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Grey seal predation mortality on three depleted stocks in the West of Scotland: What are the implications for stock assessments?

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ABSTRACTS

English:

The decrease in groundfish stocks in the North Atlantic since the mid-1900s coupled with increases in grey seal populations is responsible for an enduring controversy between fishers and conservationists regarding the role seals have played in stock declines. We used a Bayesian state-space model to investigate stock trends in the presence of grey seals and associated MSY reference points in the West of Scotland. This study provides new estimates of seal predation mortality on haddock and whiting and updates the estimates for cod, which together form the traditional main components of the mixed demersal fishery in this area. Grey seal predation mortality is greatest on cod resulting in estimates of total natural mortality higher than those used in the current ICES assessments. Seal predation mortality is low for haddock and whiting. Considering seal predation in stock assessments changes the scale of biomass and fishing mortality estimates for the three stocks. The estimates of $F_{0.1}$ and F_{MSY} are sensitive to seal predation for cod and whiting but not for haddock. In all cases MSY decreases with increased seal predation.

French:

La diminution des stocks de poissons démersaux dans l'Atlantique Nord depuis le milieu des années 1900, couplé à l'augmentation des populations de phoques gris, a entrainé une controverse durable entre les pêcheurs et les défenseurs de l'environnement concernant le rôle des phoques dans le déclin des stocks. Nous avons utilisé un model Bayésien état-espace afin d'investiguer l'évolution des stocks en présence des phoques dans l'ouest de l'Ecosse mais aussi les points de références de rendement maximal soutenu (RMS) associés. Cette étude estime la mortalité de l'aiglefin et du merlan due à la prédation des phoques gris, et met à jour les estimations pour la morue. Ces trois espèces représentent les principaux poissons démersaux traditionnellement péchés dans cette région. La mortalité de la morue due à la prédation des phoques gris est la plus importante et engendre des estimations de mortalité naturelle totale plus larges que celles actuellement utilisées par le CIEM dans l'évaluation des stocks. A l'inverse, la mortalité de l'aiglefin et du merlan est faible. Considérer la prédation des phoques dans le modèle d'évaluation des stocks change l'estimation de la biomasse et de la mortalité de pêche pour les trois stocks de poissons. L'estimation de $F_{0.1}$ et F_{MSY} pour la morue et le merlan est sensible à la prédation des phoques mais ne l'est pas pour l'aiglefin. Dans les trois cas, RMS diminue avec l'augmentation de la prédation des phoques.

INTRODUCTION

In the North Atlantic, the 20th century has seen a marked decline in fish stocks of high commercial value (Christensen et al. 2003). Atlantic cod (*Gadus morhua*), previously one of the most abundant and valuable demersal species, has declined substantially in much of Europe while some stocks in the western Atlantic collapsed (Myers et al. 1996) leading to the introduction of a moratorium on fishing in 1993. In the West of Scotland (ICES Division 6a) and the North Sea (ICES Subarea 4), the landings of demersal species have decreased substantially. In the 1980s, cod, haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) were the dominant species in the fishing catch (ICES 2013). In response to their decline, the West of Scotland fishery now targets mainly Norway lobster (*Nephrops norvegicus*) as a high value alternative species (ICES 2016) but haddock is still one of the main fish caught (ICES 2015). Whilst many fish stocks have declined, the grey seal population (*Halichoerus grypus*) has doubled around the UK (Thomas 2012) and has grown exponentially on the Canadian east coast (Bowen et al. 2003). This situation has created substantial conflicts between fishers and conservationists regarding the role that grey seals may have played in the stock depletion (Harwood 1984; Read 2008).

Grey seal predation mortality on cod has been estimated in the eastern Canada (Benoît et al. 2011; O'Boyle and Sinclair 2012) and the West of Scotland (ICES Division 6a) (Cook et al. 2015). On the Canadian east coast, the cod collapse in the early 1990s is widely accepted as being due to overfishing (Buren et al. 2014), but while seal impact on the stocks is still controversial, grey seals were recently believed to contribute to the non-recovery of the stocks despite the closure of the fishery in 1993 (Sinclair et al. 2015; Swain and Benoit 2015). Large scale seal culls were recently proposed to conserve the groundfish stocks in this area (Fisheries Resource Conservation Council 2011; Standing Senate Committee on Fisheries and Oceans 2012). In the West of Scotland, seal predation on cod is significant and may be responsible, with high levels of fishing mortality, for the non-recovery of the stock (Cook et al. 2015; Cook and Trijoulet 2016). However, cod is only one species in mixed trawl fisheries and it is important to quantify seal predation on other species that make or made a substantial contribution to the catch on which the fishery depends.

Cod is usually caught in mixed demersal fisheries along with other commercial species which appear in the grey seal diet (Bowen and Harrison 1994; Hammond and Grellier 2006; Harris 2007) and may be subject to significant seal predation. The West of Scotland area represents an opportunity to investigate grey seal predation on other species following seal diet studies carried out in 1985 and 2002 (Grellier and Hammond 2006; Harris 2007). This allows the role, if any, that grey seals may have played in the decline of haddock and whiting in the area to be investigated. It has been suggested that the weight of cod consumed by grey seals (7 565 tonnes) can be of similar magnitude to estimated spawning stock biomass (SSB) (Harris 2007) and that seal predation mortality on cod may be large (Cook et al. 2015; Cook and Trijoulet 2016). In 2002, the weight of whiting and haddock consumed by seals (Harris 2007) was estimated to be very similar to the landings for each species and may generate a mortality as large as the fishery (ICES 2013). Grey seal predation on these two other demersal species may therefore be high in this area.

At present, seal predation is considered within a multispecies stock assessment in the North Sea which provides estimates of total predation on a range of commercial species including cod, haddock and whiting (ICES 2015). However, no comparable multispecies estimates are made for the West of Scotland stocks. This could have important consequences if grey seal predation is high since these assessments are used to inform fisheries management.

Our study presents estimates of grey seal predation mortality on the three traditional principal commercial demersal species in the West of Scotland, cod, haddock and whiting. This extends and updates the study on cod by Cook et al. (2015) and Cook and Trijoulet (2016) and provides for the first time, values for predation mortality on haddock and whiting. Using these estimates we examined potential competition between the fishery and seals and the implications of considering seal predation for stock assessments in the area through the estimation of two management reference points: fishing mortality corresponding to 10% of the slope of the yield per recruit curve at the origin ($F_{0.1}$) and fishing mortality at maximum sustainable yield (F_{MSY}). The study is not an attempt to calculate multispecies reference points but rather to see how the single species assessments, as currently used in the West of Scotland, may vary with the consideration of seal predation.

MATERIALS AND METHODS

We performed the analysis in two stages. Firstly, using single species stock assessment models we estimated essential population parameters such as current stock size, fishing mortality and seal predation mortality. Secondly we used the values from the stock assessment models to calculate conventional equilibrium reference points such as $F_{0.1}$ and F_{MSY} under differing assumptions of seal predation.

Parameter estimation

For all three species we used the age-structured stock assessment model described in Cook et al. (2015) and Cook and Trijoulet (2016) to quantify the effect of fishing and seal predation on the three fish stocks. The model treats seals as an additional fishing fleet and uses observations of their catch of fish by age to estimate an associated mortality. In this study, the model is applied separately to cod, haddock and whiting. The data from standard ICES stock assessments used to fit each model and the seal data are given in Table 1. The main equations of the assessment model are given in Table 2. We configured the model in the same way as described in Cook and Trijoulet (2016) but minor modifications were made to allow application to the different species without changing the structural model or priors. These are explained below.

The model was fitted over the period 1985-2012 to include the first year when seal diet data are available and the last year when a full assessment of haddock is available for the West of Scotland. Since 2013, the haddock in the West of Scotland and the North Sea have been assessed as a single unit, so in order to retain geographical integrity with the seal diet data we used the data from the last 6a haddock stock assessment (ICES 2013). For consistency we used the same 2013 assessment for cod and whiting.

Four research vessel surveys from the West of Scotland were used in the assessments (Table 1). In 1999, the Scottish survey vessel was replaced and the length of the tow was reduced from 60 minutes to 30 minutes (ICES 2013). Hence the quarter 1 Scottish survey was split into two periods (1985-1998 and 1999-2010). This was not applied for the quarter 4 survey since it would result in a survey of only three years from 1996 to 1998. Preliminary model runs for whiting gave exceptionally large seal predation or fishing mortality estimates in 2004 and 2005 (Figure S1.1 in Supplementary material 1. Supplementary data are available online through journal) which appear to be related to the survey data. Similar unrealistically high mean fishing mortalities for the same years are obtained from the whiting ICES stock assessment model unless a persistent trend in survey catchability is assumed (ICES 2014b). Consequently, for whiting the final analysis was run with the survey data from 2001 to 2005 omitted (see Supplementary material 1 for further explanation).

We fitted models to the landings (T2.12), discards (T2.13) and research vessel indices (T2.14) age composition data under different assumptions of seal predation for each stock in turn using the same Bayesian statistical methods as described in Cook et al. (2015). The models were:

A. Seal predation rate (q) was allowed to vary annually according to a simple time series model (T2.8). This parameter determines the ability of seals to find and consume fish and may change over time if affected, for example, by the abundance of prey.

B. The seal predation rate was fixed over time (i.e. the process error standard deviation in the equation (T2.8) was set equal to 0). This model was included because of uncertainties in estimating annual values of q since the model A may over-fit the data.

C. Seal predation was considered as subsumed within natural mortality M and was not explicitly estimated in the model (i.e. Z=F+M). This most closely resembles the standard ICES assessments and was used as a baseline to determine the implication of considering seal predation in stock assessments.

Priors were either taken from Cook et al. (2015) or were modified to be applicable to the species of interest. The modified priors included the initial population size or the seal selectivity parameters. The priors are shown in Supplementary material 2 (Table S2.1).

The model was fitted separately for the three fish species using the WinBUGS 1.4.3 software (Lunn et al. 2000) run from the software R (R Core Team 2016) using the R2WinBUGS package (Sturtz et al. 2005). Preliminary runs of 10 000 iterations and 3 chains indicated convergence after 5 000 to 8 000 iterations. Final runs consisted of 1 chain, 40 000 iterations and a burn-in period of 10 000 iterations for each fish species. The last 5 000 replicates of the estimated parameters were saved for further analysis. Standard statistics recorded after each simulation were the mean, median, and 95% credible interval for all variables of interest. The Deviance Information Criterion (DIC) (Spiegelhalter et al. 2002) was calculated to compare the models A and B which explicitly considered seal predation.

The estimates of total non-fishing mortality (i.e. the sum of seal predation mortality, P and residual natural mortality, M) were compared with the estimates of M from ICES

(2013) used for ICES Division 6a stock assessments. The latter do not explicitly account for seal predation. We also compared the estimates with those from the North Sea (ICES Sub-area 4) as the ecosystems and fisheries share many similarities with the West of Scotland (ICES 2015). The North Sea estimates consider predation by fish, seals, harbour porpoises and seabirds and are based on multispecies assessment (SMS) (ICES 2014a).

Equilibrium analyses

In order to investigate how inclusion of seal predation changes perceptions of stock productivity and therefore the estimation of management reference points, two equilibrium analyses were performed These were a per recruit analysis to estimate $F_{0.1}$ and full population model to estimate MSY that used the outputs from the stock assessment model and published data. The stock assessment outputs needed for both analyses were the fishing mortality F, the Lorenzen parameters to calculate the natural mortality, the seal selectivity parameters (γ and δ) and the seal predation rate (q). The fishing selectivity at age used was derived from the average F at age taken over 2008 to 2012 to represent the most recent fishery selectivity. Because only two years of seal diet data are available and the variations in grey seal diet for the recent years are not well determined, an average seal predation rate (q) of the two years 1985 and 2002 was used as the input values. These years are informed by real observations and will be better determined. A test on the sensitivity of the results to the omission of survey data for whiting showed that this did not affect the estimates for the years 1985 and 2002 (Supplementary material 3).

Published data (Thomas 2012) on the average number of seals between 2008 and 2012 were used to scale the seal predation rate to seal predation mortality representative of recent years. An average over the same years was used for weight at age obtained from ICES (2013).

The MSY analysis requires a stock-recruitment relationship. To simulate recruitment dynamics, the replicates of the SSB and recruitment values from the stock assessment model outputs were used to fit a Ricker (1954) model from which recruitment could be predicted.

By default, for the three species the seal predation rate (q) and the seal selectivity (s) were kept constant in the projection period. In addition, for cod, the replicates of q and the partial biomass (*PB,* equation (T2.9)) from the model A were also used to fit a type II functional response (Holling 1959) by seals to cod biomass, following Cook and Trijoulet (2016). This will be referred to as the "type II" model in the MSY analysis. If θ and ρ are constants q can be expressed as:

(1) $$q_y = \frac{\theta}{1+\theta\rho PB_y}$$

The estimates of θ and ρ are available in Supplementary material 4. The poor fit of this model for haddock and whiting (Supplementary material 4) limited the functional response scenario to cod.

The per recruit analysis was used to calculate the fishing mortality at which the slope of the yield per recruit curve is 10% of the slope of the curve at its origin ($F_{0.1}$) following the method of Thompson and Bell (1934). The median measurements and 90% credible intervals were obtained by estimating $F_{0.1}$ from the 5 000 replicates obtained from the stock assessment model. This is a simple way of quantifying a MSY proxy reference point in response to changes in biological parameters without being affected by the uncertainties associated with estimating the stock-recruitment function.

The MSY analysis was performed where the stock-recruitment relationship was modelled. The fish populations were projected forward over 150 years (time long enough to reach a steady state for at least 50 years for the three species) under different scenarios of fishing and seal predation mortality. The projection model uses the same age-structured model as in the stock assessment (Table 2) except that recruitment is projected from a structural stock-recruitment model. Annually, to account for estimation error, the projection model bootstraps the 5 000 replicates of fitted Ricker stock-recruitment relationships. Stochasticity was added to the stock-recruitment curve by bootstrapping the residuals to account for process errors. In the projections if the simulated SSB exceeded the maximum observed SSB in the sample, recruitment was capped at the value given by the maximum observed SSB. This was to avoid predicting very large values of recruitment when the simulated SSB extended beyond the range of observations. We found that using another common relationship such as Beverton-Holt (Beverton and Holt 1957) gave similar management reference point estimates and therefore we only show the result for a Ricker curve. When the type II functional response was considered, the samples of q and PB were used to fit equation (1) and the residuals from the fitted relationship bootstrapped to account for process errors. The projection model provided 5 000 replicate values of yield and SSB which were averaged over the last 50 years of projection. For each replicate Maximum Sustainable Yield (MSY), fishing mortality at MSY (F_{MSY}) and SSB at MSY (SSB_{MSY}) were calculated and used to obtain posterior distributions.

RESULTS

Estimated trends in stock biomass and fishing mortality

The assessment model fitted the observed landings, discards and survey indices for the three models closely, notably for the landings (Supplementary material 5). The discard data was less well fitted, especially when only a few age classes were available. Best fits of abundance indices were to the longest running surveys. Seal diet data was also well fitted for models A and B although for haddock some points of the data lie outside the 95% credible intervals (Figures S5.48-S5.49). All the models typically estimated a larger SSB than the ICES assessments but with similar general trends (Figure 1). The estimated fishing mortality is lower than the ICES values for all species.

For haddock and whiting, the trends in F are similar to ICES assessments. For cod, however, ICES estimates a fishing mortality which is fairly constant and high while our models show a fishing mortality more variable but with a tendency to decline until an increase from 2005. Also for cod, model A, that allowed seal predation rate to vary, gave lower estimates of fishing mortality in all years than the run with this value fixed (model B) or with no explicit seal predation (model C).

Seal consumption and predation mortality

For the three species, the variable predation rate scenario (model A) gives a better fit to the estimates of consumption of fish by seals than the fixed rate model (B) most notably for cod and haddock in 2002 (Figure 2). The DIC indicates that the overall fit for model A is preferred (Table 3) but the improvement over model B is very small. In these models there is very little seal data to inform the predation estimates and the very large fluctuations in predicted fish consumption by seals are somewhat speculative. The very large estimated increase in the consumption of whiting is especially implausible.

The estimated trend in seal predation mortality along the time series varies substantially with the model considered (Figure 3). In the case of a fixed seal predation rate (model B), the mortality due to seals on the three species is almost constant reflecting the small change in the size of the seal population. For the variable predation rate scenario (model A), the estimated grey seal predation is smaller in the early years but subsequently increases and exceeds the fixed *q* estimates substantially.

Age dependent natural, seal predation and fishing mortalities

For cod, fishing mortality is the largest source of mortality for the two years seal consumption data are available except at young age classes in 2002 (Figure 4). Seal predation mortality is highest at ages 2 and 3, while fishing reaches its maximum on fish one year older.

Seal predation mortality is typically larger for cod compared to that for haddock and whiting. For these two species, seal predation mortality is the smallest component of total mortality. Seal predation mortality and fishing mortality increase with fish age for both species.

Table 4 compares mean values of seal predation mortality on cod obtained from this study to estimates made previously by Holmes and Fryer (2011) and for Canada made by Trzcinski et al. (2006) for the same years. The estimates are all of a similar magnitude.

Estimated total natural mortality

The estimates of non-fishing mortality at age (in effect the total natural mortality typically used in ICES assessments) obtained from the model A are larger than those obtained from the model B for cod, but slightly smaller for haddock and whiting (Figure 5). Models B and C give similar values for haddock and whiting. However models that consider grey seal predation explicitly estimate larger non-fishing mortalities for cod no matter the seal predation rate assumption. For the West of Scotland, generally the estimated non-fishing mortalities in this study were larger across all ages than those from ICES (M_{WoS} in Figure 5). Mortality estimates for young age classes are higher for the North Sea (M_{NS} in Figure 5) than our estimates for the West of Scotland.

Equilibrium analyses

The estimated reference points for the three species assuming the current number of grey seals in the West of Scotland are shown in Figure 6. The corresponding values are given in Supplementary material 6. The values of $F_{0.1}$ for the three models differ little from the values of F_{MSY} for cod and haddock as their distributions overlap. There is a large difference, however, for whiting. The current value of mean fishing mortality on cod is near $F_{0.1}$ and F_{MSY}, while for whiting it is below $F_{0.1}$ and close to F_{MSY}. For haddock, current mean F is well below both reference points.

For whiting, and to a lesser degree for cod, considering seal predation in the model (model A and type II) has a large effect on the estimates of MSY and SSB_{MSY} though these effects are in opposite directions for the two species. There is little effect of seal predation on these values for haddock.

Changes in MSY and F_{MSY} are shown as a function of relative seal population size for the four models (Figure 7). As expected an increase in seal numbers results in an overall decrease in MSY and F_{MSY} for the three species. However, for haddock, the change in MSY is small and F_{MSY} is almost constant no matter the change in predation mortality or the choice of model. This is consistent with the little change in overall non-fishing mortality observed in Figure 5 for this species. The type II model shows a steeper decrease in F_{MSY} and the collapse of cod occurs when the current seal predation is multiplied by a factor between 1.9 and 2. The results for whiting are similar to those for cod but less dramatic with a clear decrease in MSY and F_{MSY} when the grey seal population is increased.

DISCUSSION

Accounting for seal predation in stock assessments results in higher estimates of the total non-fishing mortality affecting the stocks compared to values used by ICES in annual assessments. As a consequence, the fishing mortality is generally lower and the corresponding estimates of SSB higher than the ICES assessments. These differences are typical for increased values of natural mortality that in effect rescale the biomass to explain the observed catches. The trend in SSB over time is less affected although the peaks and troughs are amplified. For haddock and whiting the trends in fishing mortality are similar to the ICES assessments, while for cod the trends differ more, especially in the case where model A is employed. Using model A, fishing mortality reduces on average between 1985 and 2005 while it is stable or increasing according to the ICES assessment. However, all three models in our analysis indicate an upward trend in fishing mortality for cod post 2005 while the ICES assessment, if anything, shows a downward trend.

When the seal predation rate is treated as a constant, only small variations in seal mortality estimates are observed which arise from annual fluctuations in fish size at age and small changes in seal numbers. However, there are large fluctuations when the predation rate is allowed to vary. The small number of years with seal diet data and the small difference in the DIC mean it is very difficult to distinguish between the assumptions of constant or variable seal predation rate with any confidence especially as some of the fluctuations appear implausibly large. However, the decline in the cod stock between 1985 and 2002 (ICES 2013) while seal per capita consumption rates are of the same order of magnitude between the two years (Grellier and Hammond 2006; Harris 2007) would support a variable predation rate. The fact that the seal per capita consumption rate of haddock increased significantly between 1985 and 2002 (Grellier and Hammond 2006; Harris 2007) while the haddock population was similar in both years strongly suggests a change in the predation rate. Consequently, the results presented here offer some support for the use of a variable seal predation rate in the stock assessment model. The estimates of seal predation mortality for 1985 and 2002 are likely to be the most reliable since these are years when actual observations exist. For other years the estimates need to be treated with care and are at best illustrative.

In the current West of Scotland ICES cod assessment, the average natural mortality (age 1-6) used is 0.308 and implicitly includes the mortality due to seal predation. The average non-fishing mortality on cod estimated from models A and B in this study is larger than this value suggesting that the current cod natural mortality values considered in ICES assessments for the Division 6a may be too low. Unlike recent studies in the North Atlantic where seal predation was considered as insignificant compared to the total mortality on fish stocks (Boyd and Hammond 2010; MacKenzie et al. 2011; Alexander et al. 2014) these values seem of sufficient magnitude to matter in evaluating stock status for fishery management.

The estimates of seal predation mortality at age for haddock and whiting are much lower than those for cod. While it may be indicative of a species preference, it may in part be an effect of size. Haddock and whiting have much lower size at age and the highest predation mortality is on the oldest fish (ages 6-7) while for cod it reaches a maximum at ages 2-3. These ages correspond to a similar mean length; a two year old cod has a mean length of 45.8 cm while six year old haddock and whiting have mean lengths of 43.4 cm and 38.5 cm respectively. It is suggestive of a size preference by seals since fish below and above this size have lower predation mortality rates, although for large fish this is only discernible in cod. The consequence of the apparent size preference is that, for cod, seals remove smaller fish before they are selected by the fishery leading to sequential competition. For haddock and whiting size selection increases along with the fishery and is closer to scramble competition.

The West of Scotland stocks are adjacent to those of the same species in the North Sea and it might be expected that similar non-fishing mortality rates would prevail in both areas. This is of further relevance given there is now one unified haddock stock assessment covering the West of Scotland and North Sea. Separate estimates of non-fishing mortality that include seal and other predation, have been made from multispecies models and provide a comparison to our estimates (ICES 2015). They are very similar for whiting but show marked differences for cod and haddock mostly in the shape of the mortality rate by age rather than the overall scale. Clearly in the case of haddock, however, the conventional ICES value of 0.2 used previously for the West of Scotland appears too low both in relation to our estimates and those derived for the North Sea. The recent amalgamation of the West of Scotland and the North Sea stock assessments by ICES will overcome this problem (ICES 2015). The estimated total non-fishing mortality at young ages in the North Sea is larger than that in the West of Scotland for all species. This difference arises due to the methodology used in the two areas. Our analysis assumes size dependent natural mortality based on the Lorenzen meta-analysis whereas the North Sea values are based on multispecies modelling which accounts explicitly for predatory interactions.

For cod and whiting, the mean F in the reference period 2008-2012 is not distinguishable from F_{MSY} but the corresponding SSB is smaller than SSB_{MSY}. This suggests there is potential for the stocks to recover. However, the estimated catch at MSY for these stocks is below the historical mean catches of 19 516 t and 17 178 t respectively for the period 1981-1990 when landings were at their maximum, indicating that the fishery is unlikely to return to these high values. For haddock, the current fishing mortality is well below F_{MSY} so the stock may recover in the future, but the current SSB is larger than SSB_{MSY}, so reaching the equilibrium may result in a decrease in the current SSB. Similarly to the two other stocks, while the yield may increase compared to the current catch if fished at MSY, the yield will still be below the historical level (17 178 t).

For cod and haddock estimates of $F_{0.1}$ and F_{MSY} are generally similar regardless of the model used suggesting that the estimation of fishing reference points is relatively insensitive to whether a yield per recruit ($F_{0.1}$) or a stock-recruitment relationship dependent reference point (F_{MSY}) is considered. In contrast, for whiting $F_{0.1}$ is typically much larger than F_{MSY} showing that the choice of considering a stock-recruitment relationship or not for target reference points is important. It should be noted, however, that the anomalies in the whiting stock assessment (i.e. the omission of some survey data) mean that these reference points are particularly uncertain.

Over much of the study period the grey seal population in the West of Scotland has been fairly stable and the estimates of MSY reference points in Figure 6 assume no change in seal numbers. Given the controversy surrounding the effect of seal predation on the fishery it is of interest to consider the effect of changed seal population size on these reference points. As might be expected, in all cases increased seal populations result in lower MSY catches with the most dramatic effect on cod where the stock comes close to collapse when the seal population doubles. The high sensitivity of cod to seal predation is partly an effect of scale (*P* is much larger compared to that for haddock and whiting) and partly the domed selection pattern which effectively removes fish one age earlier than the fishery.

Within the obvious limitations of the analysis, F_{MSY} appears little changed for haddock regardless of model choice under quite large changes to the seal population. Cod shows the most extreme variation where, over the range of seal populations examined, F_{MSY} has a four-fold change. Whiting is intermediate with a two-fold change. From a stock assessment perspective, this means if seal numbers change significantly, MSY values would need to be revised for cod and perhaps whiting but not for haddock.

MSY equilibrium reference points often provide the basis for long term fishing mortality targets. However, changing seal predation may affect short and long term fishery objectives differently depending on the competition between seals and the fishery (Legault and Palmer 2016). The value of increasing *F* in the short term when seal predation increases in order to catch the fish before the seals, will depend in the state of the stocks. In the species considered here, seal predation has increased with declining stocks, so increasing *F* is unlikely to be appropriate.

In the popular press the scale of seal predation is often judged by comparing catches from the fishery to estimated quantities consumed by seals. The small effect of changes in seal predation on haddock revealed in this study highlights the limits of assessing the impact of seals on a stock simply by comparing seal catches (Harris 2007) with fishing catches (ICES 2013). Even in the case of whiting, although seal predation appears to affect reference point calculations, the magnitude of seal predation mortality is small compared to other sources of mortality, including fishing.

With the exception of the cod functional response scenario, all the projections assume the seal predation mortality values are fixed which is an over-simplification if seals respond dynamically to the abundance of prey as suggested by previous studies (Matthiopoulos et al. 2003; Middlemas et al. 2006; Smout et al. 2014). Our results should therefore be seen more as an indication of sensitivity to seal predation rather than absolute quantitative predictions. The consideration of a seal functional response to cod biomass heightens the sensitivity of cod to an increase in fishing and seal predation mortality. However, the type II response was fitted to the seal predation and partial biomass estimates for which only two years of seal data over the time series of 28 years were available. The limited seal diet data brings uncertainty to the seal response and prevented a three parameter type III functional response being fitted despite the reported switching behaviour in seals (Smout et al. 2014).

For whiting we used the stock assessment outputs where abundance indices for some years were removed due to an apparent anomaly in the estimated values of seal predation. It is debatable whether this is fully justified because censoring the data is based purely on a perception of how seal predation should change. Omitting the data affected the estimated biomass and mortality rates in 2004-2005 but for other years the omission had little effect. As we used estimated values for seal predation from 1985 and 2002 in subsequent analyses our results are fairly insensitive to this problem, though it does mean that estimated stock trends during this period are subject to particularly large uncertainty.

Only two years of seal diet data inevitably means that the estimates of seal predation mortalities obtained in our analysis are subject to large uncertainty. Furthermore, the estimates are predicated on sampling seal scats from which the size and species of fish in the diet is derived from otoliths and these techniques are also subject to bias (Bowen and Iverson 2013). Nevertheless, the estimates of seal predation that we have obtained show similarities with values derived from other methods such as the stochastic multispecies model SMS (ICES 2015) and the energetic model (Trzcinski et al. 2006) offering some independent corroboration of the analysis considered here. Given the apparent importance of seal predation mortality, at least for cod, there is clearly a need to obtain more data on seal diet so that the grey seal predation estimates can be improved and lead to more robust assessments.

This study only considers the direct effect of seal predation on the mortality rates of the three species and the potential implications for routine stock assessments. In the case of cod the implications appear important, for whiting the impact on stock perception is slightly smaller and for haddock even less so. However, there is a more general question of the economic impact of seal predation on the fishery. Even if the implications seem less important for haddock and whiting, as mentioned earlier the seal catches are of comparable scale to that of the fisheries (Harris 2007), so it is premature to conclude that seal predation on haddock and whiting is unimportant simply because predation mortalities are fairly low. An economic analysis of the fishery would be needed to address this issue.

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TABLES

Table 1: Summary of empirical data used in the stock assessment model.

Data type	Years	Reference
Proportion of mature fish at age	1985-2012	ICES (2013)
Mean fish weight at age in the total catch	1985-2012	ICES (2013)
Fish landings at age (numbers)	1985-2012	ICES (2013)
Fish discards at age (numbers)	1985-2012	ICES (2013)
Scottish groundfish quarter 1 survey	1985-2010	ICES (2013)
Scottish groundfish quarter 4 survey	1996-2009	ICES (2013)
Irish groundfish quarter 4 survey	1993-2002	ICES (2013)
Irish groundfish quarter 4 survey	2003-2012	ICES (2013)
Fish weight to length conversion parameters		Coull et al. (1989)
Average seal per capita consumption rates	1985 and 2002	SMRU
Numbers of fish consumed at age by seals	1985 and 2002	SMRU
Seal numbers	1985-2011	Thomas (2012)

Table 2: Main equations of the stock assessment model. A full description of the model is given in Cook et al. (2015).

Equation number	Name	Equation	Comments
(T2.1)	Fish abundance	$N_{a+1,y+1} = N_{a,y}e^{-Z_{a,y}}$	a is the age and y the year
(T2.2)	Total mortality	$Z_{a,y} = F_{a,y} + M_{a,y} + P_{a,y}$	
(T2.3)	Fishing mortality	$F_{a,y} = sel_{a,y}E_y$	*sel* is the fishing selectivity
(T2.4)	Fishing effort	$E_y = E_{y-1}e^{\varepsilon_{E_y}}$	Random effect $\varepsilon_E \sim Normal(0,\sigma^2_E)$, $y \neq 1$
(T2.5)	Natural mortality	$M_{a,y} = \alpha(w_{a,y})^{\beta}$	w is the fish weight and α and β the Lorenzen (1996) constants
(T2.6)	Seal predation mortality	$P_{a,y} = s_{a,y}q_yG_y$	G is the number of seals
(T2.7)	Seal selectivity	$s_{a,y} = \left(\frac{l_{a,y}}{(\gamma-1)\delta}\right)^{\gamma-1} e^{\left(\gamma-1-\frac{l_{a,y}}{\delta}\right)}$	l is the fish length, γ and δ are the Gamma curve constants
(T2.8)	Seal predation rate	$q_{y+1} = q_ye^{\varepsilon_{q_y}}$	Random effect $\varepsilon_q \sim Normal(0,\sigma^2_q)$
(T2.9)	Fish partial biomass	$PB_y = \sum_a(s_{a,y}w_{a,y}N_{a,y})$	
(T2.10)	Seal catches	$H_{a,y} = \frac{P_{a,y}}{Z_{a,y}}N_{a,y}(1 - e^{Z_{a,y}})$	Baranov equation for seal mortality
(T2.11)	Fishing catches	$C_{a,y} = \frac{F_{a,y}}{Z_{a,y}}N_{a,y}(1 - e^{Z_{a,y}})$	Classic Baranov equation
(T2.12)	Landings	$L_{a,y} = r_{a,y}C_{a,y}$	r is the proportion of fish retained
(T2.13)	Discards	$D_{a,y} = (1 - r_{a,y})C_{a,y}$	
(T2.14)	Abundance index	$I_{k,a,y} = \zeta_{k,a}\eta_kN_{a,y}e^{-\theta_kZ_{a,y}}$	k is the survey, ζ the survey selectivity, η the survey catchability and θ the proportion of the year elapsed before survey

Table 3: DIC estimates for the different seal predation simulations. A lower DIC illustrates a better fit (Spiegelhalter et al. 2002).

Species	Model A (variable *q*)	Model B (fixed *q*)
Cod	3 480.31	3 495.65
Haddock	8 639.97	8 701.90
Whiting	6 917.11	7 030.69

Table 4: Average grey seal predation mortality estimates on cod (between ages 1 and 5) compared with the literature. The estimates from the current analysis correspond to the values obtained from the seal predation models A and B.

Year	Current analysis	Holmes and Fryer (2011)	Trzcinski et al. (2006)
1985	0.12-0.2	0.22-0.23	0.09
2002	0.28-0.47	0.27-0.32	0.32

FIGURE LEGENDS

Figure 1: Estimated spawning stock biomass (SSB) and mean fishing mortality (mean F) for cod, haddock and whiting from three assessment models and the ICES assessment. The average F is taken for ages 2-5 for cod, 2-6 for haddock and 2-4 for whiting following ICES (2013).

Figure 2: Estimated weight of fish consumed (in tonnes) by grey seals along the time series for the variable (model A) and fixed (model B) seal predation rate assumptions. The black line is the median consumption and the grey area is the 95% credible interval. The dots are the two years of seal diet data.

Figure 3: Comparison of grey seal predation mortality estimates averaged across all ages for the variable (model A) and fixed (model B) seal predation rate assumptions. The black line is the median predation mortality and the grey area is the 95% credible interval.

Figure 4: Estimated seal predation (P), natural (M) and fishing (F) mortality at age in 1985 and 2002 for the variable seal predation rate assumption (model A).

Figure 5: Comparison of estimated total non-fishing mortality at age (models A, B and C) with the ICES values in West of Scotland (M_{WoS}) (ICES, 2013) and the natural mortality estimated in the North Sea (ICES, 2015) which includes seal predation (M_{NS}). When seal predation is considered the outputs come from the model with the lowest DIC (variable seal predation rate, model A).

Figure 6: Estimated management reference points when the current seal predation mortality is assumed. All values correspond to median measurements and the segments represent the 90% credible interval. The dashed horizontal lines show the mean yield over the years 1981-1990, a period of high yields from the area. $F_{08\text{-}12}$ and $SSB_{08\text{-}12}$ are

the same for model A and type II because both models use the same stock assessment outputs.

Figure 7: Estimated median values of maximum sustainable yield (MSY) in tonnes and fishing mortality at MSY (F_{MSY}) as a function of the seal population relative to the mean population 2008-2012 (x-axis equals 1). The grey horizontal lines represent MSY and F_{MSY} when seal predation is not explicitly considered (model C values in Figure 6). For models A and B the scaling factor on the seal population size is equivalent to the same change in seal predation mortality.

FIGURES

Figure 1

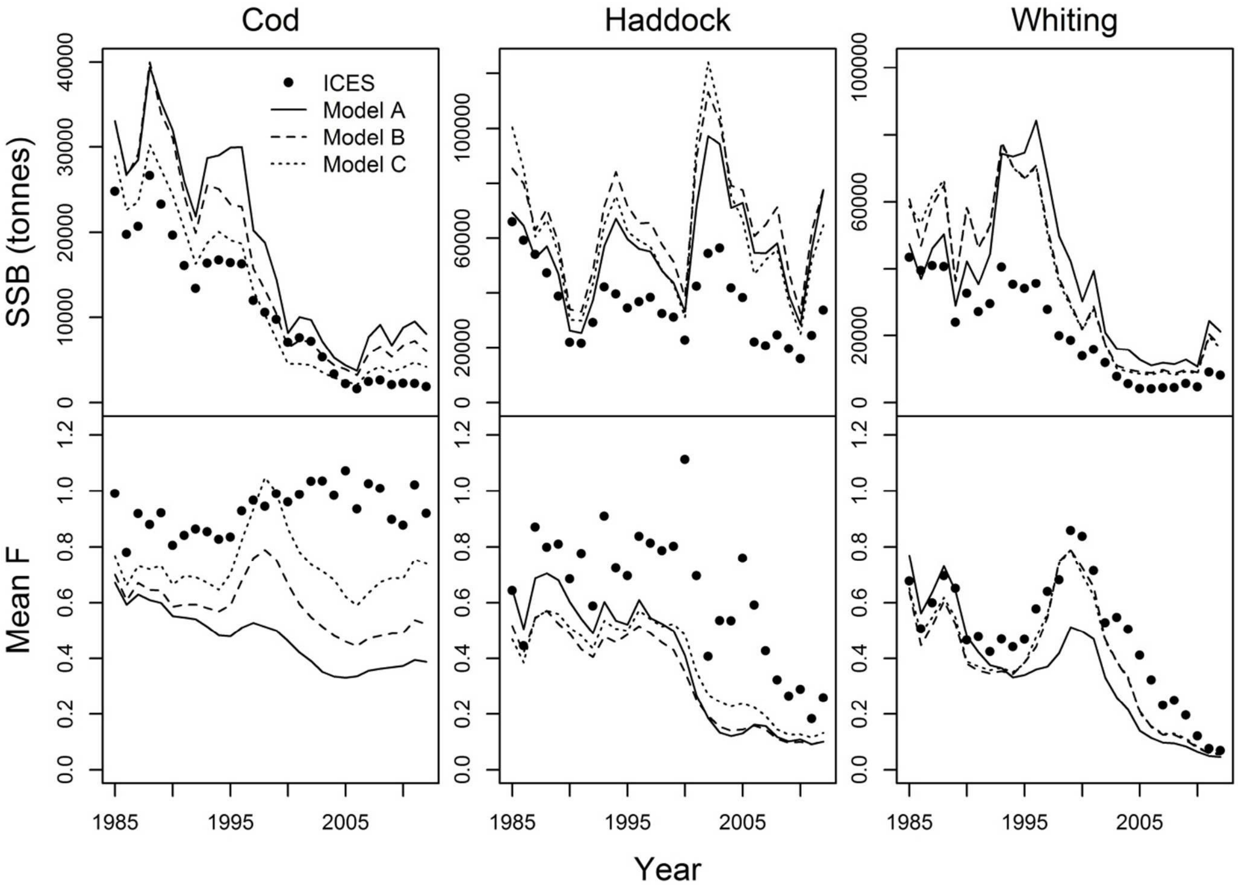


Figure 2

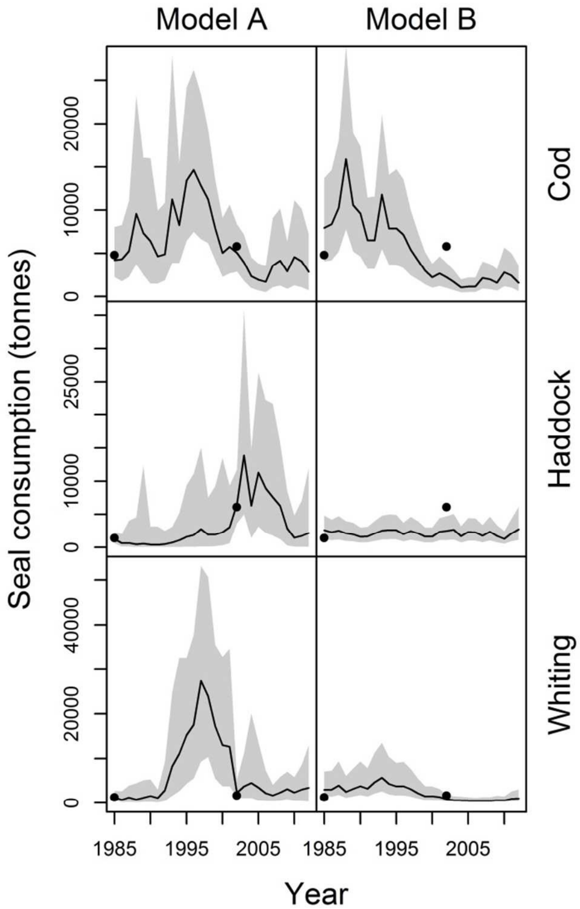

Model A
Model B
Cod
Haddock
Whiting
Seal consumption (tonnes)
0
10000
20000
0
10000
25000
0
20000
40000
1985
1995
2005
1985
1995
2005
Year

Figure 3

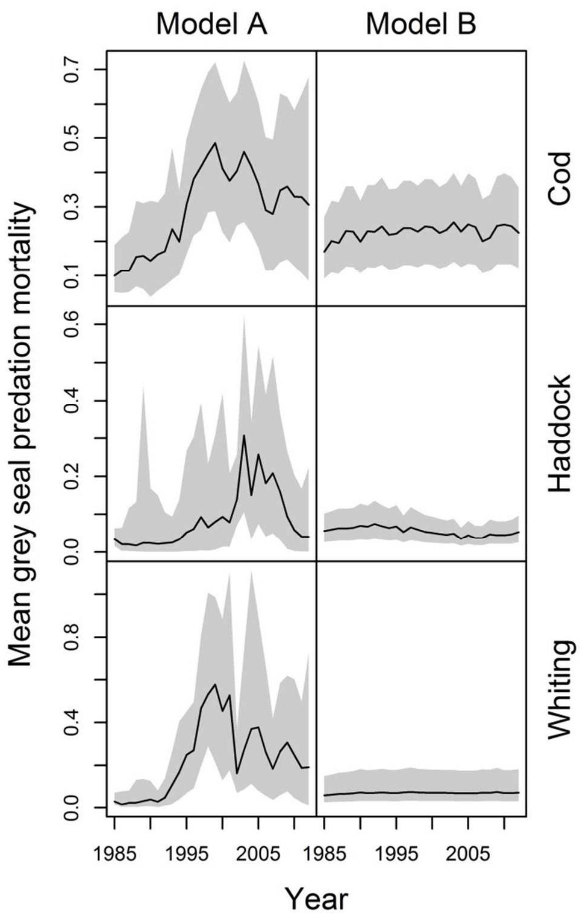

Model A
Model B
Mean grey seal predation mortality
Cod
Haddock
Whiting
0.1
0.3
0.5
0.7
0.0
0.2
0.4
0.6
0.0
0.4
0.8
1985
1995
2005
1985
1995
2005
Year

Figure 4

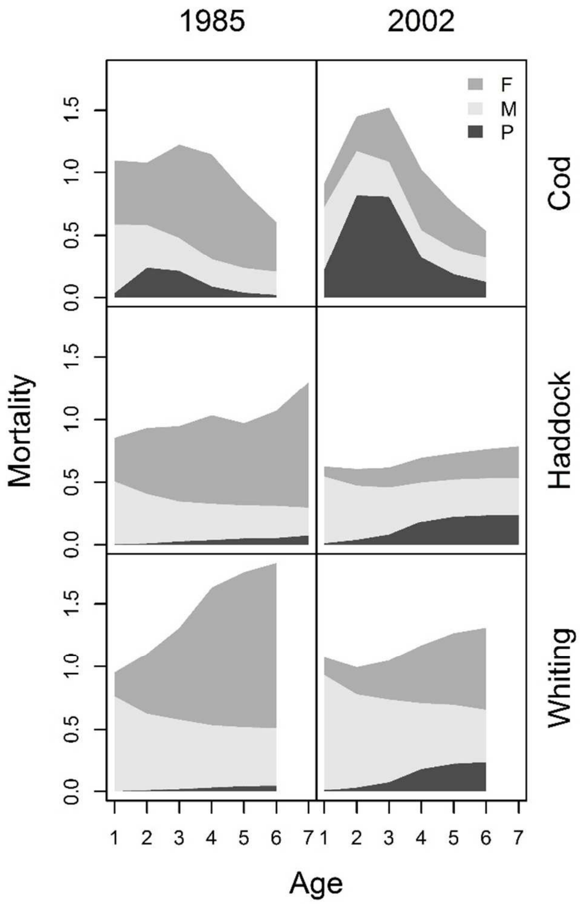

1985
2002
F
M
P
Cod
Haddock
Whiting
Mortality
0.0
0.5
1.0
1.5
1 2 3 4 5 6 7
Age

Figure 5

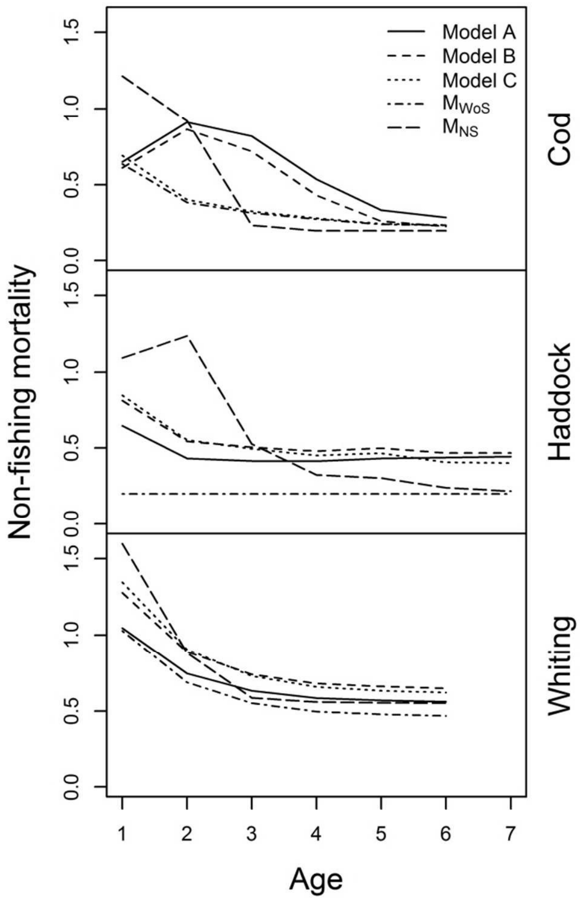
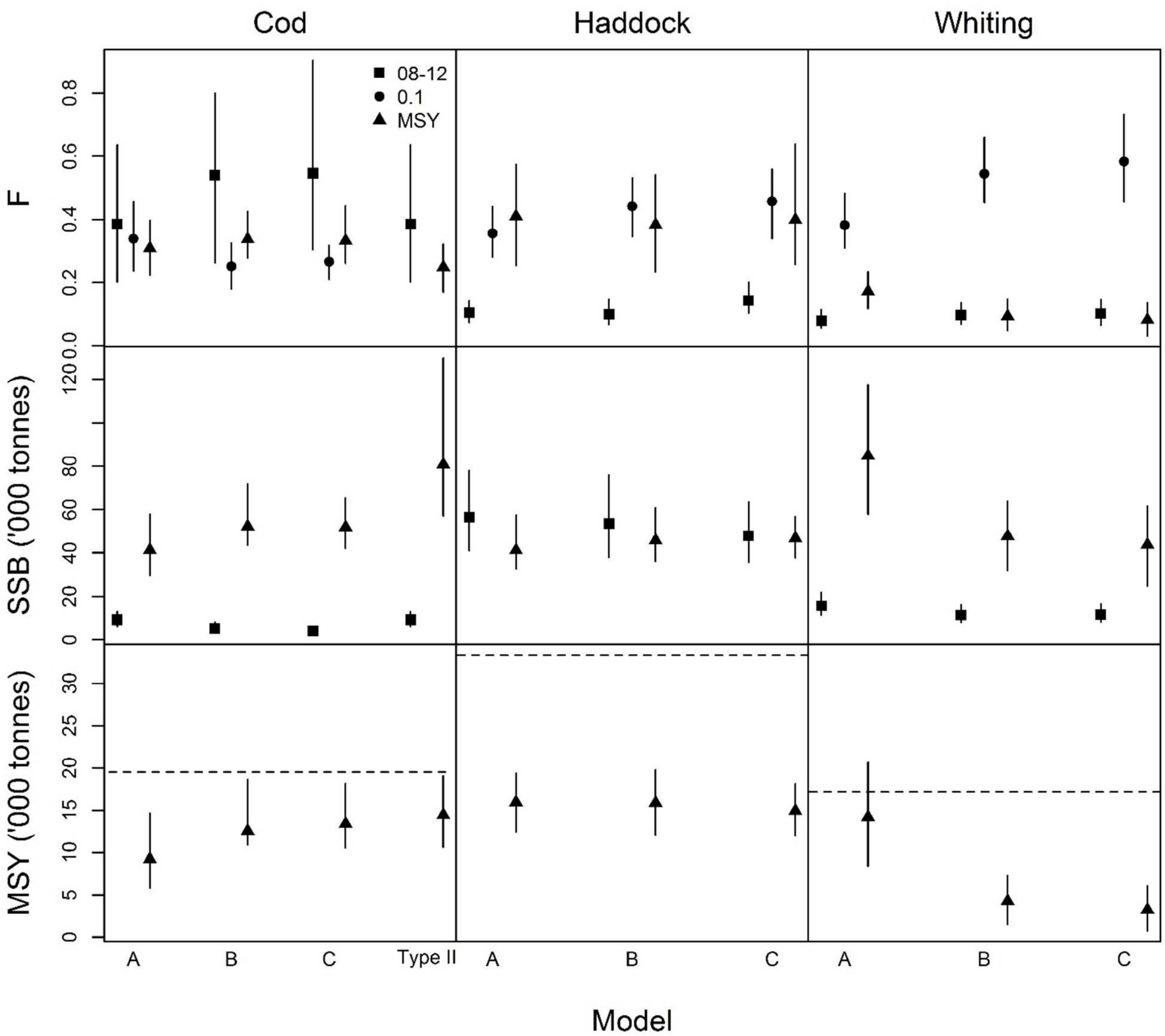
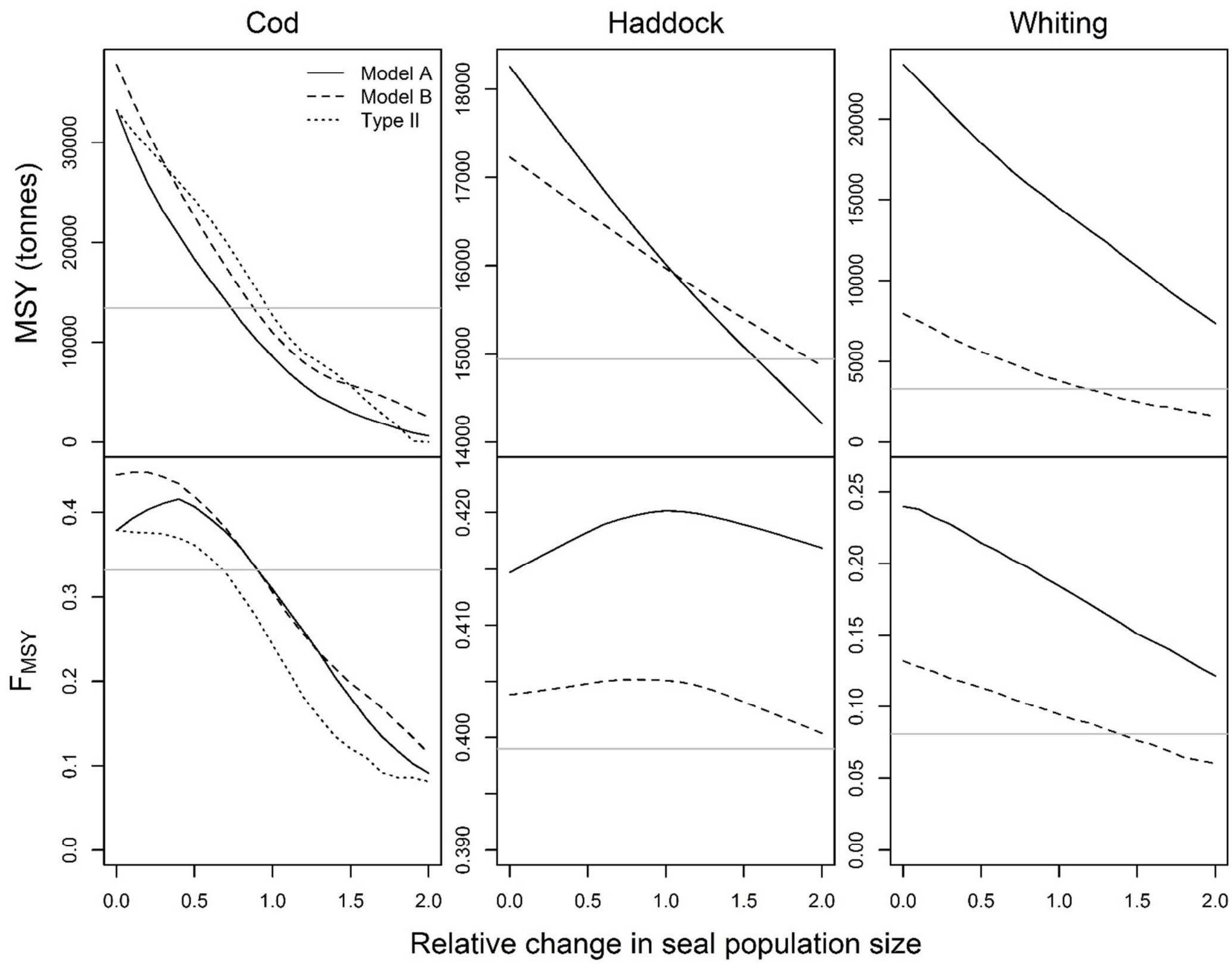

Model A
Model B
Model C
M_WoS
M_NS
Cod
Haddock
Whiting
Non-fishing mortality
Age
0.0
0.5
1.0
1.5
1
2
3
4
5
6
7

Figure 6


Cod
Haddock
Whiting
08-12
0.1
MSY
F
SSB ('000 tonnes)
MSY ('000 tonnes)
0.0
0.2
0.4
0.6
0.8
0
20
40
60
80
120
0
5
10
15
20
25
30
A
B
C
Type II
A
B
C
A
B
C
Model

14 Figure 7



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