

1 **Grey seal predation mortality on three depleted stocks in the West of Scotland:**

2 **What are the implications for stock assessments?**

3 Vanessa Trijoulet^{1,a}, Steven J. Holmes² and Robin M. Cook¹

4 ¹ Department of Mathematics and Statistics, University of Strathclyde, Livingstone

5 Tower, 26 Richmond Street, Glasgow G1 1XH, UK

6 ² Joint Research Centre, European Commission, Ispra, Lombardia, Italy

7 Corresponding author: Vanessa Trijoulet, vanessa.trijoulet@noaa.gov, Tel: +1 508-495-

8 2018, Fax: +1 508-495-2335

9 Co-authors emails: steven.holmes@jrc.ec.europa.eu, robin.cook@strath.ac.uk

10 ^a Current address: Integrated Statistics, under contract to Northeast Fisheries Science

11 Center, National Marine Fisheries Service, National Oceanic and Atmospheric

12 Administration, 166 Water St., Woods Hole, MA 02543, USA

13

14 **ABSTRACTS**15 English:

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

30 French:

31 La diminution des stocks de poissons démersaux dans l'Atlantique Nord depuis le
32 milieu des années 1900, couplé à l'augmentation des populations de phoques gris, a
33 entraîné une controverse durable entre les pêcheurs et les défenseurs de
34 l'environnement concernant le rôle des phoques dans le déclin des stocks. Nous avons
35 utilisé un model Bayésien état-espace afin d'investiguer l'évolution des stocks en
36 présence des phoques dans l'ouest de l'Ecosse mais aussi les points de références de
37 rendement maximal soutenu (RMS) associés. Cette étude estime la mortalité de l'aiglefin

38 et du merlan due à la prédation des phoques gris, et met à jour les estimations pour la
39 morue. Ces trois espèces représentent les principaux poissons démersaux
40 traditionnellement pêchés dans cette région. La mortalité de la morue due à la
41 prédation des phoques gris est la plus importante et engendre des estimations de
42 mortalité naturelle totale plus larges que celles actuellement utilisées par le CIEM dans
43 l'évaluation des stocks. A l'inverse, la mortalité de l'aiglefin et du merlan est faible.
44 Considérer la prédation des phoques dans le modèle d'évaluation des stocks change
45 l'estimation de la biomasse et de la mortalité de pêche pour les trois stocks de poissons.
46 L'estimation de $F_{0.1}$ et F_{MSY} pour la morue et le merlan est sensible à la prédation des
47 phoques mais ne l'est pas pour l'aiglefin. Dans les trois cas, RMS diminue avec
48 l'augmentation de la prédation des phoques.

49 INTRODUCTION

50 In the North Atlantic, the 20th century has seen a marked decline in fish stocks of high
51 commercial value (Christensen et al. 2003). Atlantic cod (*Gadus morhua*), previously one
52 of the most abundant and valuable demersal species, has declined substantially in much
53 of Europe while some stocks in the western Atlantic collapsed (Myers et al. 1996)
54 leading to the introduction of a moratorium on fishing in 1993. In the West of Scotland
55 (ICES Division 6a) and the North Sea (ICES Subarea 4), the landings of demersal species
56 have decreased substantially. In the 1980s, cod, haddock (*Melanogrammus aeglefinus*)
57 and whiting (*Merlangius merlangus*) were the dominant species in the fishing catch
58 (ICES 2013). In response to their decline, the West of Scotland fishery now targets
59 mainly Norway lobster (*Nephrops norvegicus*) as a high value alternative species (ICES
60 2016) but haddock is still one of the main fish caught (ICES 2015). Whilst many fish
61 stocks have declined, the grey seal population (*Halichoerus grypus*) has doubled around

62 the UK (Thomas 2012) and has grown exponentially on the Canadian east coast (Bowen
63 et al. 2003). This situation has created substantial conflicts between fishers and
64 conservationists regarding the role that grey seals may have played in the stock
65 depletion (Harwood 1984; Read 2008).

66 Grey seal predation mortality on cod has been estimated in the eastern Canada (Benoît
67 et al. 2011; O'Boyle and Sinclair 2012) and the West of Scotland (ICES Division 6a)
68 (Cook et al. 2015). On the Canadian east coast, the cod collapse in the early 1990s is
69 widely accepted as being due to overfishing (Buren et al. 2014), but while seal impact
70 on the stocks is still controversial, grey seals were recently believed to contribute to the
71 non-recovery of the stocks despite the closure of the fishery in 1993 (Sinclair et al.
72 2015; Swain and Benoit 2015). Large scale seal culls were recently proposed to
73 conserve the groundfish stocks in this area (Fisheries Resource Conservation Council
74 2011; Standing Senate Committee on Fisheries and Oceans 2012). In the West of
75 Scotland, seal predation on cod is significant and may be responsible, with high levels of
76 fishing mortality, for the non-recovery of the stock (Cook et al. 2015; Cook and Trijoulet
77 2016). However, cod is only one species in mixed trawl fisheries and it is important to
78 quantify seal predation on other species that make or made a substantial contribution
79 to the catch on which the fishery depends.

80 Cod is usually caught in mixed demersal fisheries along with other commercial species
81 which appear in the grey seal diet (Bowen and Harrison 1994; Hammond and Grellier
82 2006; Harris 2007) and may be subject to significant seal predation. The West of
83 Scotland area represents an opportunity to investigate grey seal predation on other
84 species following seal diet studies carried out in 1985 and 2002 (Grellier and Hammond
85 2006; Harris 2007). This allows the role, if any, that grey seals may have played in the

86 decline of haddock and whiting in the area to be investigated. It has been suggested that
87 the weight of cod consumed by grey seals (7 565 tonnes) can be of similar magnitude to
88 estimated spawning stock biomass (SSB) (Harris 2007) and that seal predation
89 mortality on cod may be large (Cook et al. 2015; Cook and Trijoulet 2016). In 2002, the
90 weight of whiting and haddock consumed by seals (Harris 2007) was estimated to be
91 very similar to the landings for each species and may generate a mortality as large as
92 the fishery (ICES 2013). Grey seal predation on these two other demersal species may
93 therefore be high in this area.

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

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

110 the single species assessments, as currently used in the West of Scotland, may vary with
111 the consideration of seal predation.

112 **MATERIALS AND METHODS**

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

118 ***Parameter estimation***

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

129 The model was fitted over the period 1985-2012 to include the first year when seal diet
130 data are available and the last year when a full assessment of haddock is available for
131 the West of Scotland. Since 2013, the haddock in the West of Scotland and the North Sea
132 have been assessed as a single unit, so in order to retain geographical integrity with the

133 seal diet data we used the data from the last 6a haddock stock assessment (ICES 2013).
134 For consistency we used the same 2013 assessment for cod and whiting.

135 Four research vessel surveys from the West of Scotland were used in the assessments
136 (Table 1). In 1999, the Scottish survey vessel was replaced and the length of the tow
137 was reduced from 60 minutes to 30 minutes (ICES 2013). Hence the quarter 1 Scottish
138 survey was split into two periods (1985-1998 and 1999-2010). This was not applied for
139 the quarter 4 survey since it would result in a survey of only three years from 1996 to
140 1998. Preliminary model runs for whiting gave exceptionally large seal predation or
141 fishing mortality estimates in 2004 and 2005 (Figure S1.1 in Supplementary material 1.
142 Supplementary data are available online through journal) which appear to be related to
143 the survey data. Similar unrealistically high mean fishing mortalities for the same years
144 are obtained from the whiting ICES stock assessment model unless a persistent trend in
145 survey catchability is assumed (ICES 2014b). Consequently, for whiting the final
146 analysis was run with the survey data from 2001 to 2005 omitted (see Supplementary
147 material 1 for further explanation).

148 We fitted models to the landings (T2.12), discards (T2.13) and research vessel indices
149 (T2.14) age composition data under different assumptions of seal predation for each
150 stock in turn using the same Bayesian statistical methods as described in Cook et al.
151 (2015). The models were:

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

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

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

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

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

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

180 (2013) used for ICES Division 6a stock assessments. The latter do not explicitly account
181 for seal predation. We also compared the estimates with those from the North Sea (ICES
182 Sub-area 4) as the ecosystems and fisheries share many similarities with the West of
183 Scotland (ICES 2015). The North Sea estimates consider predation by fish, seals,
184 harbour porpoises and seabirds and are based on multispecies assessment (SMS) (ICES
185 2014a).

186 ***Equilibrium analyses***

187 In order to investigate how inclusion of seal predation changes perceptions of stock
188 productivity and therefore the estimation of management reference points, two
189 equilibrium analyses were performed. These were a per recruit analysis to estimate $F_{0.1}$
190 and full population model to estimate MSY that used the outputs from the stock
191 assessment model and published data. The stock assessment outputs needed for both
192 analyses were the fishing mortality F , the Lorenzen parameters to calculate the natural
193 mortality, the seal selectivity parameters (γ and δ) and the seal predation rate (q). The
194 fishing selectivity at age used was derived from the average F at age taken over 2008 to
195 2012 to represent the most recent fishery selectivity. Because only two years of seal diet
196 data are available and the variations in grey seal diet for the recent years are not well
197 determined, an average seal predation rate (q) of the two years 1985 and 2002 was
198 used as the input values. These years are informed by real observations and will be
199 better determined. A test on the sensitivity of the results to the omission of survey data
200 for whiting showed that this did not affect the estimates for the years 1985 and 2002
201 (Supplementary material 3).

202 Published data (Thomas 2012) on the average number of seals between 2008 and 2012
203 were used to scale the seal predation rate to seal predation mortality representative of

204 recent years. An average over the same years was used for weight at age obtained from
 205 ICES (2013).

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

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

$$216 \quad (1) \quad q_y = \frac{\theta}{1 + \theta \rho P B_y}$$

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

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

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

248 **RESULTS**

249 *Estimated trends in stock biomass and fishing mortality*

250 The assessment model fitted the observed landings, discards and survey indices for the
251 three models closely, notably for the landings (Supplementary material 5). The discard
252 data was less well fitted, especially when only a few age classes were available. Best fits
253 of abundance indices were to the longest running surveys. Seal diet data was also well
254 fitted for models A and B although for haddock some points of the data lie outside the
255 95% credible intervals (Figures S5.48-S5.49). All the models typically estimated a larger
256 SSB than the ICES assessments but with similar general trends (Figure 1). The estimated
257 fishing mortality is lower than the ICES values for all species.

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

264 ***Seal consumption and predation mortality***

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

272 The estimated trend in seal predation mortality along the time series varies
273 substantially with the model considered (Figure 3). In the case of a fixed seal predation

274 rate (model B), the mortality due to seals on the three species is almost constant
275 reflecting the small change in the size of the seal population. For the variable predation
276 rate scenario (model A), the estimated grey seal predation is smaller in the early years
277 but subsequently increases and exceeds the fixed q estimates substantially.

278 ***Age dependent natural, seal predation and fishing mortalities***

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

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

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

291 ***Estimated total natural mortality***

292 The estimates of non-fishing mortality at age (in effect the total natural mortality
293 typically used in ICES assessments) obtained from the model A are larger than those
294 obtained from the model B for cod, but slightly smaller for haddock and whiting (Figure
295 5). Models B and C give similar values for haddock and whiting. However models that
296 consider grey seal predation explicitly estimate larger non-fishing mortalities for cod no
297 matter the seal predation rate assumption. For the West of Scotland, generally the

298 estimated non-fishing mortalities in this study were larger across all ages than those
299 from ICES (M_{WoS} in Figure 5). Mortality estimates for young age classes are higher for
300 the North Sea (M_{NS} in Figure 5) than our estimates for the West of Scotland.

301 ***Equilibrium analyses***

302 The estimated reference points for the three species assuming the current number of
303 grey seals in the West of Scotland are shown in Figure 6. The corresponding values are
304 given in Supplementary material 6. The values of $F_{0.1}$ for the three models differ little
305 from the values of F_{MSY} for cod and haddock as their distributions overlap. There is a
306 large difference, however, for whiting. The current value of mean fishing mortality on
307 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,
308 current mean F is well below both reference points.

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

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

321 cod but less dramatic with a clear decrease in MSY and F_{MSY} when the grey seal
322 population is increased.

323 **DISCUSSION**

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

337 When the seal predation rate is treated as a constant, only small variations in seal
338 mortality estimates are observed which arise from annual fluctuations in fish size at age
339 and small changes in seal numbers. However, there are large fluctuations when the
340 predation rate is allowed to vary. The small number of years with seal diet data and the
341 small difference in the DIC mean it is very difficult to distinguish between the
342 assumptions of constant or variable seal predation rate with any confidence especially
343 as some of the fluctuations appear implausibly large. However, the decline in the cod
344 stock between 1985 and 2002 (ICES 2013) while seal per capita consumption rates are

345 of the same order of magnitude between the two years (Grellier and Hammond 2006;
346 Harris 2007) would support a variable predation rate. The fact that the seal per capita
347 consumption rate of haddock increased significantly between 1985 and 2002 (Grellier
348 and Hammond 2006; Harris 2007) while the haddock population was similar in both
349 years strongly suggests a change in the predation rate. Consequently, the results
350 presented here offer some support for the use of a variable seal predation rate in the
351 stock assessment model. The estimates of seal predation mortality for 1985 and 2002
352 are likely to be the most reliable since these are years when actual observations exist.
353 For other years the estimates need to be treated with care and are at best illustrative.

354 In the current West of Scotland ICES cod assessment, the average natural mortality (age
355 1-6) used is 0.308 and implicitly includes the mortality due to seal predation. The
356 average non-fishing mortality on cod estimated from models A and B in this study is
357 larger than this value suggesting that the current cod natural mortality values
358 considered in ICES assessments for the Division 6a may be too low. Unlike recent
359 studies in the North Atlantic where seal predation was considered as insignificant
360 compared to the total mortality on fish stocks (Boyd and Hammond 2010; MacKenzie et
361 al. 2011; Alexander et al. 2014) these values seem of sufficient magnitude to matter in
362 evaluating stock status for fishery management.

363 The estimates of seal predation mortality at age for haddock and whiting are much
364 lower than those for cod. While it may be indicative of a species preference, it may in
365 part be an effect of size. Haddock and whiting have much lower size at age and the
366 highest predation mortality is on the oldest fish (ages 6-7) while for cod it reaches a
367 maximum at ages 2-3. These ages correspond to a similar mean length; a two year old
368 cod has a mean length of 45.8 cm while six year old haddock and whiting have mean

369 lengths of 43.4 cm and 38.5 cm respectively. It is suggestive of a size preference by seals
370 since fish below and above this size have lower predation mortality rates, although for
371 large fish this is only discernible in cod. The consequence of the apparent size
372 preference is that, for cod, seals remove smaller fish before they are selected by the
373 fishery leading to sequential competition. For haddock and whiting size selection
374 increases along with the fishery and is closer to scramble competition.

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

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

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

411 Over much of the study period the grey seal population in the West of Scotland has been
412 fairly stable and the estimates of MSY reference points in Figure 6 assume no change in
413 seal numbers. Given the controversy surrounding the effect of seal predation on the
414 fishery it is of interest to consider the effect of changed seal population size on these
415 reference points. As might be expected, in all cases increased seal populations result in

416 lower MSY catches with the most dramatic effect on cod where the stock comes close to
417 collapse when the seal population doubles. The high sensitivity of cod to seal predation
418 is partly an effect of scale (P is much larger compared to that for haddock and whiting)
419 and partly the domed selection pattern which effectively removes fish one age earlier
420 than the fishery.

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

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

434 In the popular press the scale of seal predation is often judged by comparing catches
435 from the fishery to estimated quantities consumed by seals. The small effect of changes
436 in seal predation on haddock revealed in this study highlights the limits of assessing the
437 impact of seals on a stock simply by comparing seal catches (Harris 2007) with fishing
438 catches (ICES 2013). Even in the case of whiting, although seal predation appears to

439 affect reference point calculations, the magnitude of seal predation mortality is small
440 compared to other sources of mortality, including fishing.

441 With the exception of the cod functional response scenario, all the projections assume
442 the seal predation mortality values are fixed which is an over-simplification if seals
443 respond dynamically to the abundance of prey as suggested by previous studies
444 (Matthiopoulos et al. 2003; Middlemas et al. 2006; Smout et al. 2014). Our results
445 should therefore be seen more as an indication of sensitivity to seal predation rather
446 than absolute quantitative predictions. The consideration of a seal functional response
447 to cod biomass heightens the sensitivity of cod to an increase in fishing and seal
448 predation mortality. However, the type II response was fitted to the seal predation and
449 partial biomass estimates for which only two years of seal data over the time series of
450 28 years were available. The limited seal diet data brings uncertainty to the seal
451 response and prevented a three parameter type III functional response being fitted
452 despite the reported switching behaviour in seals (Smout et al. 2014).

453 For whiting we used the stock assessment outputs where abundance indices for some
454 years were removed due to an apparent anomaly in the estimated values of seal
455 predation. It is debatable whether this is fully justified because censoring the data is
456 based purely on a perception of how seal predation should change. Omitting the data
457 affected the estimated biomass and mortality rates in 2004-2005 but for other years the
458 omission had little effect. As we used estimated values for seal predation from 1985 and
459 2002 in subsequent analyses our results are fairly insensitive to this problem, though it
460 does mean that estimated stock trends during this period are subject to particularly
461 large uncertainty.

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

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

483 **ACKNOWLEDGMENTS**

484 This work was supported by funds from the University of Strathclyde, Marine Scotland
485 and MASTS through the Scottish Funding Council (grant reference 388 HR09011) to V.T

486 and by MASTS through the Scottish Funding Council (grant reference HR09011) to
487 R.M.C. We thank Helen Dobby for her comment on the manuscript.

488 **REFERENCES**

489 Alexander, K. A., Heymans, J. J., Magill, S., Tomczak, M. T., Holmes, S. J., and Wilding, T. A.
490 2014. Investigating the recent decline in gadoid stocks in the west of Scotland shelf
491 ecosystem using a foodweb model. *ICES Journal of Marine Science: Journal du Conseil*:
492 14.

493

494 Benoît, H. P., Swain, D. P., Bowen, W. D., Breed, G. A., Hammill, M. O., and Harvey, V. 2011.
495 Evaluating the potential for grey seal predation to explain elevated natural mortality in
496 three fish species in the southern Gulf of St. Lawrence. *Marine Ecology Progress Series*,
497 442: 149-167. doi: 10.3354/meps09454.

498

499 Beverton, R. J. H., and Holt, S. J. 1957. *On the dynamics of exploited fish populations*,
500 Springer.

501

502 Bowen, W., and Iverson, S. 2013. Methods of estimating marine mammal diets: A review
503 of validation experiments and sources of bias and uncertainty. *Marine Mammal Science*,
504 29: 719-754.

505

506 Bowen, W. D., and Harrison, G. D. 1994. Offshore diet of grey seals *Halichoerus grypus*
507 near Sable Island, Canada. *Marine ecology progress series*. Oldendorf, 112: 1-11.

508

509 Bowen, W. D., McMillan, J., and Mohn, R. 2003. Sustained exponential population growth
510 of grey seals at Sable Island, Nova Scotia. *ICES Journal of Marine Science: Journal du*
511 *Conseil*, 60: 1265-1274.

512

513 Boyd, I. L., and Hammond, P. S. 2010. Seals and fish stocks in Scottish waters. European
514 Parliament, Directorate General for Internal Policies Policy Department B: Structural
515 and Cohesion Policies.

516

517 Buren, A. D., Koen-Alonso, M., and Stenson, G. B. 2014. The role of harp seals, fisheries
518 and food availability in driving the dynamics of northern cod. *MEPS*, 511: 265-284.

519

520 Christensen, V., Guenette, S., Heymans, J. J., Walters, C. J., Watson, R., Zeller, D., and Pauly,
521 D. 2003. Hundred-year decline of North Atlantic predatory fishes. *Fish and Fisheries*, 4:
522 1-24.

523

524 Cook, R. M., Holmes, S. J., and Fryer, R. J. 2015. Grey seal predation impairs recovery of
525 an over-exploited fish stock. *Journal of Applied Ecology*. doi: doi: 10.1111/1365-
526 2664.12439.

527

528 Cook, R. M., and Trijoulet, V. 2016. The effects of grey seal predation and commercial
529 fishing on the recovery of a depleted cod stock. *Canadian Journal of Fisheries and*
530 *Aquatic Sciences*. doi: 10.1139/cjfas-2015-0423.

531

532 Coull, K. A., Jermyn, A. S., Newton, A. W., Henderson, G. I., and Hall, W. B. 1989.
533 Length/weight relationships for 88 species of fish encountered in the North East

534 Atlantic. Ed. by Department of Agriculture and Fisheries for Scotland. Scottish Fisheries
535 Research Report.

536

537 Fisheries Resource Conservation Council. 2011. Towards Recovered and Sustainable
538 Groundfish Fisheries in Eastern Canada: A Report to the Minister of Fisheries and
539 Oceans. ICES Document FRCC.11.R1 72 pp.

540

541 Grellier, K., and Hammond, P. S. 2006. Robust digestion and passage rate estimates for
542 hard parts of grey seal (*Halichoerus grypus*) prey. Canadian Journal of Fisheries and
543 Aquatic Sciences, 63: 1982-1998.

544

545 Hammond, P., and Grellier, K. 2006. Grey seal diet composition and prey consumption in
546 the North Sea. Final report to Department for Environment and Rural Affairs on project
547 MF0319.

548

549 Harris, R. N. 2007. Assessing grey seal (*Halichoerus grypus*) diet in western Scotland.
550 University of St Andrews, NERC Sea Mammal Research Unit (SMRU) Theses.

551

552 Harwood, J. 1984. Seals and Fisheries. ICES Document 12: 15, Great Britain 426-429 pp.

553

554 Holling, C. S. 1959. The components of predation as revealed by a study of small-
555 mammal predation of the European pine sawfly. The Canadian Entomologist, 91: 293-
556 320.

557

558 Holmes, S. J., and Fryer, R. J. 2011. Significance of seal feeding on cod west of Scotland –
559 results from a state space stock assessment model. *In* ICES Annual Science Conference
560 2011. Ed. by I. CM/I:22.

561

562 ICES. 2013. Report of the Working Group for Celtic Seas Ecoregion (WGCSE). 8–17 May
563 2013, Copenhagen, Denmark. ICES CM 2013/ACOM:12 1986 pp.

564

565 ICES. 2014a. Interim Report of the Working Group on Multispecies Assessment Methods
566 (WGSAM). 20–24 October 2014, London, UK. ICES CM 2014/SSGSUE:11 104 pp.

567

568 ICES. 2014b. Report of the Working Group for Celtic Seas Ecoregion (WGCSE). 13-22
569 May 2014, Copenhagen, Denmark. ICES CM 2014/ACOM:12 2010 pp.

570

571 ICES. 2015. Report of the Working Group on the Assessment of Demersal Stocks in the
572 North Sea and Skagerrak (WGNSSK). 28 April-7 May, ICES HQ, Copenhagen, Denmark.
573 ICES CM 2015/ACOM:13 1031 pp.

574

575 ICES. 2016. Report of the Working Group for the Celtic Seas Ecoregion (WGCSE). 12–21
576 May 2015, Copenhagen, Denmark. ICES CM 2015/ACOM:12 1432 pp.

577

578 Legault, C. M., and Palmer, M. C. 2016. In what direction should the fishing mortality
579 target change when natural mortality increases within an assessment? *Canadian Journal*
580 *of Fisheries and Aquatic Sciences*, 73: 349-357. doi: 10.1139/cjfas-2015-0232.

581

582 Lorenzen, K. 1996. The relationship between body weight and natural mortality in
583 juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *Journal of*
584 *Fish Biology*, 49: 627-642.

585

586 Lunn, D. J., Thomas, A., Best, N., and Spiegelhalter, D. 2000. WinBUGS-a Bayesian
587 modelling framework: concepts, structure, and extensibility. *Statistics and computing*,
588 10: 325-337.

589

590 MacKenzie, B. R., Eero, M., and Ojaveer, H. 2011. Could seals prevent cod recovery in the
591 Baltic Sea? *PloS one*, 6: e18998.

592

593 Matthiopoulos, J., Smout, S., and Harwood, J. 2003. Modelling the functional response of
594 British grey seals. *In Scientific Advice on Matters Related to the Management of Seal*
595 *Populations: 2003*. Ed. by SCOS.

596

597 Middlemas, S. J., Barton, T. R., Armstrong, J. D., and Thompson, P. M. 2006. Functional
598 and aggregative responses of harbour seals to changes in salmonid abundance.
599 *Proceedings of the Royal Society of London B: Biological Sciences*, 273: 193-198.

600

601 Myers, R. A., Hutchings, J. A., and Barrowman, N. 1996. Hypotheses for the decline of cod
602 in the North Atlantic. *Marine ecology progress series*. Oldendorf, 138: 293-308.

603

604 O'Boyle, R., and Sinclair, M. 2012. Seal-cod interactions on the Eastern Scotian Shelf:
605 Reconsideration of modelling assumptions. *Fisheries Research*, 115-116: 1-13. doi:
606 10.1016/j.fishres.2011.10.006.

607

608 R Core Team 2016. R: A language and environment for statistical computing. Ed. by R
609 Foundation for Statistical Computing. Vienna, Austria.

610

611 Read, A. J. 2008. The looming crisis: interactions between marine mammals and
612 fisheries. *Journal of Mammalogy*, 89: 541-548.

613

614 Ricker, W. E. 1954. Stock and recruitment. *Journal of the Fisheries Board of Canada*, 11:
615 559-623.

616

617 Sinclair, M., Power, M., Head, E., Li, W. K. W., McMahon, M., Mohn, R., O'Boyle, R., et al.
618 2015. Eastern Scotian Shelf trophic dynamics: A review of the evidence for diverse
619 hypotheses. *Progress in Oceanography*, 138, Part A: 305-321. doi:
620 <http://dx.doi.org/10.1016/j.pocean.2015.09.005>.

621

622 Smout, S., Rindorf, A., Hammond, P. S., Harwood, J., and Matthiopoulos, J. 2014.
623 Modelling prey consumption and switching by UK grey seals. *ICES Journal of Marine*
624 *Science*, 71: 81-89. doi: 10.1093/icesjms/fst109.

625

626 Spiegelhalter, D. J., Best, N. G., Carlin, B. P., and Van Der Linde, A. 2002. Bayesian
627 measures of model complexity and fit. *Journal of the Royal Statistical Society: Series B*
628 (Statistical Methodology), 64: 583-639.

629

630 Standing Senate Committee on Fisheries and Oceans. 2012. The sustainable
631 management of grey seal populations: A Path towards the recovery of cod and other
632 groundfish stocks. 42 pp.

633

634 Sturtz, S., Ligges, U., and Gelman, A. E. 2005. R2WinBUGS: a package for running
635 WinBUGS from R. *Journal of Statistical software*, 12: 1-16.

636

637 Swain, D. P., and Benoit, H. P. 2015. Extreme increases in natural mortality prevent
638 recovery of collapsed fish populations in a Northwest Atlantic ecosystem. *Marine
639 Ecology Progress Series*, 519: 165-182. doi: 10.3354/meps11012.

640

641 Thomas, L. 2012. Estimating the size of the UK grey seal population between 1984 and
642 2011. SCOS Briefing Papers 12/01.

643

644 Thompson, W. F., and Bell, F. H. 1934. Biological statistics of the Pacific halibut fishery.
645 (2) Effect of changes in intensity upon total yield and yield per unit of gear. ICES
646 Document 8 49 pp.

647

648 Trzcinski, M. K., Mohn, R., and Bowen, W. D. 2006. Continued decline of an Atlantic cod
649 population: How important is gray seal predation? *Ecological applications*, 16: 2276-
650 2292.

651

652

653 **TABLES**

654 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)

655

656 Table 2: Main equations of the stock assessment model. A full description of the model
 657 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	$q_{y+1} = q_y e^{\varepsilon q_y}$	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	$I_{k,a,y} = \zeta_{k,a}\eta_k N_{a,y} e^{-\theta_k Z_{a,y}}$	k is the survey, ζ the survey selectivity, η the survey catchability and θ the proportion of the year elapsed before survey

658

659 Table 3: DIC estimates for the different seal predation simulations. A lower DIC
660 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

661

662 Table 4: Average grey seal predation mortality estimates on cod (between ages 1 and 5)
 663 compared with the literature. The estimates from the current analysis correspond to the
 664 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

665

666 **FIGURE LEGENDS**

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

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

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

679 Figure 4: Estimated seal predation (P), natural (M) and fishing (F) mortality at age in
680 1985 and 2002 for the variable seal predation rate assumption (model A).

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

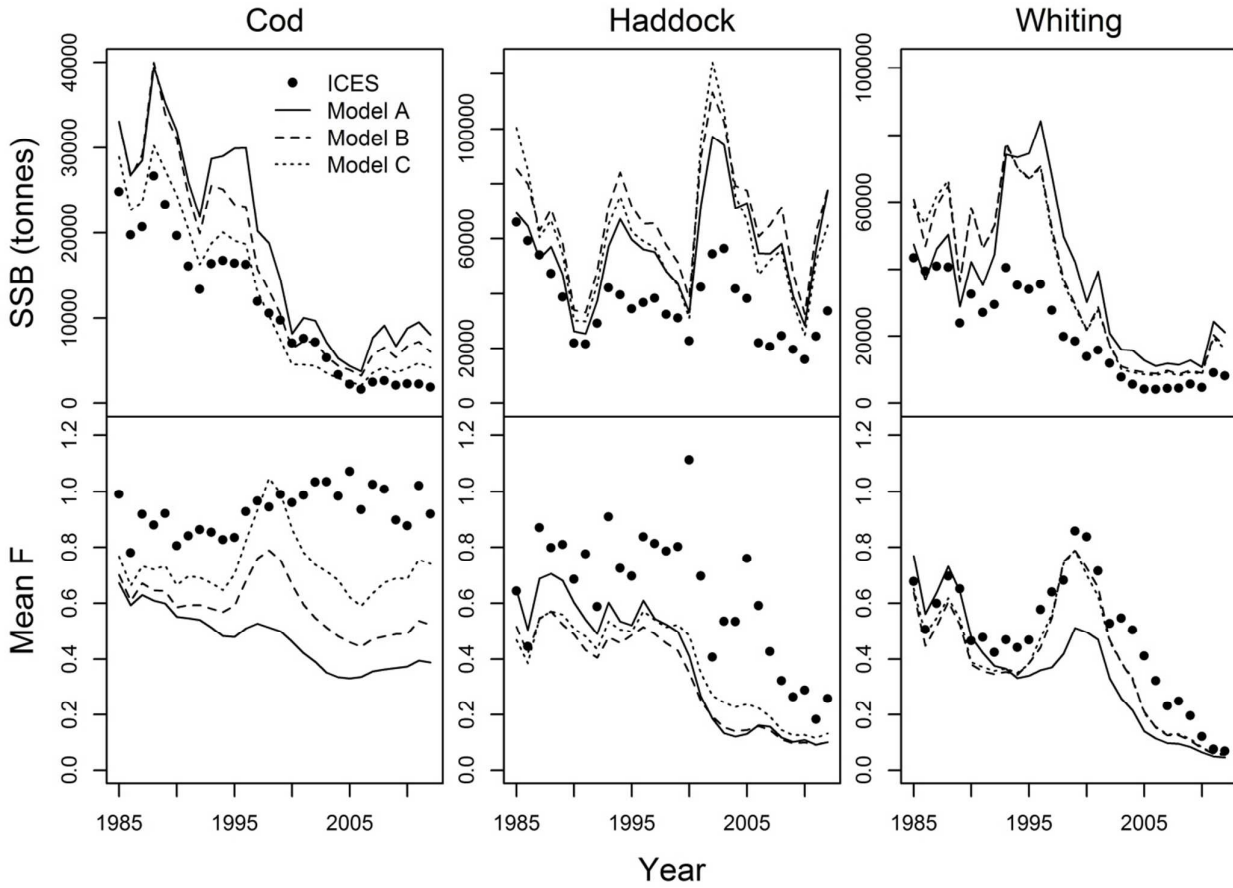
686 Figure 6: Estimated management reference points when the current seal predation
687 mortality is assumed. All values correspond to median measurements and the segments
688 represent the 90% credible interval. The dashed horizontal lines show the mean yield
689 over the years 1981-1990, a period of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

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

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

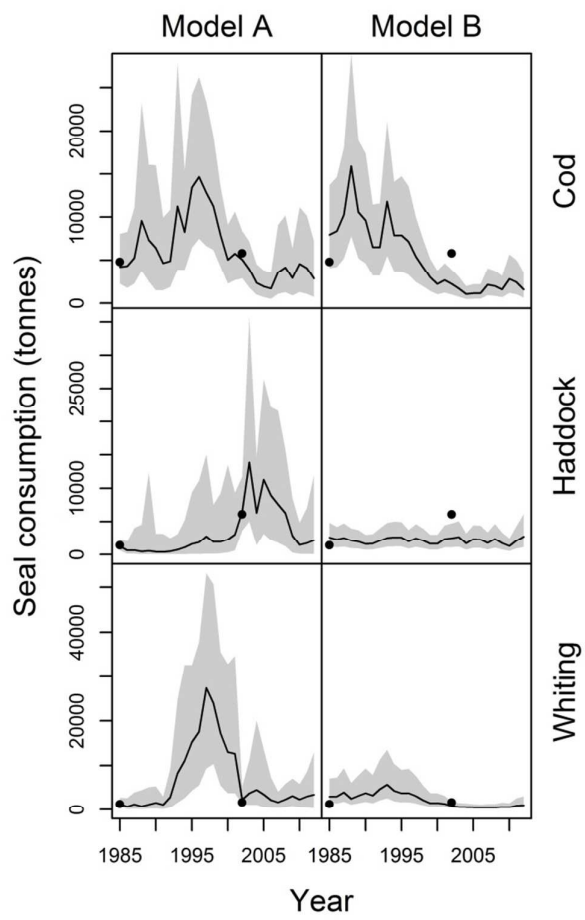
1 FIGURES

2 Figure 1



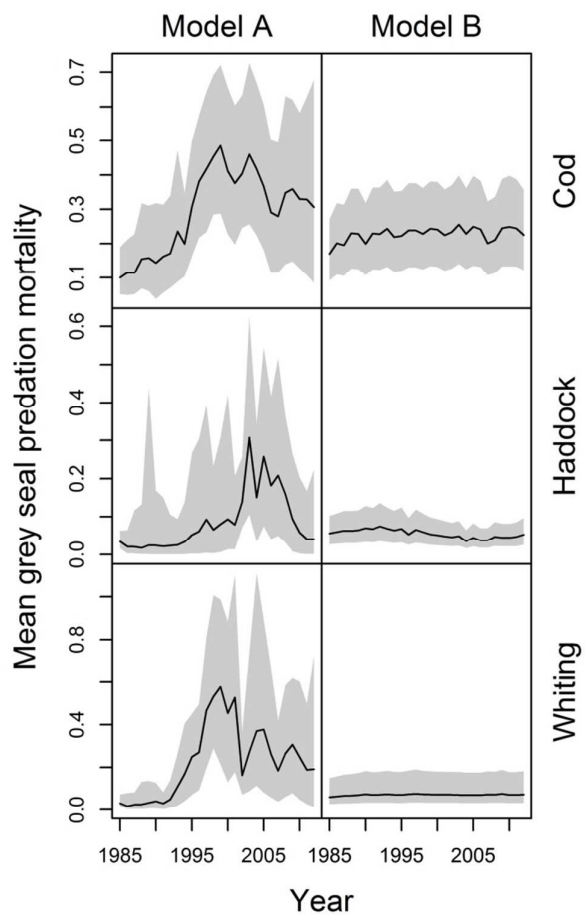
3

4 Figure 2



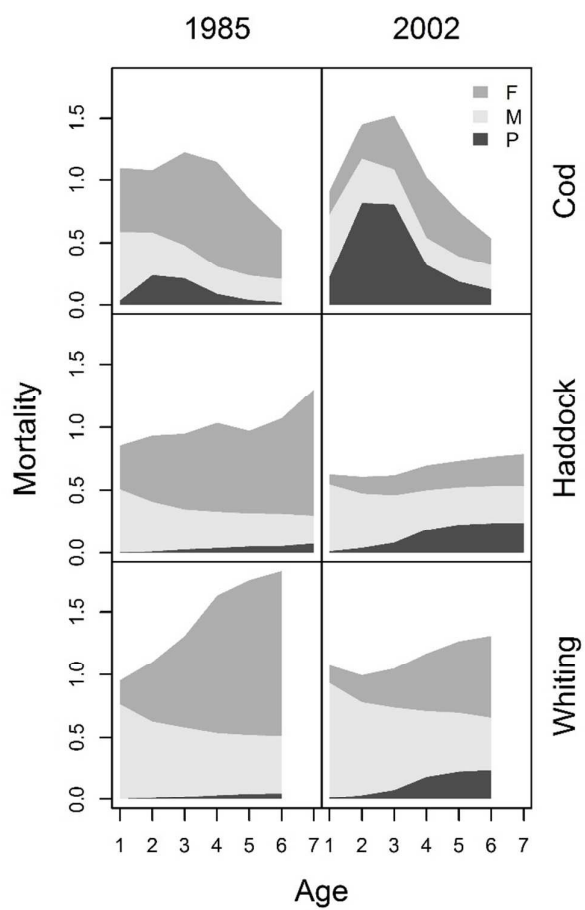
5

6 Figure 3



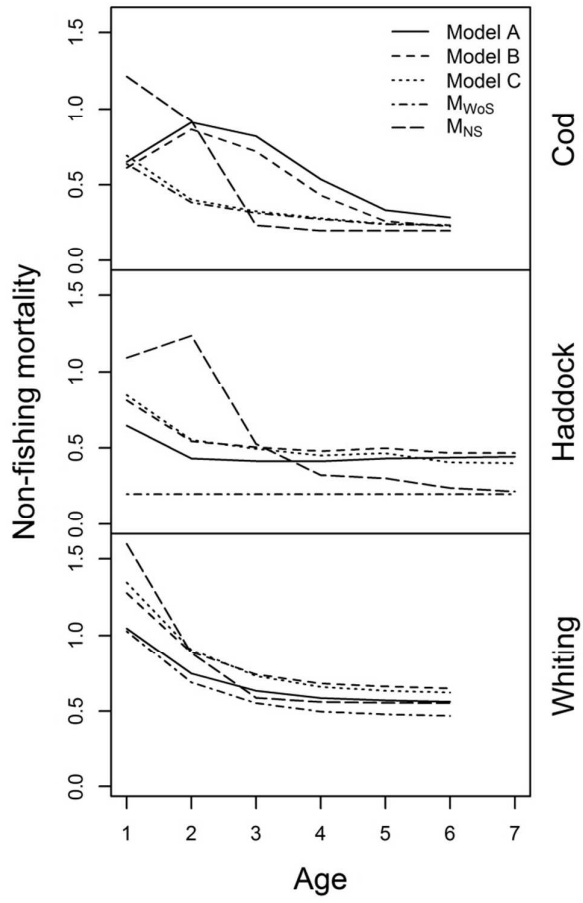
7

8 Figure 4



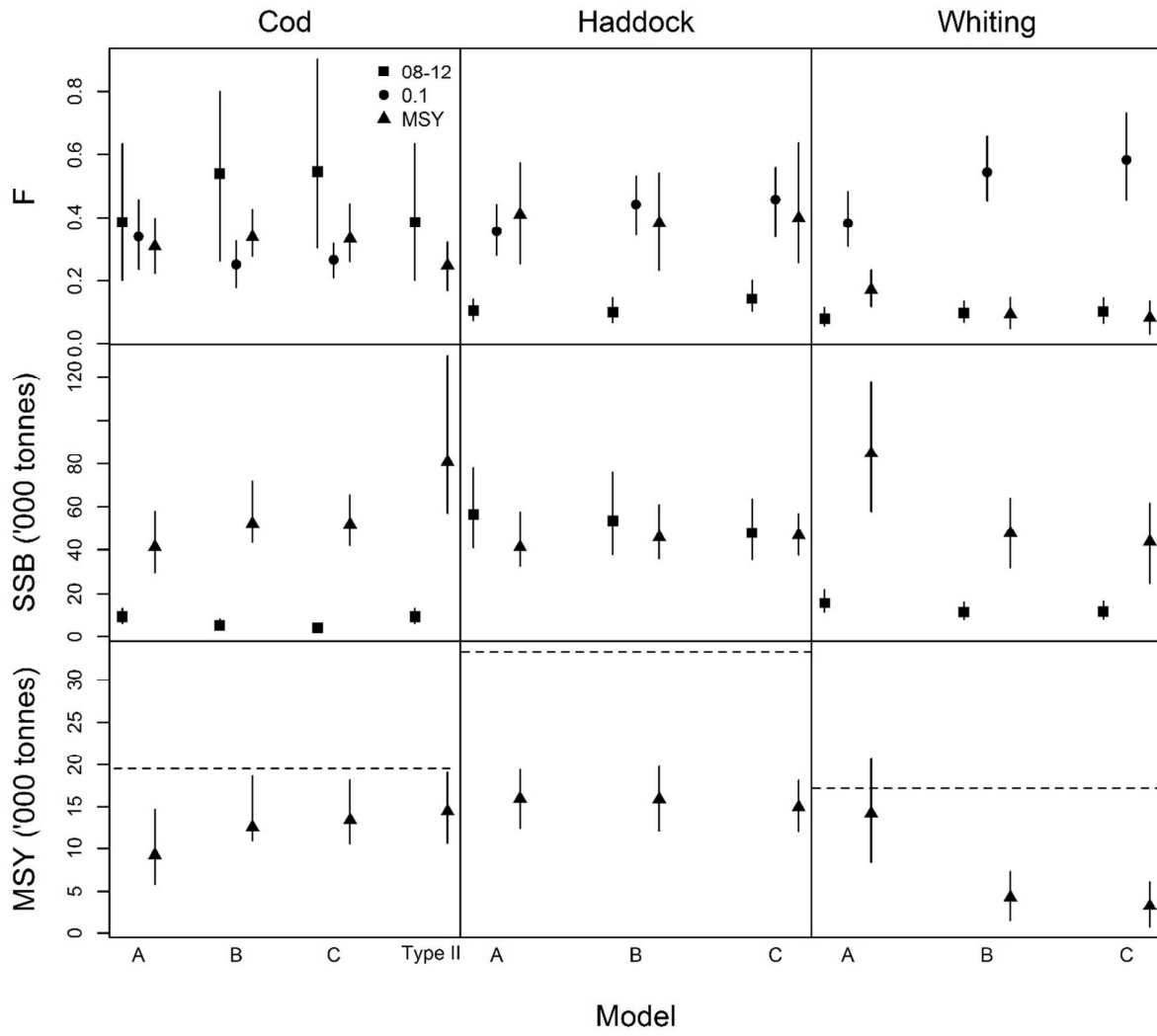
9

10 Figure 5



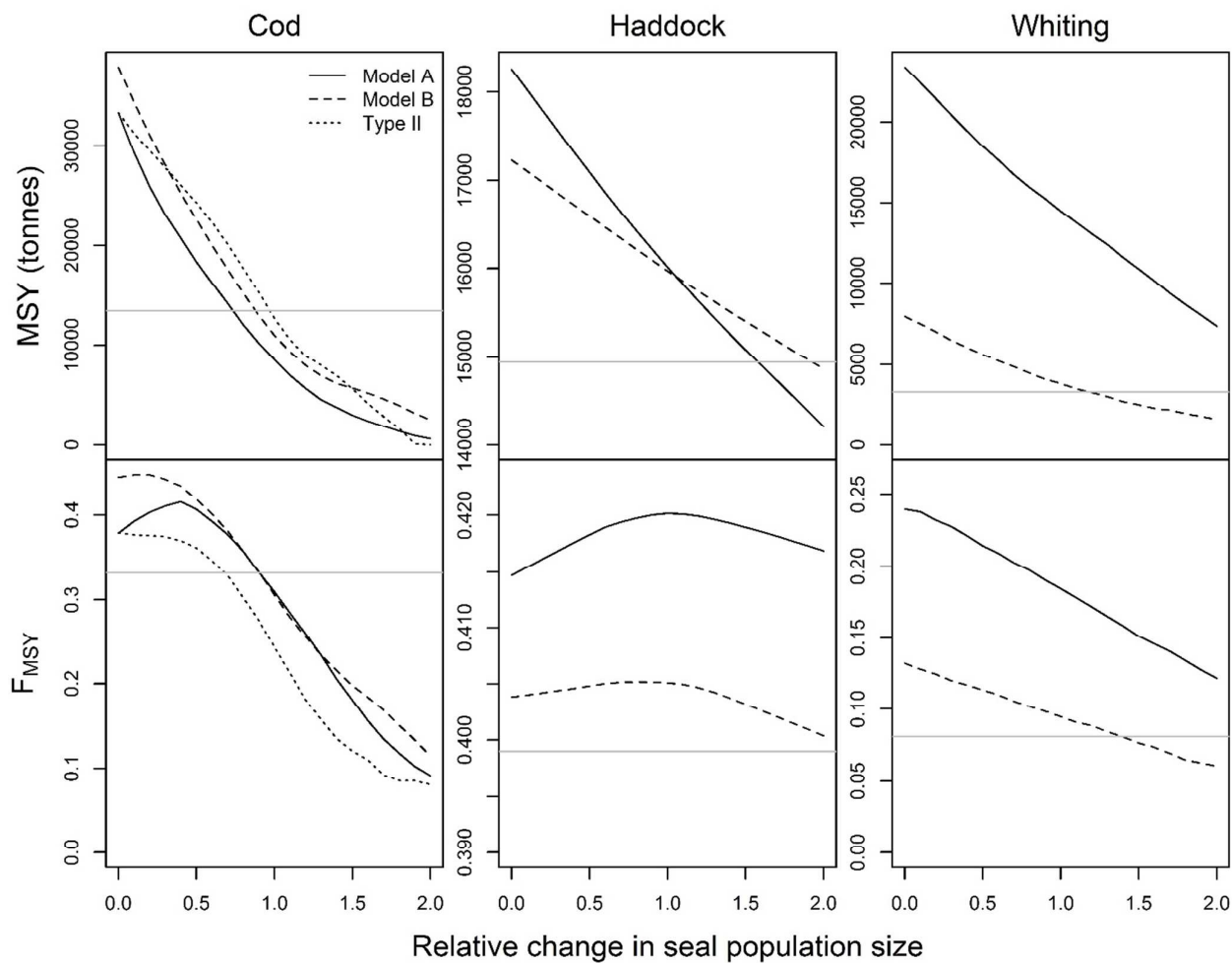
11

12 Figure 6



13

14 Figure 7



15