Grey seal predation impairs recovery of an over-exploited fish stock

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Summary

1. Grey seal predation has been blamed by fishers for the decline of Atlantic cod stocks and has led to calls for seal culls. In the West of Scotland area, estimates of cod consumption by seals have exceeded reported catches and spawning biomass, focussing attention on the interaction between fishers and seals.
2. Bayesian models making different assumptions about seal predation were used to estimate the size of the West of Scotland cod stock between 1985 and 2005 and the mortalities due to fishing and seal foraging. A simple population model was used to identify the likely direction of cod population change at recent mortality rates.
3. All model configurations suggest that the total mortality of cod has remained fairly stable and high for many years regardless of the assumptions on seal predation. The high mortality explains the long term decline of the stock.
4. The best fitting model suggests that mortality due to fishing reduced substantially in the decade up to 2005, but has been replaced by increased seal predation mortality on a smaller cod stock. Given total mortality estimates, the stock is unlikely to recover even at present reduced levels of fishing.
5. *Synthesis and applications:* Our model offers a method of estimating seal predation mortality as part of routine stock assessments that inform fishery management. The analysis shows that predation by seals can be an important component of the total stock mortality. It also shows that assuming invariant natural mortality, as adopted in many standard fish stock assessments, may lead to incorrect perceptions of fishing mortality, over-estimating the benefits of reducing fishing mortality when there is density dependent predation. It is essential to consider predation by top predators when formulating appropriate advice for managing the fishery.

Keywords: Bayesian modelling, cod, fishery management, grey seals, misreported catch, mortality rate, predation, stock assessment

Introduction

The diet of the grey seal *Halichoerus grypus* Fabricius, 1791 contains many commercially exploited fish species including cod, *Gadus morhua* Linnaeus, 1758 (Prime & Hammond 1990; Hammond, Hall & Prime 1994a, 1994b; Hammond & Grellier 2006). The competition between fishers and seals for the same resource has led to controversy over the impact of seal predation on fisheries (Harwood 1984). With the decline in many cod stocks in the North Atlantic (Myers *et al* 1996; Myers, Hutchings & Barrowman 1996; Cook, Sinclair & Stefánsson1997) fishers have blamed seals for economic losses and stock decline, leading to seal culls in Europe (Harwood 1984) and Canada (Yodzis 2001). Studies on Canadian cod stocks suggest that, while seal predation may be large, it was not responsible for stock decline, but may inhibit recovery (Hammill, Ryg & Mohn 1995; Mohn & Bowen 1996; Fu, Mohn & Fanning 2001; Trzcinski, Mohn & Bowen 2006; O'Boyle & Sinclair 2012). In the Baltic, MacKenzie, Eero & Ojaveer (2011) concluded that seal predation need not inhibit cod stock recovery provided environmental conditions are favourable.

The consumption of cod by seals around the British Isles in 1985 and 2002 was estimated by the Sea Mammal Resarch Unit (SMRU) (Hammond & Harris 2006; Hammond & Grellier 2006). These estimates suggested that in the North Sea, consumption of cod was small relative to the commercial catch and the total stock size. However, in the West of Scotland area (Fig.1) the estimated consumption of cod in 2002 was comparable to the cod spawning stock biomass estimated from the stock assessment of the International Council for the Exploration of the Sea (ICES) , implying either a very large mortality caused by seals or an inconsistency in the assessment (ICES 2005). Conventional single species stock assessment models of the class used for West of Scotland cod do not explicitly model mortalities caused by sources other than fishing (the so-called “natural mortality”) and typically have assumed a constant value, so an inconsistency may not be surprising (ICES 2005).

Holmes & Fryer (2011) developed a state space model with a dynamic seal predation component to estimate seal predation mortality using data on the size composition of cod in the grey seal diet (Harris 2007). This was the first attempt to reconcile estimates of cod consumption by seals with the estimates of cod biomass and suggested seal predation mortality was as least as large as the assumed natural mortality. However, fishery management advice continues to be based on an assessment that excludes seal data (ICES 2013a).

Current assessments of West of Scotland cod by ICES show a major decline in spawning stock biomass (ICES 2013b) with fishing mortality high and relatively constant since the 1980s. Management advice is effectively to close the fishery (ICES 2013a). The last estimate (in 2002) of cod consumption by seals in the West of Scotland area was 6748 tonnes while the reported landings for that year were only 2245 tonnes and the spawning stock biomass was estimated to be only 5163 tonnes (ICES 2005). In these circumstances, it is important to understand the impact of seal predation and its bearing on the management and recovery of the stock.

A complication when assessing West of Scotland cod is that reported landings are thought to be biased, under-representing the true values. Estimated landings from the late 1990s to the mid-2000s can differ from the reported landings by a factor of 2–4 (ICES 2013b). However, some of these discrepancies may also be due to unaccounted mortalities such as predation by top predators.

In this paper we explore fishing and seal predation mortalities on West of Scotland cod using Bayesian models that also attempt to account for bias in catch data. Our aim is to examine the implications for fishery management of the apparently high consumption of cod by seals and to reconcile the consumption estimates with the estimates of cod biomass from conventional assessments. Finally we consider the prospects for recovery of this cod stock. With only two years of data on cod consumption by seals, our analysis is restricted to illustrating the range of interpretations of the data and the implications for management advice under different assumptions.

Materials and Methods

DATA

Cod in the West of Scotland area (Fig. 1) are caught predominantly in bottom trawls in a mixed groundfish fishery, with about 60% of the catch being taken by Scotland. Monitoring programmes collect data on catches and relative abundance which are used in annual stock assessments and provide much of the data for this study.

Catch at age data consisting of landings and discards and survey abundance indices were taken from the ICES assessment report (ICES 2013b). We used data from 1985, when systematic research vessel survey data began, to 2005. The catch data from 2006 onwards were dominated by fish dumped at sea due to quota restrictions and are problematic to quantify. Since discard data are less precise than landings data, this makes it difficult to estimate population abundances and mortalities with any precision for this period. Since no seal consumption data are available after 2002, limiting the analysis to 2005 does not lose any information on seal predation.

Four research vessel survey data series were available and are listed in Table 1 with the years and ages used. Zero indices were treated as missing to avoid problems when taking logs. This accounted for about 6% of the indices and affected older ages.

Mean stock weights at age and proportions mature at age were also taken from ICES (2013b) and were used to calculate spawning stock biomass and total catch in weight (yield). Mean stock lengths at age were derived from the mean weights at age using the inverse weight–length relationship in Coull *et al* (1989). These estimates of mean length will be biased, but should be adequate indices of size for estimating the selectivity of seals.

Length compositions of cod in the seal diet and estimates of the total biomass of cod consumed were obtained from Harris (2007). Estimates were only available for 1985 and 2002 and in both years cod represented approximately 10% of the diet. The length compositions were converted to age compositions using age-length keys from research vessel surveys. Annual estimates of the number of seals in the West of Scotland area were obtained from Thomas (2010) and are shown in Fig. S1 in Supporting Information.

For Scotland, there are data on fishing effort and misreported catches for a few years. Estimates of commercial fishing effort measured in Kilowatt-days from 2000 to 2005 were obtained from Marine Scotland (Anon, 2011) and estimates of misreported cod catch for 2001–2005 were taken from ICES (2013b). These data were not included in the model described below but were compared with the model output as an external check of consistency.

ANALYTICAL MODEL

I. Structural model

The population of cod, *N*, is assumed to decay exponentially due to a total mortality *Z*:

$$N_{a+1,y+1} = N_{a,y} \exp(-Z_{a,y}) \qquad \text{eqn 1}$$

where *a* and *y* are indices for age and year respectively. The total mortality is partitioned between fishing mortality *F*, natural mortality *M* and seal predation mortality *P* as:

$$Z_{a,y} = F_{a,y} + M_{a,y} + P_{a,y} \qquad \text{eqn 2}$$

Fishing mortality, as in many fishery models, is assumed to be the product of an age effect or selectivity, *s*, and a year effect, *f* (Pope & Shepherd 1982):

$$F_{a,y} = s_{a,y} f_y \qquad \text{eqn 3}$$

Selectivity measures the “catchability” of fish, which varies with age due to differences in retention by and availability to the fishing gear, whilst the year effect measures overall fishing mortality. Both components are modelled as a random walk with a multiplicative random term:

$$f_y = f_{y-1} \exp(\varepsilon_{f,y}), \qquad \varepsilon_{f,y} \sim Normal(0,\sigma_f^2),\ y \neq 1 \qquad \text{eqn 4}$$

$$s_{a,y} = s_{a,y-1}\exp(\varepsilon_{s,a,y}), \qquad \varepsilon_{s,a,y} \sim Normal(0,\sigma_s^2),\ y\neq 1 \qquad \text{eqn 5}$$

where σ_f and σ_s are the standard deviations of the random walks. For identifiability, the selectivity at age 3 is set to one, i.e. $s_{3,y} = 1$ for all y.

Based on a meta-analysis of worldwide fish stocks (Lorenzen 1996), natural mortality is modelled in terms of mean weight at age, $\overline{w}$:

$$M_{a,y} = c(\overline{w}_{a,y})^b \qquad \text{eqn 6}$$

where c and b are parameters that determine the change of M with weight.

Seal predation mortality is modelled in a similar way to fishing mortality as the product of a size preference (or selectivity), s_{seal}, and an "effort" component, $q_{seal}G$, where q_{seal} represents the annual *per capita* capacity of seals to prey on cod (the "predation rate"), and G is the abundance of seals:

$$P_{a,y} = s_{seal,a,y}q_{seal,y}G_y \qquad \text{eqn 7}$$

The quantity q_{seal} will depend on the ability of seals to find and catch cod, the time it takes to process prey items and the presence of other prey. Assuming there is a preferred size of cod, selectivity is modelled as a gamma function (Millar & Fryer 1999) of mean fish length at age, $\bar{l}$:

$$s_{seal,a,y}=\left(\bar{l}_{a,y}/[(\alpha-1)\beta]\right)^{(\alpha-1)}\exp(\alpha-1-\bar{l}_{a,y}/\beta) \qquad \text{eqn 8}$$

where the parameters α and β determine the shape of the curve. The parameter q_{seal} is modelled as a random walk:

$$q_{seal} = q_{seal,y-1}\exp(\varepsilon_{qseal,y}), \qquad \varepsilon_{qseal,y} \sim Normal(0,\sigma_{qseal}^2),\ y\neq 1 \qquad \text{eqn 9}$$

where σ_{qseal} is the standard deviation of the random walk. This allows values of q_{seal} to be estimated for years where there are no seal diet data and, without explicitly modelling them, assumes that the factors driving q_{seal} are serially autocorrelated.

II. Observation equations

The indices of cod abundance at age from the kth survey, U_k, are assumed to be proportional to population size, where the proportionality constant is the product of an age-specific selectivity, s_k, and an overall survey catchability, q_k, both of which are constant over time. If ρ_k is the proportion of the year elapsed before the survey, then:

$$U_{k,a,y}=s_{k,a}q_k N_{a,y} exp(-\rho_k Z_{a,y}) \qquad \text{eqn 10}$$

where the term $exp(–\rho_k Z_{a,y})$ accounts for mortality during the year up to the time of the survey . As the abundance indices are derived from trawl sampling, logistic curves are used to describe the selectivity of each survey gear. These are parameterized in terms of 50% selection ages, $A_{50,k}$, and selection ranges, SR_k (Millar & Fryer 1999):

$$ln\left(s_{k,a}/(1- s_{k,a})\right)=ln(9)(a-A_{50,k})/SR_k \qquad \text{eqn 11}$$

The observed survey indices, $\hat{U}_k$, are assumed to be log normally distributed with age-specific standard deviations $\sigma_{k,\mathrm{a}}$:

$$ln\hat{U}_{k,a,y} \sim Normal(lnU_{k,a,y}, \sigma_{k,a}^2) \qquad \text{eqn 12}$$

The catch in number, C, of fish taken by the commercial fishery is assumed to follow the Baranov catch equation:

$$C_{a,y}=F_{a,y}N_{a,y}\left(1-exp(-Z_{a,y})\right)/Z_{a,y} \qquad \text{eqn 13}$$

The catch is subject to discarding (Stratoudakis *et al.* 1999) and only the landed portion is reported, with the discarded portion estimated from observer data. During the study period almost all the discarded cod were aged one or two (Fernandes *et al.* 2011) and we therefore assume a common discarding curve over time. The proportion of fish retained, r, is modelled in a similar way to survey selectivity using a logistic curve:

$$ln\left(r_{a,y}/(1- r_{a,y})\right)=ln(9)(\bar{l}_{a,y}-D_{50})/SR_D \qquad \text{eqn 14}$$

where D_{50} and SR_D are the 50% retention length and selection range respectively. The landings L and discards D are then:

$$L_{a,y}=r_{a,y}C_{a,y} \qquad \text{eqn 15}$$

$$D_{a,y}=(1-r_{a,y})C_{a,y} \qquad \text{eqn 16}$$

However, the reported landings are subject to misreporting (ICES 2013a) and are biased. If p_y is the proportion of the landings reported in year y, we take the observed landings, $\hat{L}$, to be log-normally distributed

$$ln(\hat{L}_{a,y}) \sim Normal(ln(p_y L_{a,y}),\sigma_{L,a}^2) \qquad \text{eqn 17}$$

where $\sigma_{L,a}$ are age-specific standard deviations. The discard estimates, $\hat{D}$, are also biased, since they are scaled by the reported demersal landings (Millar & Fryer 2005). Assuming that misreporting affects all demersal species similarly, we have:

$$ln(\hat{D}_{a,y}) \sim Normal(ln(p_y D_{a,y}),\sigma_{D,a}^2) \qquad \text{eqn 18}$$

where $\sigma_{D,a}$ are age-specific standard deviations. For identifiability and model stability, we assume that $p_y = 1$ for 1985–1989 inclusive, a period when misreporting was believed to be negligible.

The catch, H, taken by seals is given by an analogue of the Baranov catch equation:

$$H_{a,y}=P_{a,y}N_{a,y}\big(1-exp(-Z_{a,y})\big)/Z_{a,y} \qquad \text{eqn 19}$$

There are observations of both the age composition of the seal catch and the total weight of cod consumed. The age composition is from a small sample, size n, and the catch at age in this sample, h, is assumed to have a multinomial distribution:

$$h_{a,y}, a=1\ldots A \sim Multinomial(n_y, p_{seal,1,y}, p_{seal,2,y},\ldots,p_{seal,A,y}) \qquad \text{eqn 20}$$

where $p_{seal,a,y}=\dfrac{H_{a,y}}{\sum_{a=1}^{A}H_{a,y}}$ is the probability that a fish in the diet has age a. The total weight of fish consumed by seals, Y_{seal}, is:

$$Y_{seal,y} = \sum_{a} H_{a,y} \overline{w}_{a,y} \qquad \text{eqn 21}$$

As with the commercial landings and discards, the observed catch, $\hat{Y}_{seal}$, is assumed to have a lognormal distribution:

$$ln\hat{Y}_{seal,y} \sim Normal(ln(Y_{seal,y}), \sigma_{seal}^2) \qquad \text{eqn 22}$$

III. Prior distributions

Priors for the model parameters are given in Table 2. Where possible, priors are taken from published information as detailed in the Table. Uniform priors are used for those parameters where only upper and lower bounds could be specified. The WinBUGS software (Lunn *et al.* 2000) used for fitting the model specifies normal distributions in terms of the mean and precision (inverse variance). Hence the priors on the precision of the landings, discards and survey observations are gamma distributions with small values for the shape and scale parameters (Lunn *et al*. 2012). Confidence intervals on the seal catch estimates (Harris 2007) are used to specify a gamma prior for the precision of the seal catch observations. We place uniform priors on the process error standard deviations as recommended by Gelman (2006). For the initial populations, the prior means are the sample means of the log catches-at-age scaled by an exploitation rate of 1.6 [based on the assessment in ICES (2013b)] and the prior precision is half the sample precision of the log catches.

MODEL FITTING AND SUMMARY STATISTICS

Exploratory runs with 3 sampling chains and between 10000 and 20000 iterations indicated that the chains converged by 10000 iterations. Posterior distributions were then calculated from two chains of 40000 iterations with a burn in period of 10000 iterations and a thinning rate of 3.

Three model configurations were run:

I. A ‘base’ model where no seal data were included. This assumes that the seal mortality is subsumed in the natural mortality and most closely resembles the ICES assessment.

II. A ‘fixed q_{seal}’ model which assumes a fixed per capita seal predation rate over time (i.e. σ_{qseal} = 0).

III. A ‘full model’ where q_{seal} followed a random walk through time (eqn 9).

The Deviance Information Criterion (DIC) (Spiegelhalter *et al*. 2002) was used to summarize overall model fit.

Standard fish stock summary statistics were calculated within the model estimation procedure to obtain posterior median values and 95% credible intervals. The statistics are the mean annual fishing mortality, spawning stock biomass, total catch in weight, total misreported catch in weight and the partial biomass exploited by seals (Table 3). The latter is defined as the weighted sum of the cod stock biomass at each age, where the ‘weights’ are the seal selectivities (s_{seal}) and represent the size ‘preference’ of seals.

Some of the model output was compared to data not used in the model as an external check for consistency. The estimates of misreported catch were compared with figures on misreporting in ICES (2013b). The commercial fishing effort data were normalized to the same mean as the mean F from the full model for the period 2000–2005 and the trends compared.

To assess the longer term persistence of the cod stock, the replacement line (Sissenwine & Shepherd 1987; Cook 1998) for the mean total mortality over the period 2001–2005 was superimposed on the spawning stock-recruitment plot. This corresponds to the inverse value of spawning stock biomass per recruit calculated at the current total mortality. If the replacement line lies above the recruitment values for the range of stock sizes observed, the stock will tend to decline. This analysis was based on the median values from the posterior distributions from the full model.

Results

The overall fit to the three models is summarized in Table 4. The base model does not use seal data so the DIC is not comparable to the other models. Of the models using the seal data, the full model had a lower DIC offering some support for a change in predation rate per seal over time. Fits to the catch and survey data and the posterior distributions for the full model parameters are given in Supporting Information (Figs. S2 and S3). Good fits were obtained for the data on landings, Scottish surveys and discards at age 1. The fits to the Irish surveys were poor and their respective selectivity parameters were not well estimated. However, these surveys have little effect on the estimates of the main quantities of interest since they contribute little to the total likelihood.

Summary statistics from the three models and from the ICES assessment are shown in Fig. 2. All models estimate a nearly continuous decline in SSB with only a change of scale to separate them. As described below, this change of scale is due to the differing ways in which the models apportion mortality to fishing or non-fishing deaths. The fishing mortality rate in the base and fixed q_{seal} models and in the ICES assessment change little over time. The full model, which suggests a decline in F, is the most consistent with the trend in recorded effort. However, given the large credible intervals, trends are difficult to discern with confidence. The median misreporting factor for the full model shows little change for most of the period but reduces sharply between 2002 and 2005. The base and fixed q_{seal} models suggest greater misreporting from 1998 onwards. The recent estimates of misreported catch for Scottish vessels are consistent with the median values from the full model though there is high uncertainty.

The age composition of the seal diet in the two sampled years is shown in Fig. 3 (upper panels) with the median values for the full model. The model fits the age composition in the diet well. The fixed q_{seal} model gave almost identical results and is not shown. Fig. 3 (lower panels) shows the corresponding estimates of seal predation mortality. Both the full and fixed q_{seal} models give similar results for 1985 with a peak mortality of 0.3–0.4 at age 2. For 2002 the full model estimates substantially higher mortality. Natural mortality (*M*) is of a similar order of magnitude to the seal predation mortality (Fig. 3) but is highest at the youngest ages.

The total weight of cod consumed by seals is shown in Fig. 4. The full model fits the consumption estimates well while the model with a fixed q_{seal} estimates much lower consumption in 2002.

The size selectivity curve for seals shows greatest selection at about 50cm (Fig. 5) which corresponds to cod of ages 2–3, about one year less than the age of highest selection in the commercial fishery. The fishery has lower selectivity at the smallest and largest sizes (or ages) in 2002. This may be associated with the introduction of gear technical measures intended to reduce the capture of young fish (Suuronen & Sarda 2007; Enever, Revill & Grant 2009) and changes in the trawl fleet composition away from vessels targeting the more offshore waters and shelf edge (STECF 2012) where older fish are more prevalent.

The functional response of seals to cod biomass as estimated from the models is shown in Fig. 6. As might be expected, the fixed q_{seal} model that assumes a constant per capita predation rate shows a roughly linear increase in biomass consumed as cod partial biomass increases. When q_{seal} is allowed to vary over time (full model), a conventional type II functional response emerges.

The total mortality for each model and for the ICES assessment, partitioned into mortality components, is shown in Fig. 7. Fishing mortality is further partitioned into reported and misreported catch. Although there are large differences in the estimates of fishing and seal predation mortality, the estimates of total mortality are remarkably similar. Each model partitions a similar total mortality into fishing, natural and seal predation components in different amounts depending on the assumptions made. The ICES and base model have the highest fishing mortality while the fixed q_{seal} model 're-allocates' some of this fishing mortality and natural mortality to seal predation mortality. The full model allocates more of the mortality to seal predation in the second half of the time series by, in effect, reducing the level of misreporting suggested by the other models.

Most recruitment estimates lie below the estimated replacement line for typical mortality rates (Fig. 8). This is most noticeable at the lower values of SSB where only a single year class has exceeded the replacement mortality. This suggests the stock will continue to decline.

Discussion

In common with the assessment conducted by ICES, our analysis estimates a steady decline in cod SSB from the mid-1980s to the mid-2000s (ICES 2013b). However, the interpretation of mortality rates differs, with the full model showing a decline in fishing mortality in the more recent years while the ICES assessment suggests little change. Though there remains much uncertainty, the consistency of our analysis with recent changes in fishing effort and estimates of misreported catch offers support for the assessment using the full model. Furthermore, price changes for cod in the period of greatest misreporting show little change (Fig. S4) suggesting the quantities misreported are low since high quantities would be expected to depress market price. This adds support to the full model where the misreported catch is estimated to be much lower than the fixed q_{seal} model.

All models give similar estimates of total mortality despite substantial differences in assumptions about seal predation suggesting that these estimates are robust. However, the way in which this mortality is partitioned between fishing, seal predation and natural mortality is highly relevant to the management of the fishery. If correct, the apparent reduction in fishing mortality in recent years is not sufficient to bring about a recovery in the stock because other mortalities, generally beyond the influence of managers, have increased.

Seal predation appears to be greatest at age 2 (Fig. 3) which is consistent with studies in the North Sea (ICES 2011) and Canadian waters (O’Boyle and Sinclair, 2012). In these studies, however, seal predation mortality was much lower, around 0.1–0.2, whereas the full model in the current analysis suggests values around 0.3–0.9. The three fold increase in seal predation mortality between 1985 and 2002 does not appear to be due to increasing seal population numbers. According to estimates from Thomas (2010), the seal population on the West of Scotland in 2005 was only 20% larger than 1983. However, it is consistent with a functional response as assumed by O'Boyle and Sinclair (2012), Trzcinski *et al.* (1996) or as observed by Middlemas *et al.* (2006) and Smout *et al.* (2013). It is also consistent with the functional response estimated from the full model (Fig. 6) and means that the proportion of the biomass eaten has increased at lower cod partial biomass. Clearly with only two years of seal consumption data this relationship can only be tentative.

Although the model fit to the age composition of the seal catch (Fig. 3) and to the total weight eaten in the two sample years appears close (Fig. 4) the uncertainty in the quantity eaten is large. There are further reasons to be cautious about the estimates and how they are modelled. Seals eat dead fish discarded from fishing vessels (Bergmann *et al* 2002), and if the age composition data include discarded fish, the model will be double counting some deaths. Also, bias may arise if the scat samples on which the diet is estimated are unrepresentative. Seal foraging areas reported by Matthiopoulos *et al.* (2004) include areas considered unsuitable for trawl fishing (Bailey *et al.* 2011), so seals may be exploiting parts of the cod stock not available to the fishery. Clearly these are sources of potential bias and uncertainty that merit further investigation.

If total mortality has remained high over the period of analysis and fishing mortality has declined to only 20% of the total, as suggested by the full model, there are important implications for fishery management. In common with other studies (Fu, Mohn & Fanning 2001; Mohn & Bowen 1996;Trzcinski *et al*. 1996; O'Boyle & Sinclair 2012) our analysis implies that the decline of the cod stock was mainly due to high fishing mortalities whereas the failure to recover is at least partly due to high non-fishing mortalities. The current replacement line lies above recent recruitment so, on average, population losses will exceed gains. Further reductions in fishing mortality are also unlikely to reduce the slope of the replacement line to sustainable levels.

Cod stocks both in the West of Scotland and North Sea have been subject to a “recovery plan” that is intended to reduce fishing mortality and increase the SSB through fishing effort limitation, gear modifications, and landings limits (see Kraak *et al.* 2013). This plan is based on the assumption that a reduction in fishing mortality will reduce total mortality. This is implicit in assessments where natural mortality is the only non-fishery mortality and is assumed to be constant. When other mortalities compensate for reduced fishing when stock size is low, as appears to be the case for West of Scotland cod, any projected stock recovery will be over-estimated and will undermine the basis of the recovery plan. This illustrates the importance of taking into account broader ecosystem interactions that go beyond single species analysis.

ICES advice for West of Scotland cod since 2003 has effectively been to reduce fishing mortality to zero (ICES 2013a) and our analysis suggests movement towards this goal. If however total mortality is now dominated by natural and seal predation mortalities, further reductions in fishing, while beneficial, are unlikely to achieve substantial improvements in stock size. To overcome the higher mortalities caused by seal predation, the stock is dependent on the production of a large year class, or sequence of good year classes, which will be largely determined by favourable environmental conditions.

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Data accessibility

The WinBUGS code and source data used in the analysis are available at http://dx.doi.org/10.6084/m9.figshare.1356164.

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Supporting Information

File	**Format**	**Size**	**Description**
jpe00933-supp-FigS1.pdf	**pdf**	**110**	**Fig S1. Grey seal population numbers over time**
jpe00933-supp-FigS2.pdf	**Pdf**	**181**	**Fig S2. Fit of model values to data**
jpe00933-supp-FigS3.pdf	**Pdf**	**308**	**Fig. S3. Model parameter posterior distributions**
jpe00933-supp-FigS4.pdf	**pdf**	**103**	**Fig. S4. Cod price over time adjusted for inflation**

Table 1. Research vessel surveys in the West of Scotland area used in the analysis

Survey	**Abbreviation**	**Year available**	**Years used**	**Ages used**
Scottish quarter 1	Sco1	1985–2010	1985–2005	1–6
Scottish quarter 4	Sco2	1985–2009	1996–2005	1–4
Irish quarter 4	Ire1	1993–2002	1993–2002	1–3
Irish quarter 4, revised	Ire2	2003–2012	2003–2005	1–2

Table 2. Prior distributions on the model parameters. The normal distributions are defined in terms of the mean and precision (i.e. inverse variance) as this is the formulation used by the WinBUGS software

Parameter	Description	Prior	Comment
$\ln N_{2,1}$ $\ln N_{3,1}$ $\ln N_{4,1}$ $\ln N_{5,1}$ $\ln N_{6,1}$	Log cod population for ages ≥ 2 in year 1	Normal(6.84, 0.3) Normal(6.14, 0.3) Normal(5.02, 0.3) Normal(3.73, 0.3) Normal(2.64, 0.3)	The mean is the average catch at age scaled up by 1.6. The precision is half the sample precision of the log catches rounded down to the nearest significant digit.
$\ln N_{1,y}$	Log cod population at age 1 in each year	Normal(6.98, 0.3)	As above
$s_{1,1}$ $s_{2,1}$ $s_{4,1}$ $s_{5,1}$ $s_{6,1}$	Commercial fleet selectivity at age in year 1; $a \neq 3$	Uniform(0.1, 0.8) Uniform(0.2, 1.5) Uniform(0.2, 2) Uniform(0.2, 2) Uniform(0.2, 2)	$s_{3,y}=1$ for identifiability
$\ln f_1$	Fishing year effect in year 1	Uniform(-3, 0.5)	
c b	Parameters of natural mortality function	Normal(3.69, 4) Normal(-0.305, 1250)	From Lorenzen (1996)
α	Seal selectivity function: shape parameter	Normal(20, 0.1)	The mean gives a low probability of selecting fish above the maximum observed length (75cm)
m	Seal selectivity function: mode $m=\beta(\alpha-1)$	Normal(45, 0.1)	The mean is the mid-point of the observed length distributions
$\ln q_k$	Log catchability of *k*th survey	Uniform(-7, 3)	
$A_{50,k}$	50% retention age for the *k*th survey	Uniform(-3, 6)	
SR_k	Selection range for the *k*th survey	Uniform(0.01, 2)	
D_{50}	50% retention length for the discards	Normal(35, 0.01667)	Mean is the minimum landing size for cod
SR_D	Selection range for the discards	Normal(6, 0.5)	From Cook (2013)
$\ln q_{seal,1}$	Log of seal predation rate in year 1	Uniform(-10, 0.5)	
p_y	Proportion of catch reported	Beta(2, 0.5)	Mode is at one and implies misreporting is rare. p_y was fixed at one for the years 1985-1989.
 σ_f $\sigma_{s,a}$ σ_{qseal}	Standard deviation of process error: - fishing mortality - fishing selectivity at age *a* ($a \neq 3$) - seal predation rate	 Uniform(0, 100) Uniform(0, 100) Uniform(0, 100)	Non-informative priors on σ
 $\sigma_{k,a}$ $\sigma_{L,a}$ $\sigma_{D,a}$ σ_{seal}	Standard deviation of observation error: - *k*th survey at age *a* - landings at age *a* - discards at age *a* - seal catch	 Gamma(0.01, 0.01) Gamma(0.01, 0.01) Gamma(0.01, 0.01) Gamma(4, 0.33)	Non-informative priors on $1/\sigma^2$. The prior for the seal catch gives a mean precision equal to the reciprocal of the sample variance and a 50% coefficient of variation

Table 3. Statistics used to summarize stock biomass, catch and fishing mortality

Summary Statistic	Definition
Mean fishing mortality over ages 2-5	$\frac{1}{4}\sum_{a=2}^{a=5} F_{a,y}$
Spawning stock biomass, where $p_{m,a,y}$ is the proportion mature at age *a* in year *y*.	$\sum_{a} p_{m,a,y} \overline{w}_{a,y} N_{a,y}$
Total catch in weight	$\sum_{a} \overline{w}_{a,y} C_{a,y}$
Misreported catch	$(1-p_y)\sum_{a} \overline{w}_{a,y} C_{a,y}$
Partial biomass exploited by seals	$\sum_{a} s_{seal,a,y} \overline{w}_{a,y} N_{a,y}$

Table 4. DIC values for each model

Model	DIC	Description
I. Base	2981.48	No seal data included in the model
II. Fixed q_{seal}	2987.93	Seal per capita predation rate fixed
III. Full model	2978.38	Seal per capita predation rate follows a random walk

Figure Legends

Fig. 1. Map of the West of Scotland cod stock assessment area, ICES Division Via (polygon). Most cod landings are from the northern half of the area, on or to the east of the shelf edge (indicated by the 200m contour). The distribution of grey seals is indicated by showing all haul-out sites (filled circles) where at least 2 grey seals were observed in the same year in August surveys between 2007 and 2011.

Fig. 2. Summary statistics for the cod fishery. (a) Spawning stock biomass, (b) mean fishing mortality over ages 2–5, (c) the misreporting factor, p_y, (p_y=1 from 1985–1989), (d) estimated missing or misreported catch. The solid line shows the full model, the dotted line the fixed q_{seal} model and the dashed line the base model without seal predation. The open circles are the values from the ICES assessment. The shaded area shows pointwise 95% credible intervals for the full model. In (b) the scaled fishing effort for Scottish vessels is shown as solid dots while in (d) misreported catch as estimated by ICES for Scottish vessels is shown as solid dots.

Fig. 3. Proportion by age of cod in the seal diet and seal predation mortality. Upper panels show the observed proportion of fish at each age in the two years of sampling with the median proportions from the full model (solid line) and pointwise 95% credible intervals (shaded). Lower panels show the median seal predation mortality for the full model (solid line) and fixed q_{seal} model (dotted line) and pointwise 95% credible intervals for the full model (shaded). The dashed line shows the median natural mortality (due to non-seal causes) from the full model.

Fig. 4. Estimates of seal consumption from the full model (solid line) and the fixed q_{seal} model (dotted line) with 95% credible intervals for the full model (shaded). Observed values are shown as points.

Fig. 5. The estimated seal selectivity curve from the full model (solid line) and selectivities for the commercial fishery in 1985 (dotted line) and 2002 (dashed line), the years for which there are seal

diet data. The selectivities for the fishery were converted from an age to a length scale using annual mean lengths at age.

Fig. 6. The estimated functional response of grey seals expressed as the cod consumption per seal plotted against the partial biomass of cod available. The upper and lower panels show the response for the fixed q_{seal} model and the full model respectively.

Fig. 7. The total mortality Z, partitioned according to fishing, seal predation and other sources. Estimates are shown for the base model without seal predation, the ICES assessment, the fixed q_{seal} model and the full model. Fishing mortality, F, is partitioned into the components attributable to reported and unreported catch.

Fig. 8. Stock-recruitment plot for cod estimated from the full model. The replacement line corresponding to the mean total mortality 2001–2005 is shown. Points lying below the line represent recruitment values that are insufficient to replace the stock. Points are labelled with corresponding year classes.

Figure 1

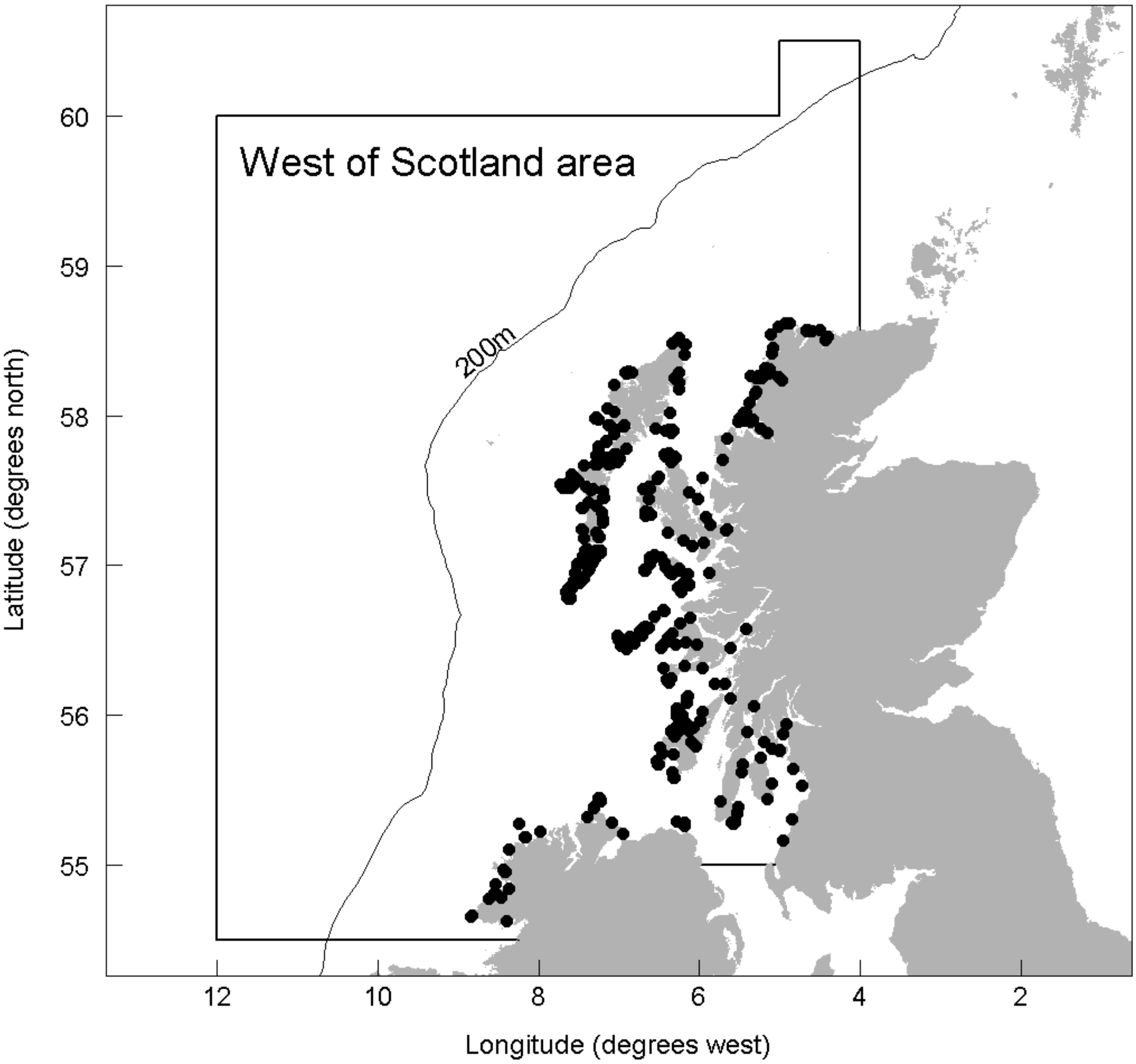

West of Scotland area
200m
60
59
58
57
56
55
Latitude (degrees north)
12
10
8
6
4
2
Longitude (degrees west)

Figure 2

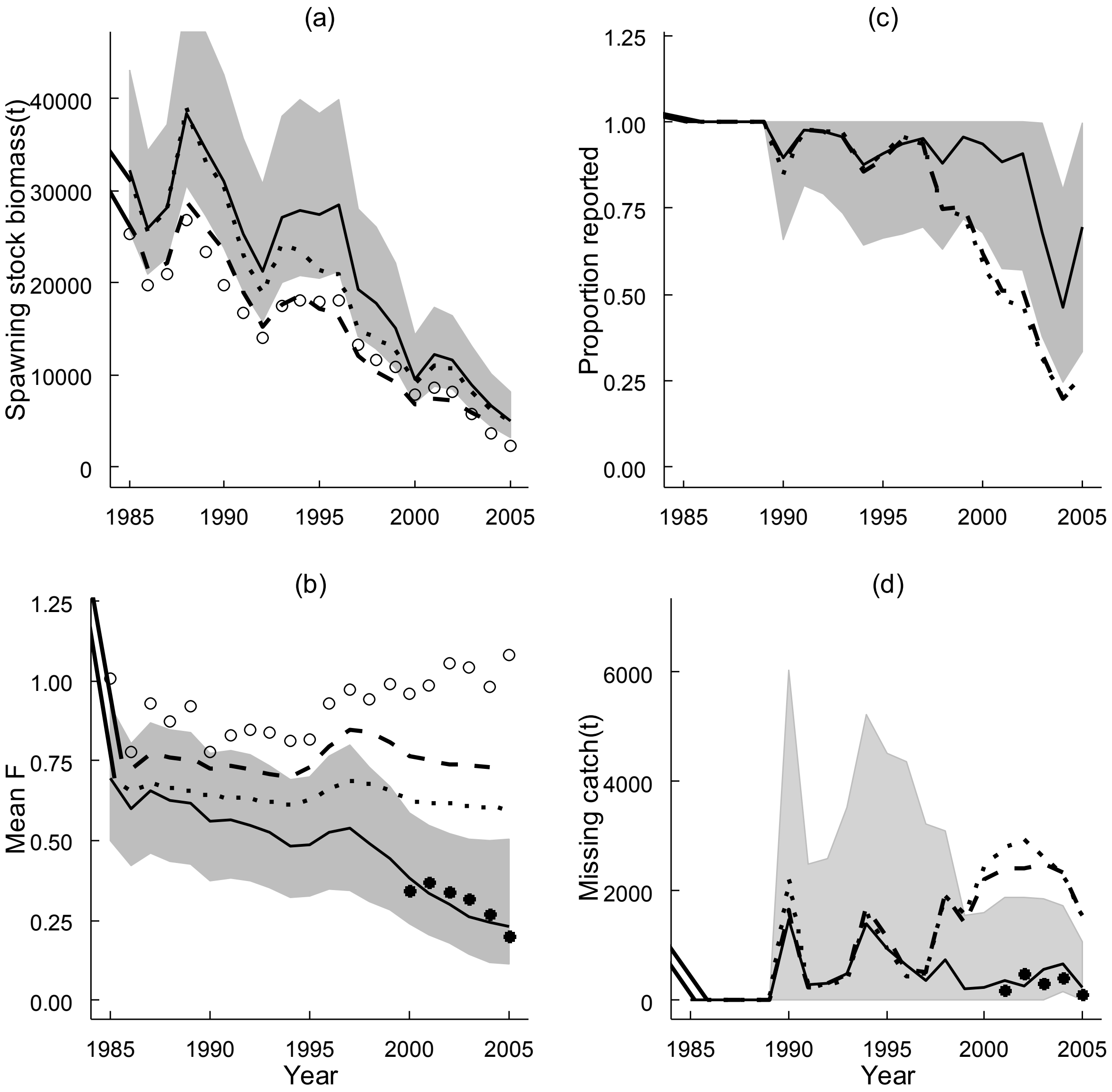

(a)
Spawning stock biomass(t)
0
10000
20000
30000
40000
1985
1990
1995
2000
2005
(c)
Proportion reported
0.00
0.25
0.50
0.75
1.00
1.25
1985
1990
1995
2000
2005
(b)
Mean F
0.00
0.25
0.50
0.75
1.00
1.25
1985
1990
1995
2000
2005
Year
(d)
Missing catch(t)
0
2000
4000
6000
1985
1990
1995
2000
2005
Year

Figure 3

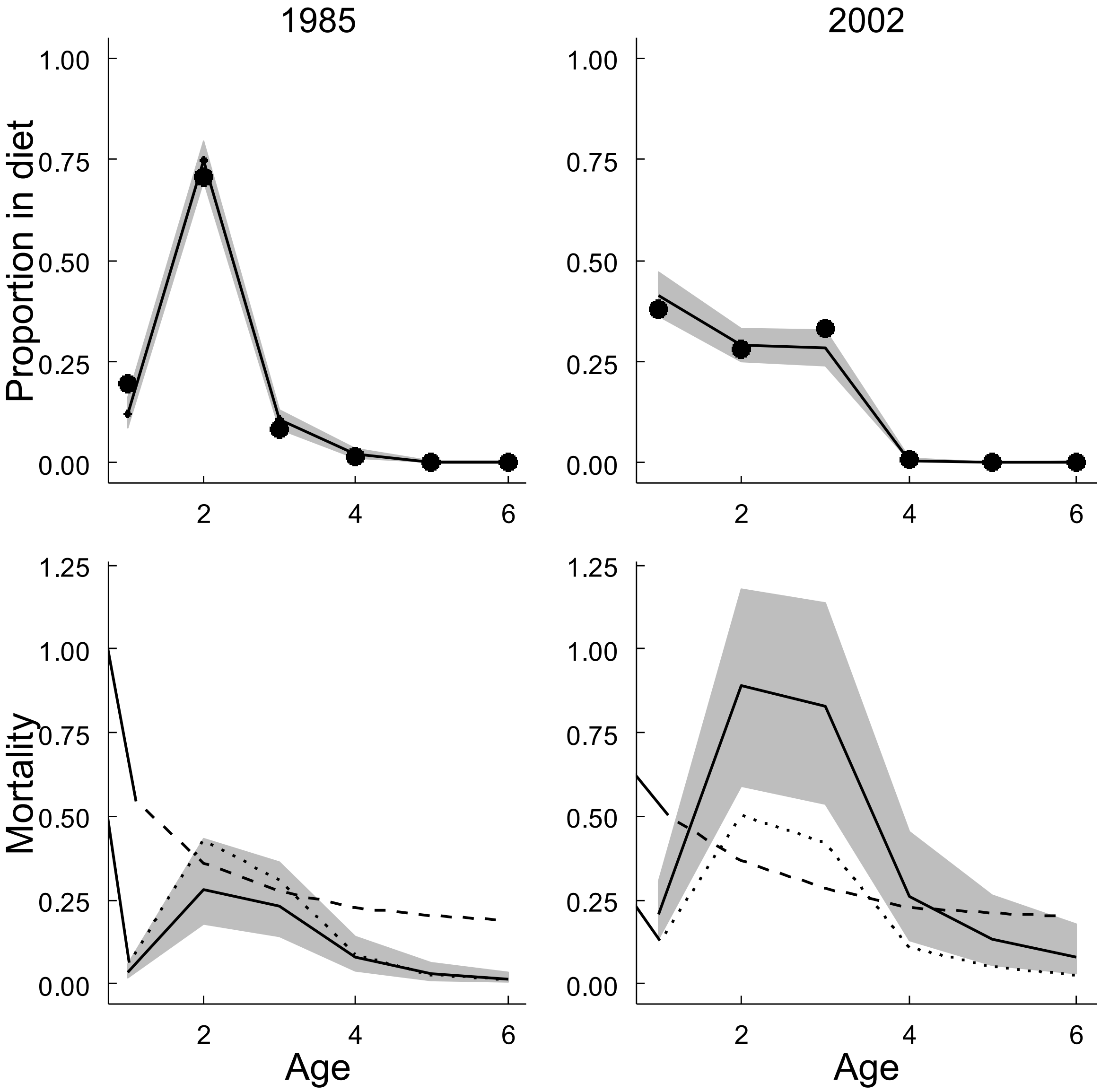
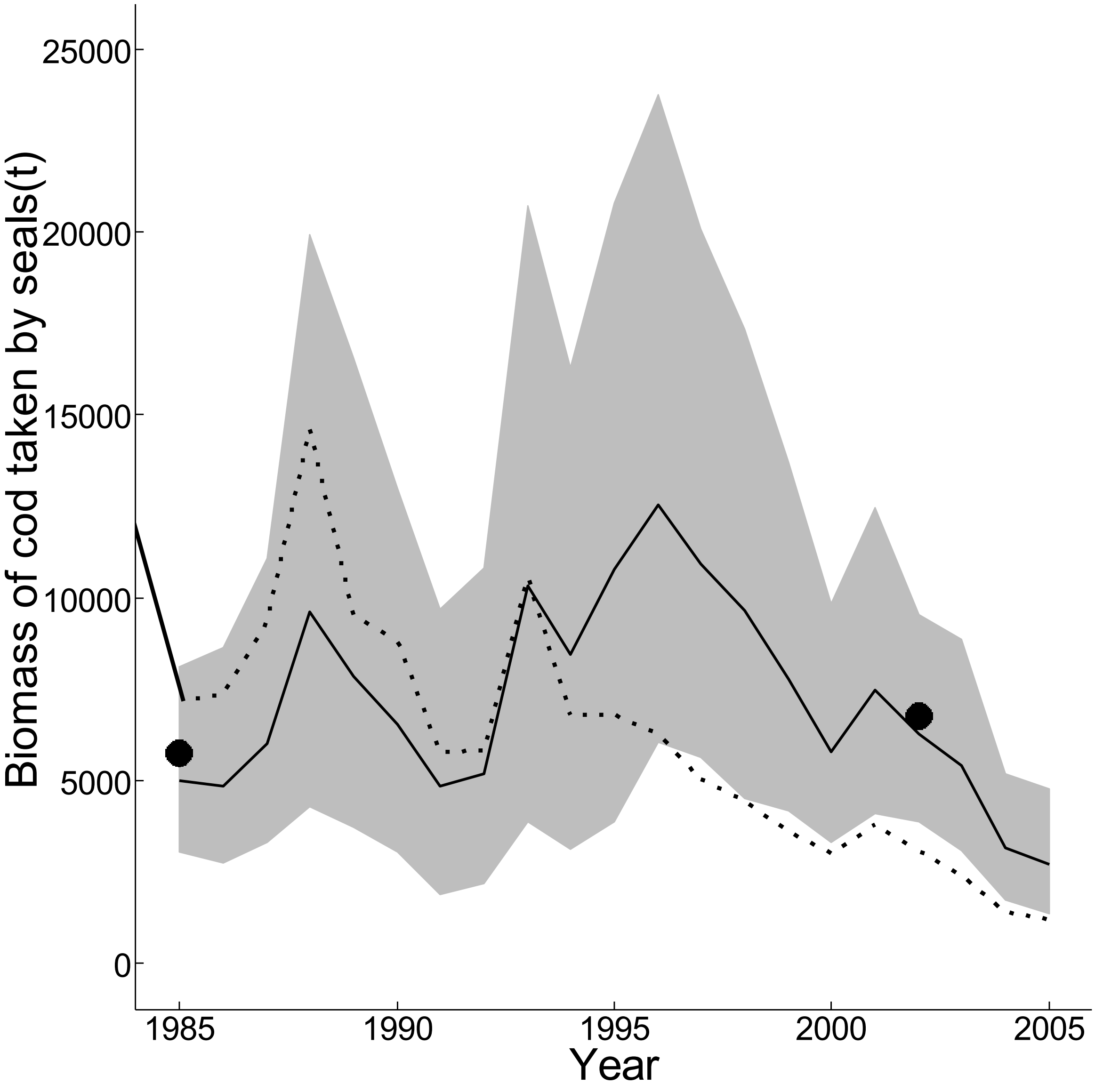
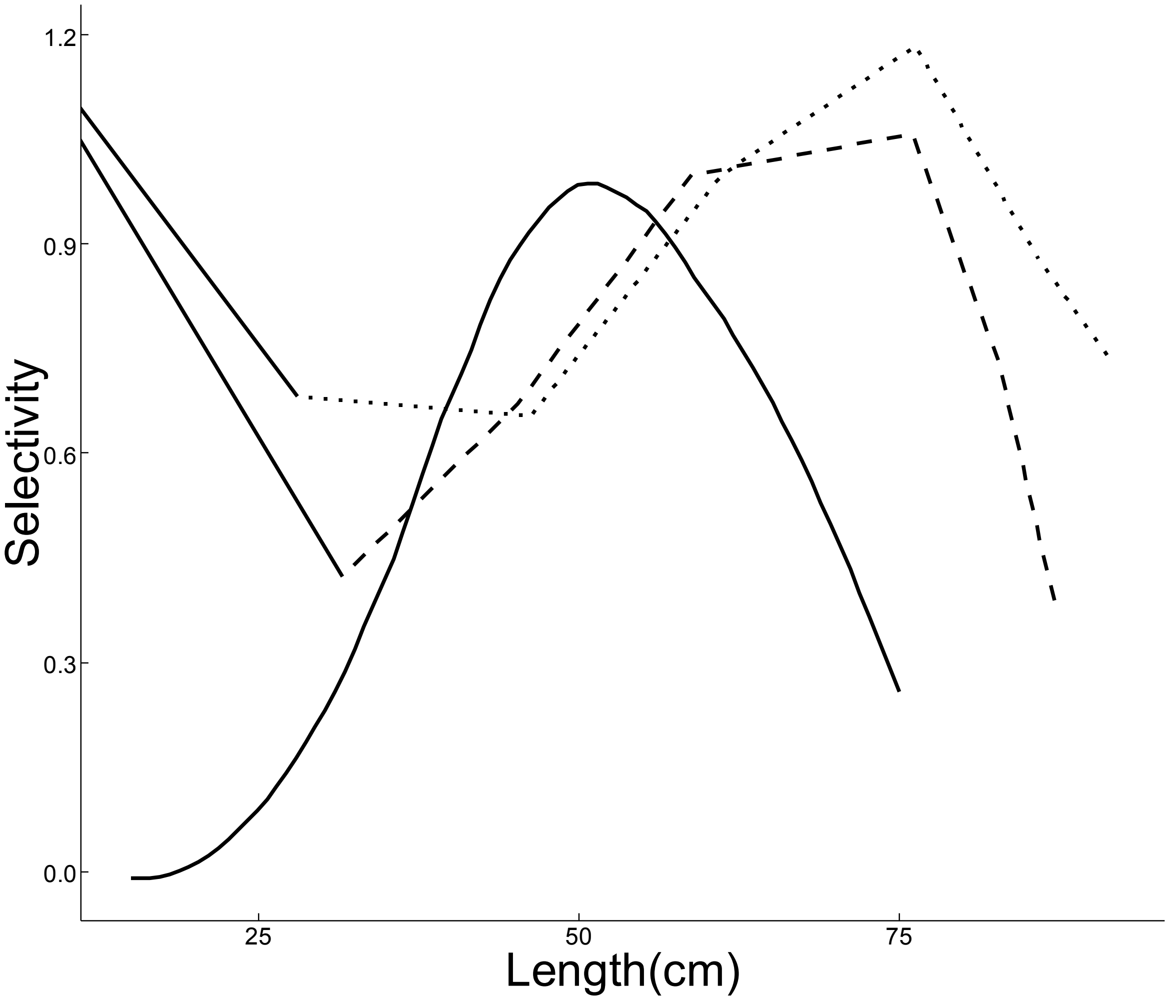

1985
2002
Proportion in diet
1.00
0.75
0.50
0.25
0.00
2
4
6
Mortality
1.25
1.00
0.75
0.50
0.25
0.00
Age
Age

Figure 4



Biomass of cod taken by seals(t)
25000
20000
15000
10000
5000
0
1985
1990
1995
2000
2005
Year

538 Figure 5



539

540

Figure 6

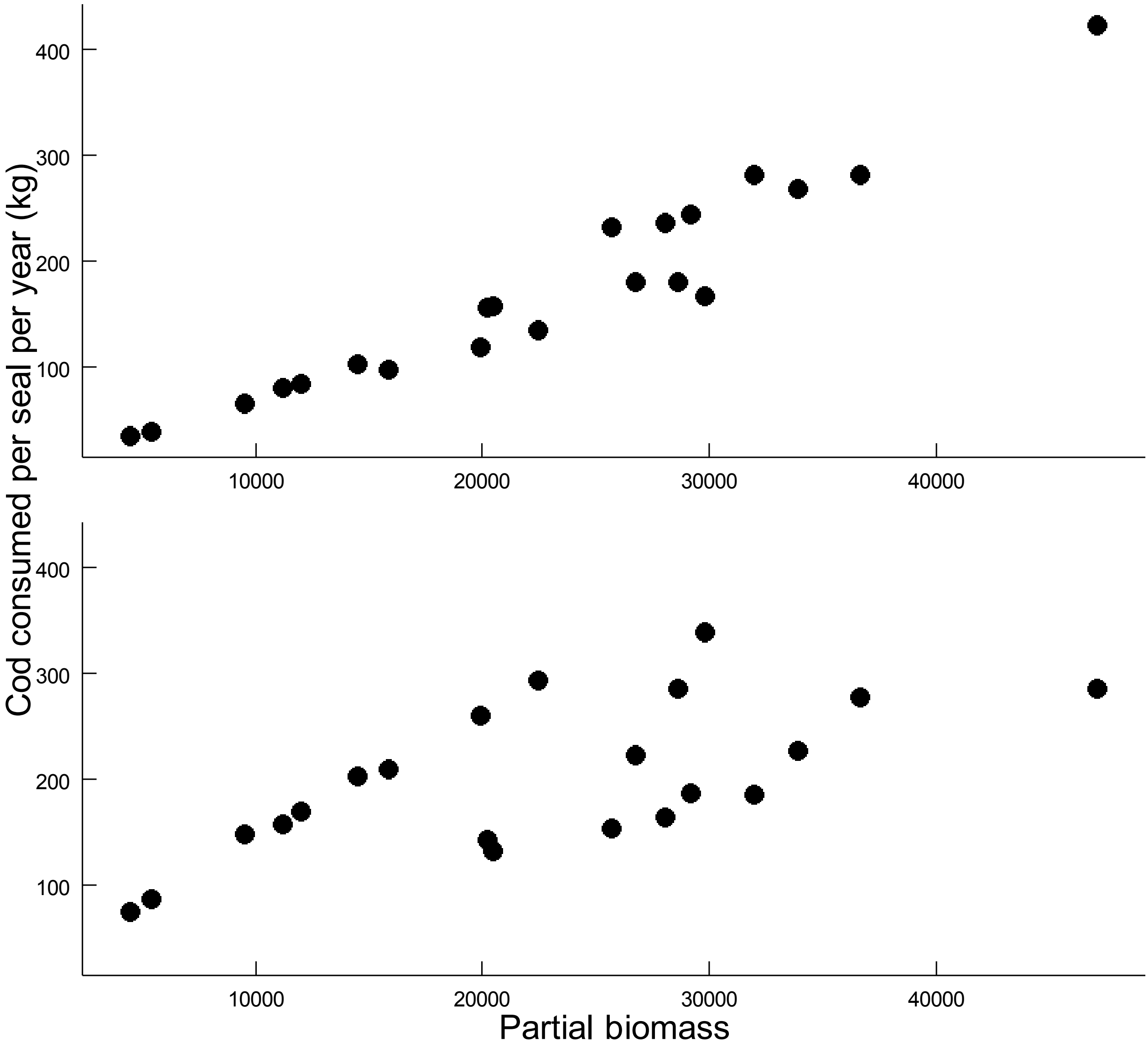

Cod consumed per seal per year (kg)
400
300
200
100
10000
20000
30000
40000
400
300
200
100
10000
20000
30000
40000
Partial biomass

Figure 7

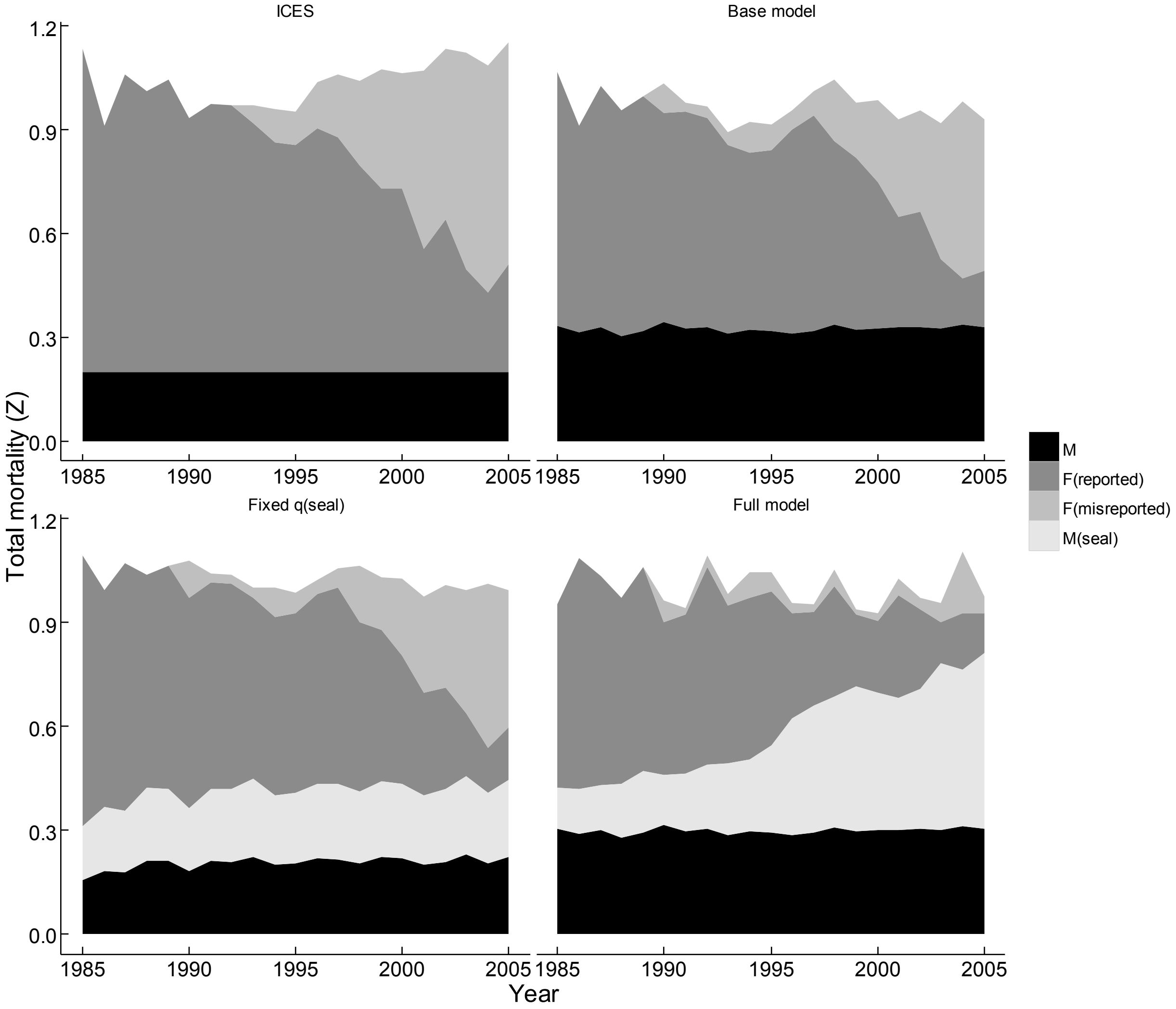
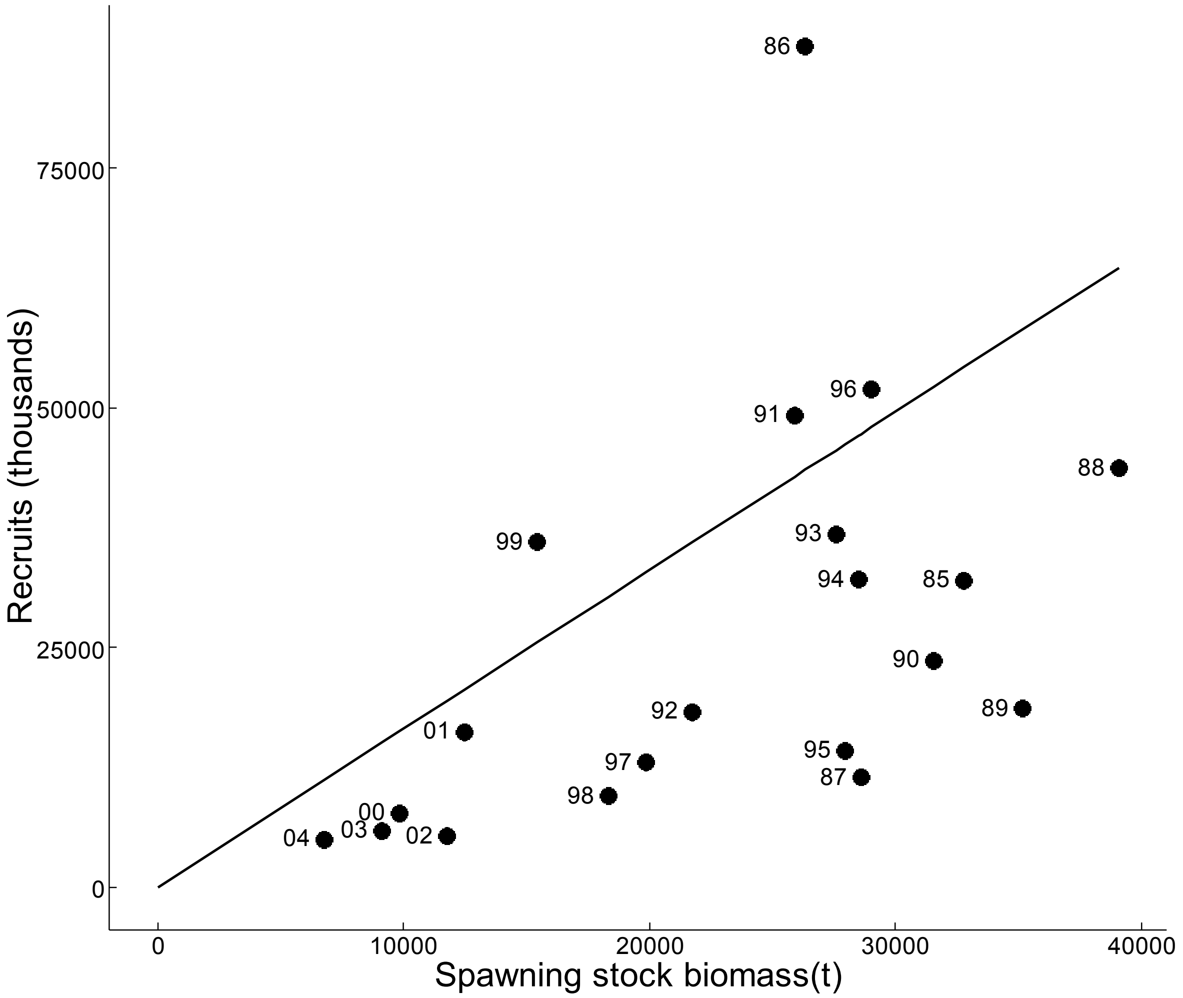

ICES
Base model
Fixed q(seal)
Full model
Total mortality (Z)
1.2
0.9
0.6
0.3
0.0
1985
1990
1995
2000
2005
Year
M
F(reported)
F(misreported)
M(seal)

Figure 8


Recruits (thousands)
75000
50000
25000
0
Spawning stock biomass(t)
0
10000
20000
30000
40000
86
96
91
88
99
93
94
85
90
92
89
01
97
95
87
98
00
03
02
04