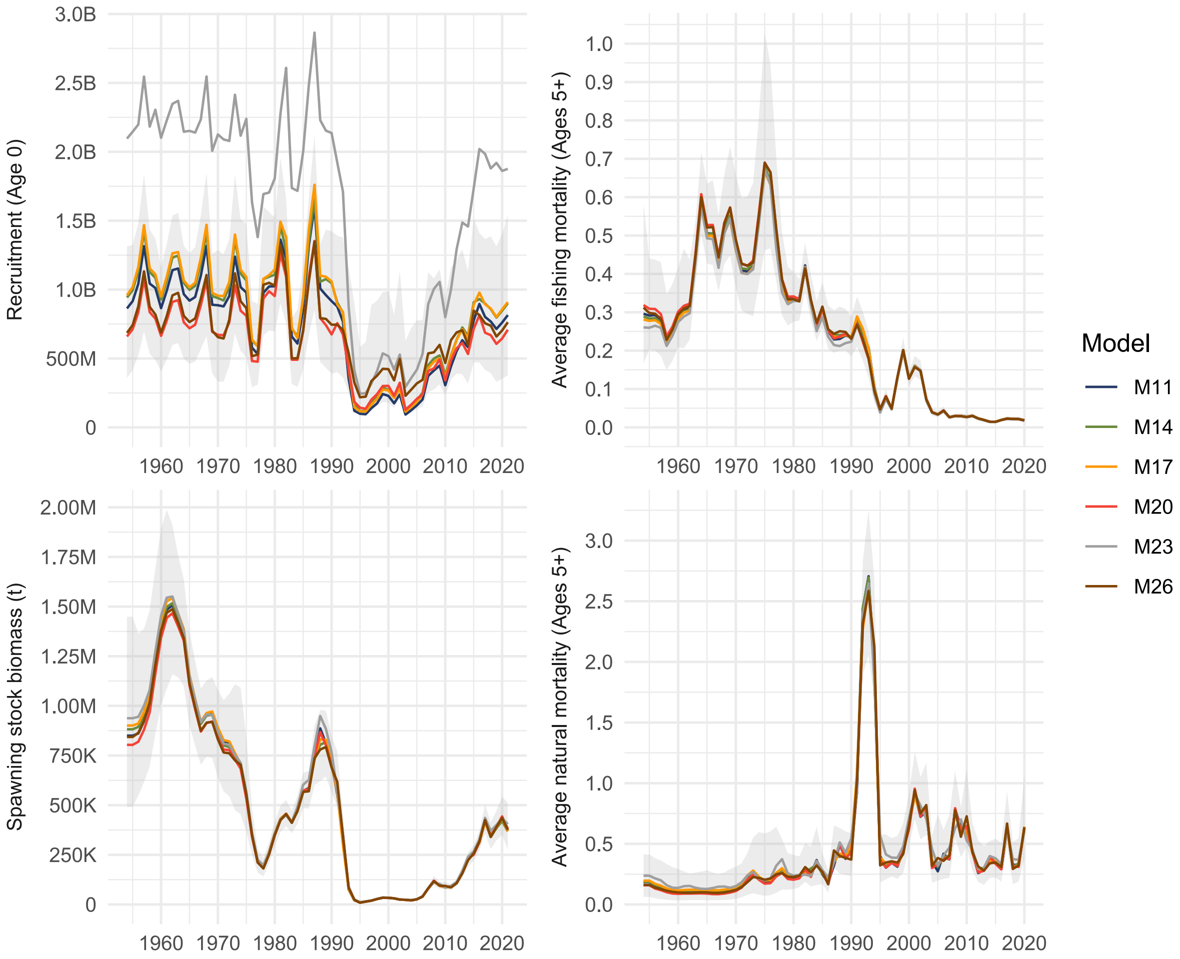

*Figure 3: Trends in recruitment, spawning stock biomass, fishing mortality, and natural mortality from models assuming constant baseline rates of M (**M11**, **M14**, **M17**, **M23**, **M20**, and **M26**). Shaded area represents the 95% confidence interval from model **M26**.*

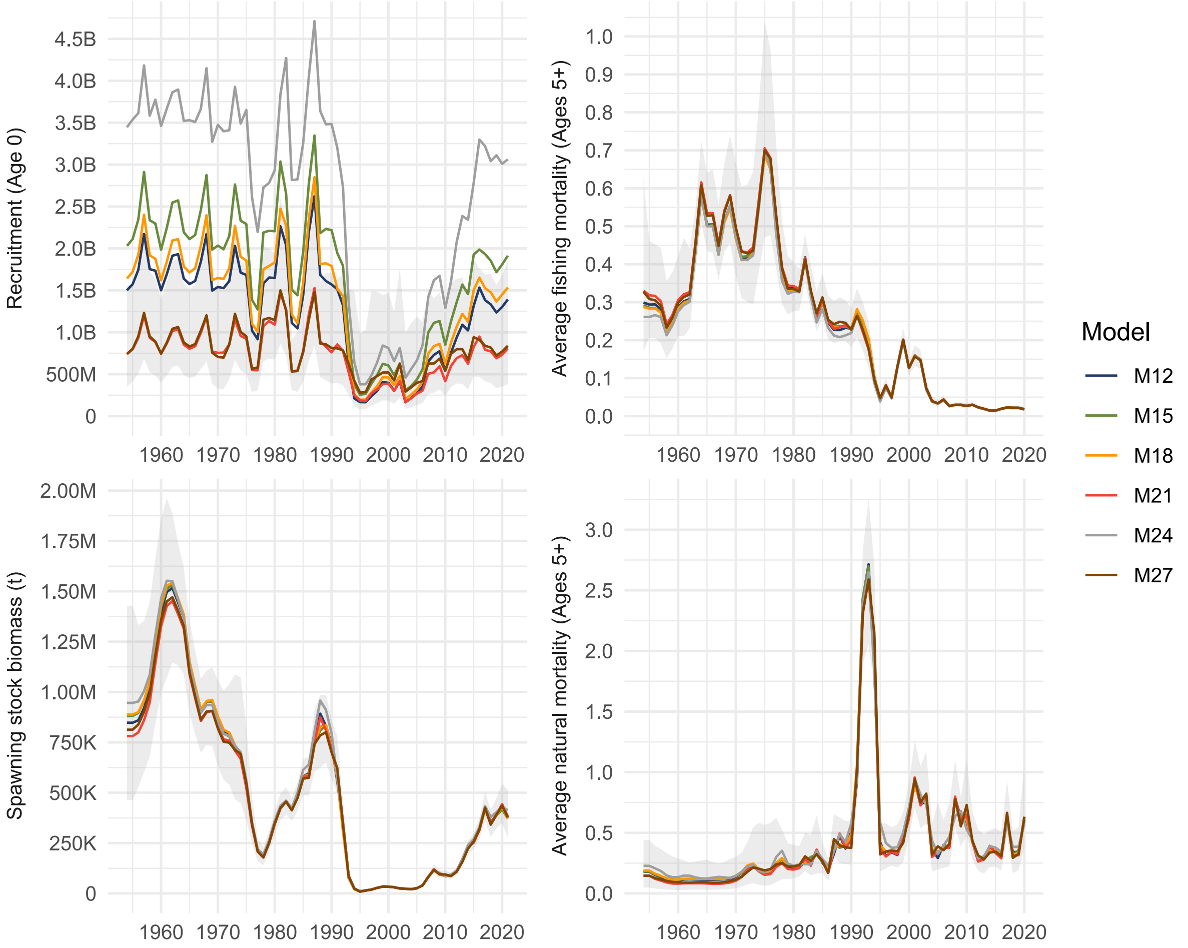

Figure 4: Trends in recruitment, spawning stock biomass, fishing mortality, and natural mortality from models assuming an allometric M *effect (**M12**, **M15**, **M18**, **M24**, **M21**, and **M27**). Shaded area represents the 95% confidence interval from model **M27**.*

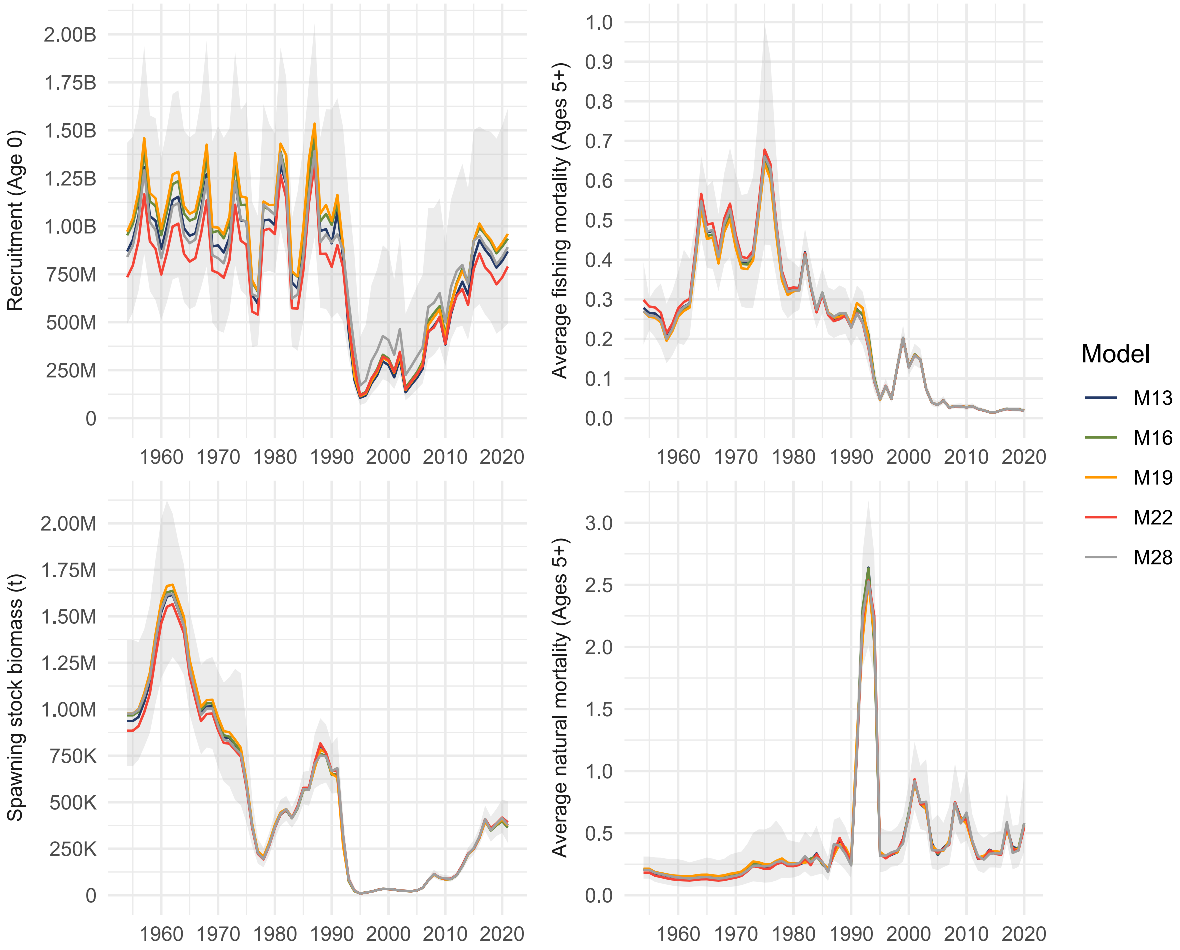

*Figure 5: Trends in recruitment, spawning stock biomass, fishing mortality, and natural mortality from models assuming shifts in baseline M (**M13**, **M16**, **M19**, **M22**, and **M28**). Shaded area represents the 95% confidence interval from model **M28**.*

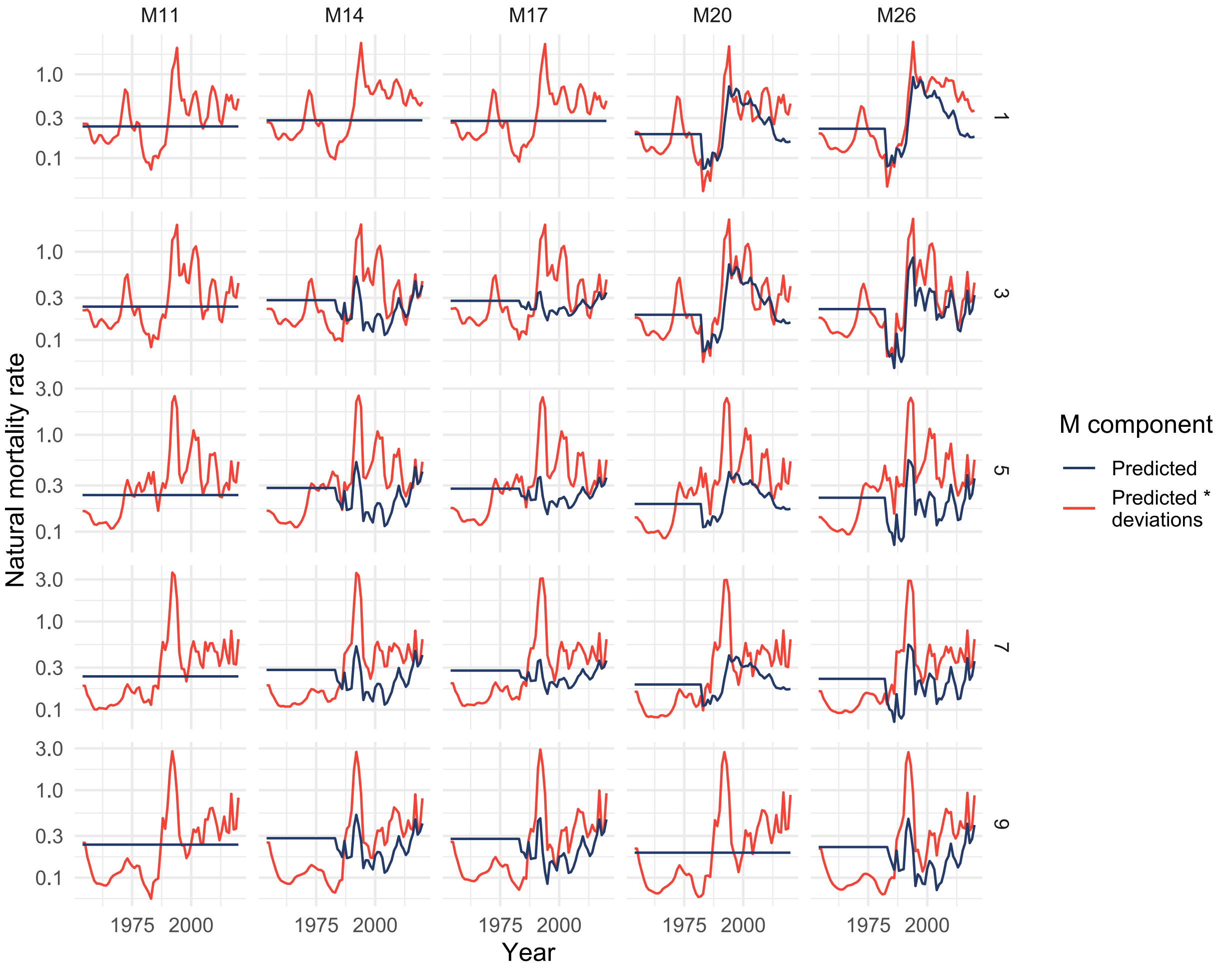

*Figure 6: Estimates of natural mortality across age 1, 3, 5, 7, and 9 from a subset of models assuming constant baseline rates of M (**M11**, **M14**, **M17**, **M20**, and **M26**). Note that y-axis is in log scale.*

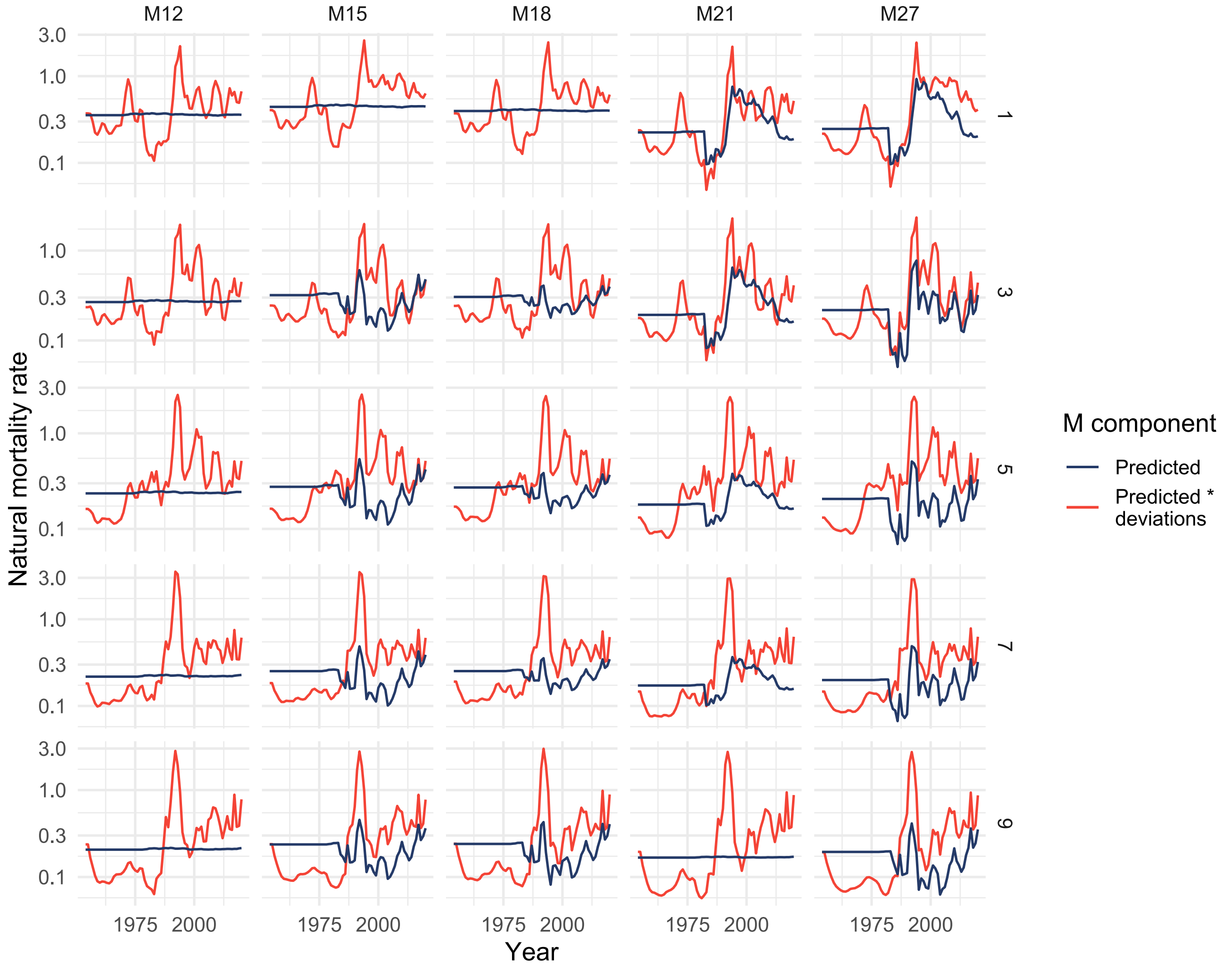

*Figure 7: Estimates of natural mortality across age 1, 3, 5, 7, and 9 from a subset of models assuming an allometric M effect (**M12**, **M15**, **M18**, **M21**, and **M27**). Note that y-axis is in log scale.*

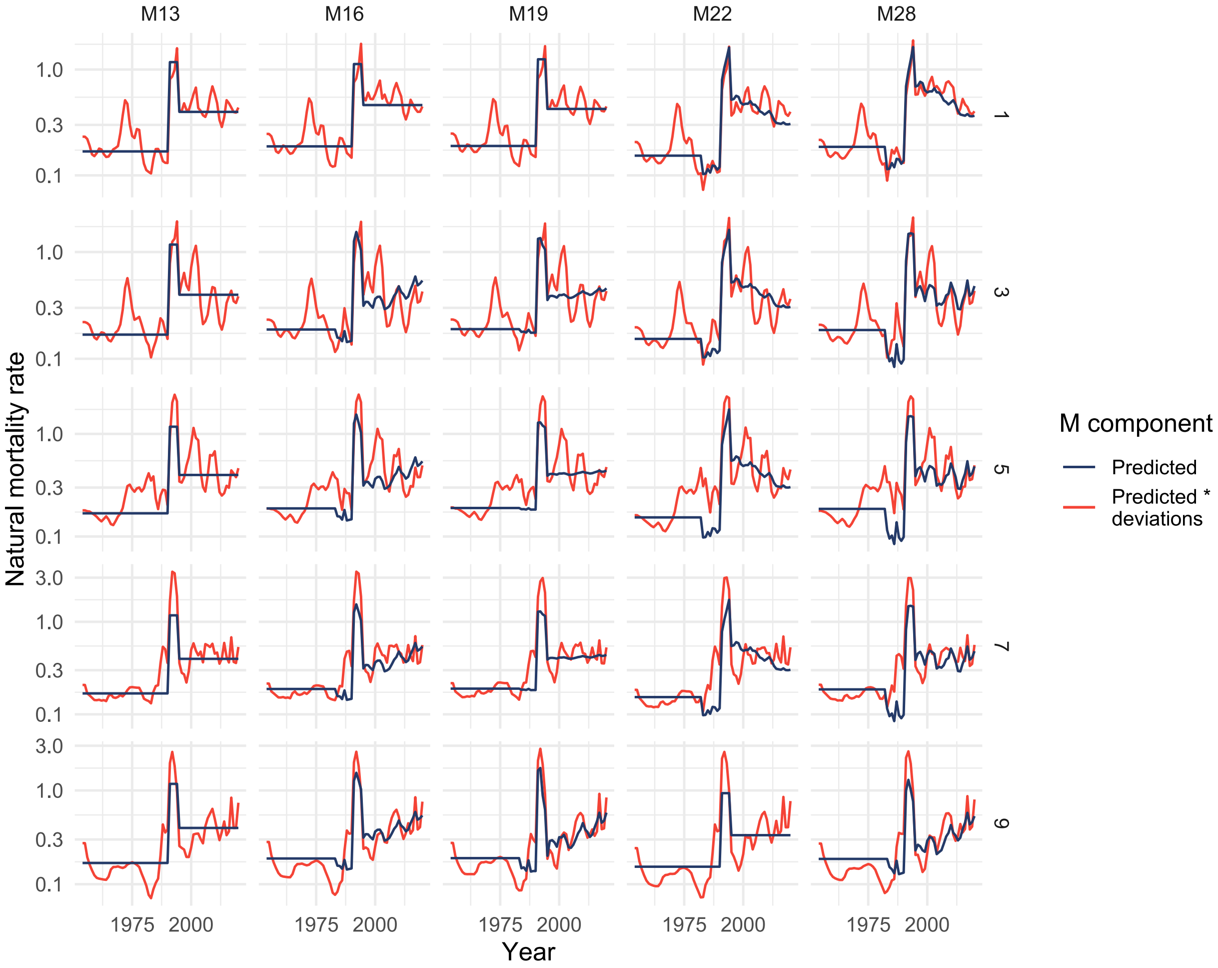

*Figure 8: Estimates of natural mortality across age 1, 3, 5, 7, and 9 from a subset of models assuming shifts in baseline rates of M (**M13**, **M16**, **M19**, **M22**, and **M28**). Note that y-axis is in log scale.*

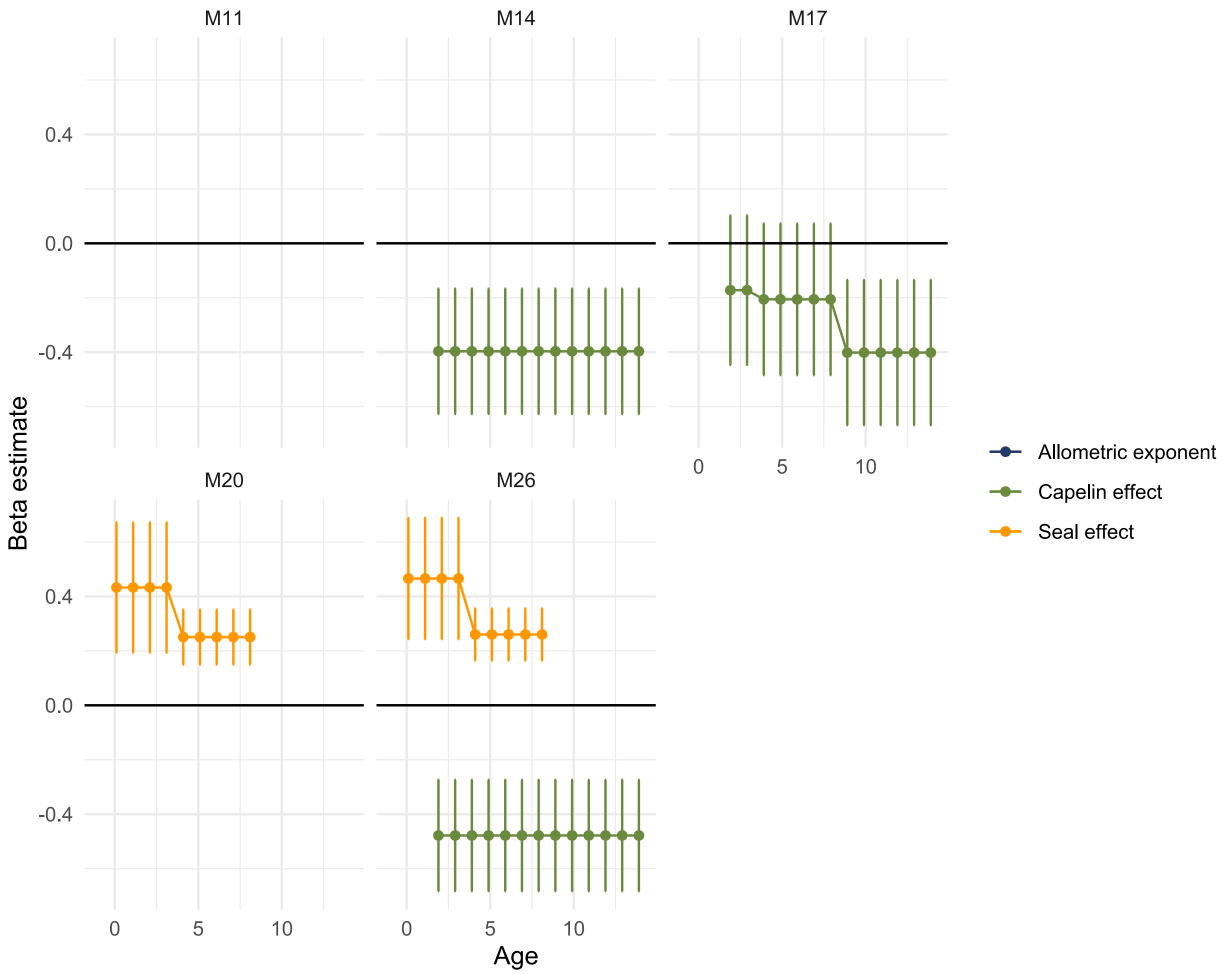

Figure 9: Beta parameter estimates from a subset of models assuming constant baseline rates of M *(**M11**, **M14**, **M17**, **M20**, and **M26**).*

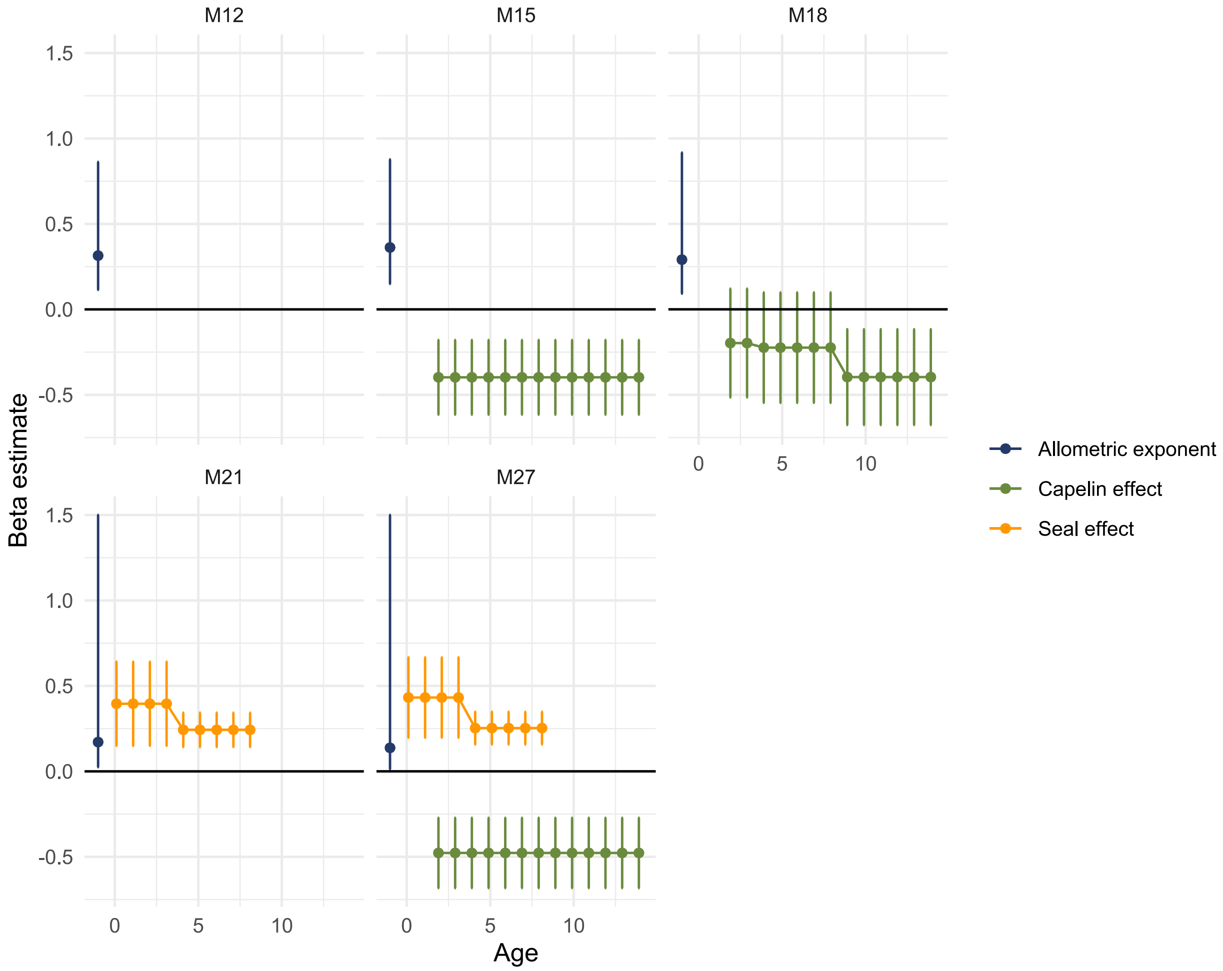

*Figure 10: Beta parameter estimates from a subset of models assuming an allometric M effect (**M12**, **M15**, **M18**, **M21**, and **M27**).*

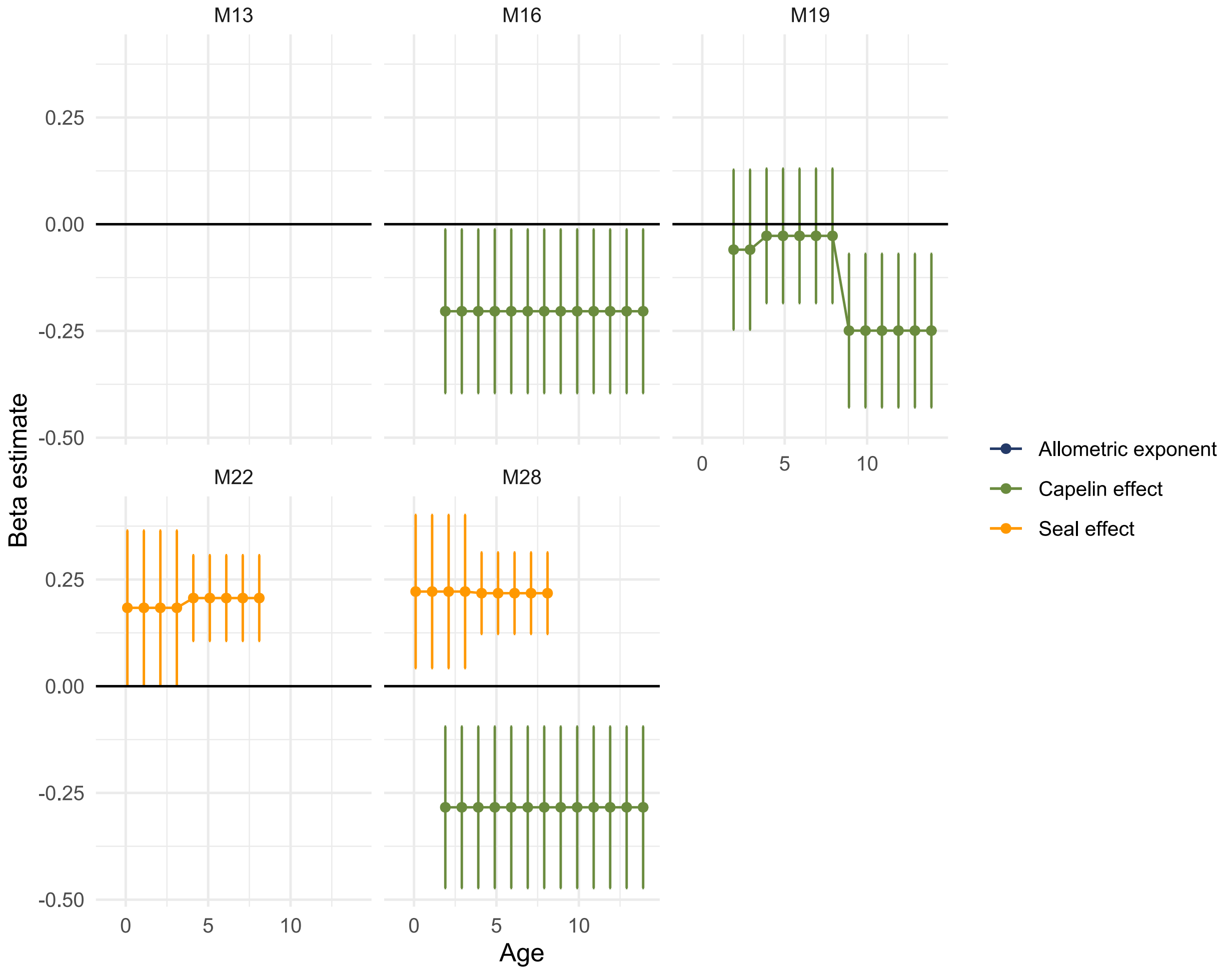

*Figure 11: Beta parameter estimates from a subset of models assuming shifts in baseline rates of M (**M13**, **M16**, **M19**, **M22**, and **M28**).*

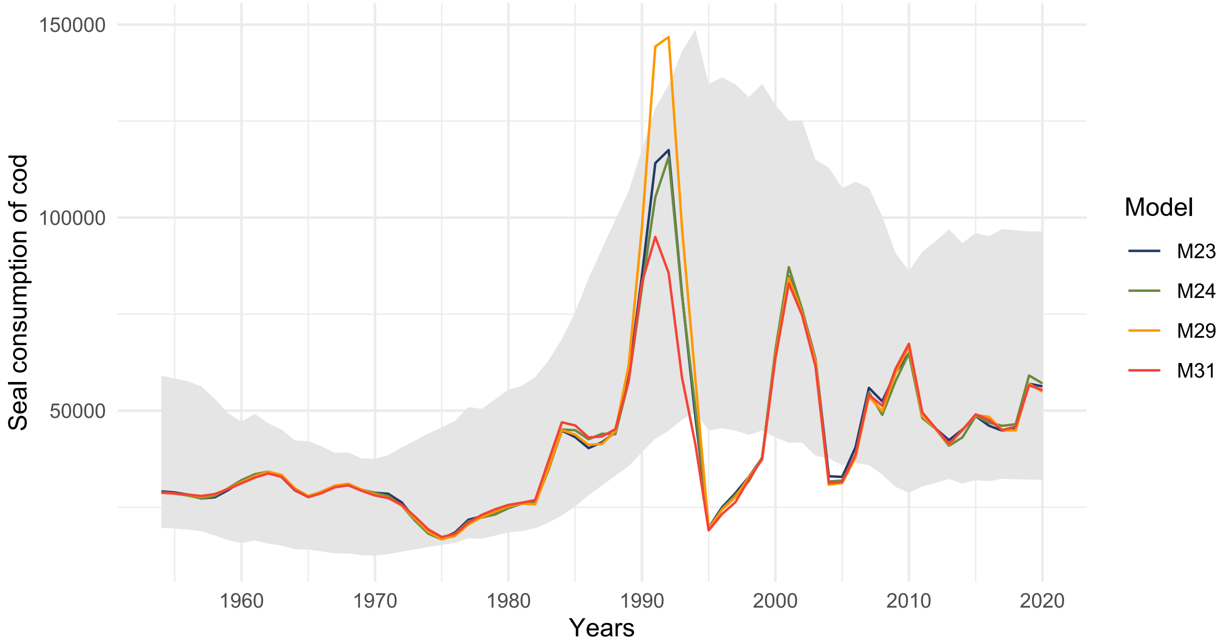

Figure 12: Prediction of consumption of cod by seal compared against estimates and bounds provided to the model.

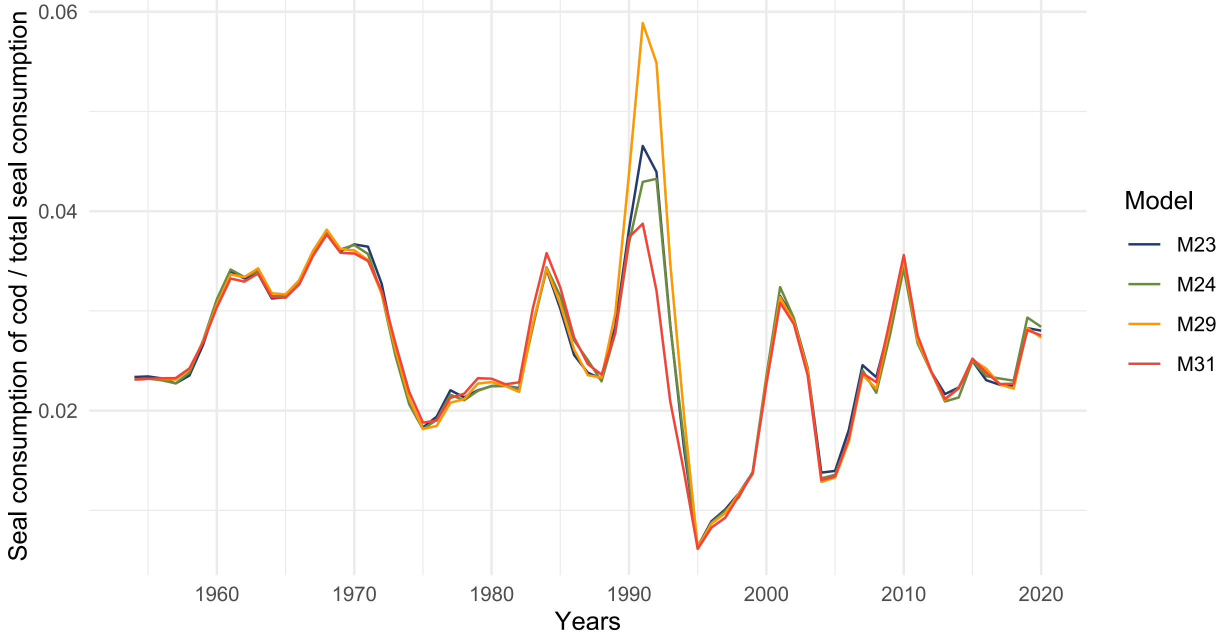

Figure 13: Prediction of consumption of cod by seal as percent of total consumption by seals.

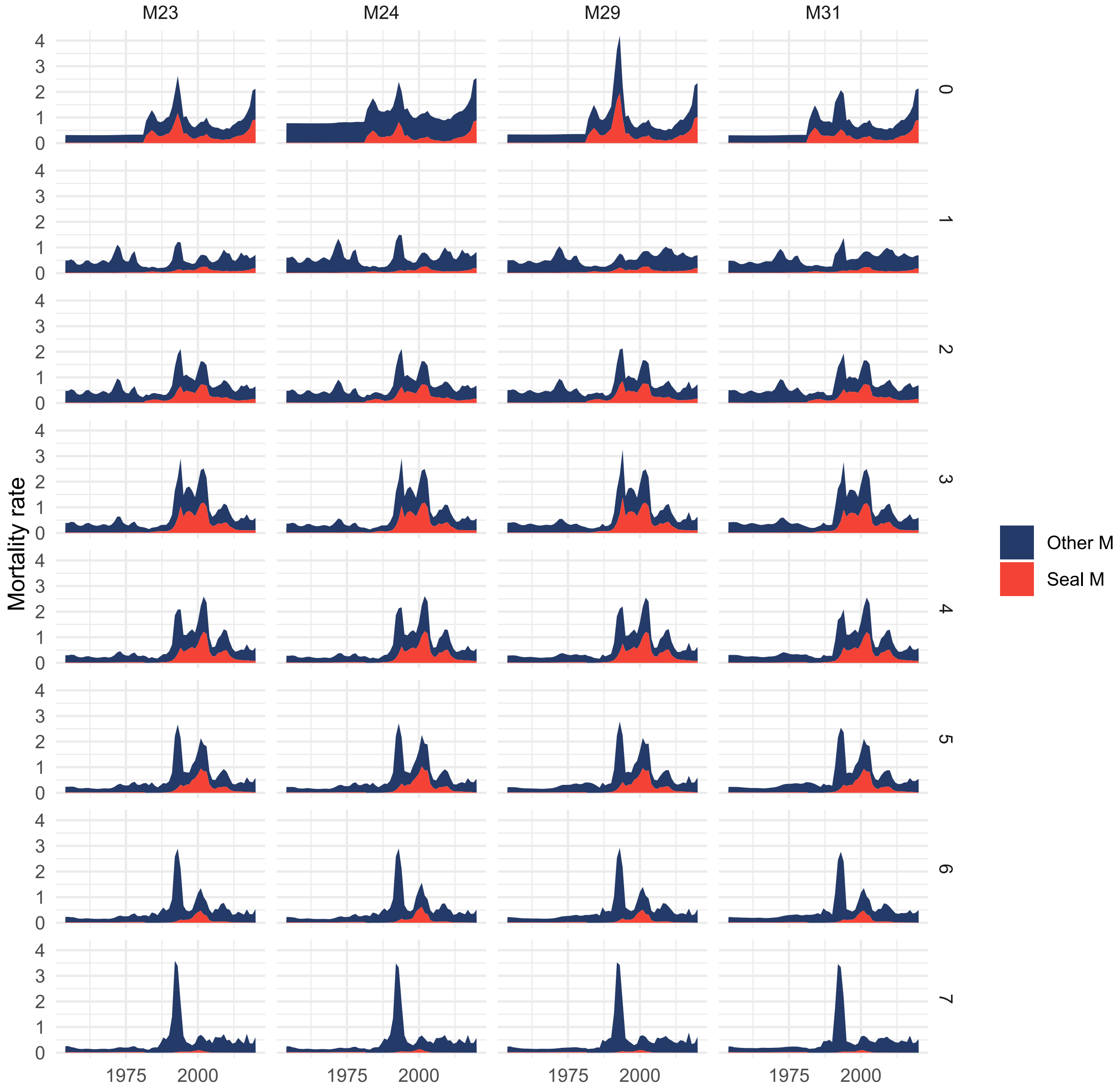

Figure 14: Estimates of natural mortality by age and across models incorporating seal effect as consumption.

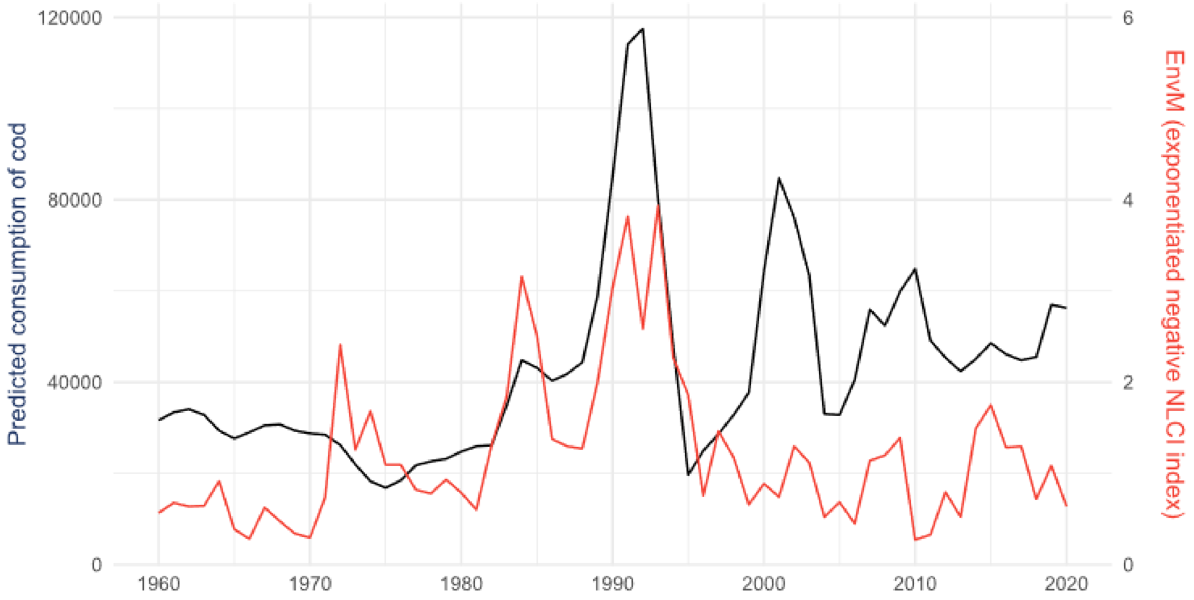

Figure 15: Comparison of prediction seal consumption of cod and a proxy environmental (EnvM) derived as the exponent of negative NLCI.

9. COLOPHON

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The computational environment that was used to generate this version is as follows:

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