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1   **The effects of grey seal predation and commercial fishing on the recovery of a depleted cod stock**

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8

9 **Abstract**

10 Cod *(Gadus morhua*) are preyed upon by grey seals (*Halichoerus grypus)* and there is debate over

11 the impact this has had on the decline of stocks and their prospects for recovery. We analysed a

12 depleted stock to the West of Scotland and show that seal predation rate is consistent with a type II

13 functional response. Forward projections of a model including the functional response under varying

14 levels of fishing and seal population size suggest that stock recovery is possible under current

15 conditions but there is a modest probability that the stock will decline further in both the short and

16 long term. The potential recovery is fragile and sensitive to relatively small increases in either fishing

17 or seal predation. Forward projection models that exclude the functional response estimate a lower

18 probability of stock decline and may underestimate the risk to the stock. At low stock sizes and high

19 fishing mortality rates functional response models project slower recovery but the opposite is true at

20 low fishing mortality.

21

1. Introduction

Fisheries for Altantic cod (*Gadus morhua*) have long existed and provide an important source of food as well as supporting valuable commercial trade (Kurlansky, 1997). Many cod stocks both in Europe and North America have declined to low levels (Cook et al.,1997; Myers et al. 1996) and the species is currently classified as "vulnerable" in the IUCN Red List (IUCN, 2014). Grey seals (*Halichoerus grypus),* classified as "least concern" by the IUCN (IUCN 2014), are predators on cod (Prime & Hammond 1990; Hammond, Hall & Prime 1994; Hammond & Grellier 2006) and potentially compete with fisheries for the same resource. As a result there is controversy over the impact of seal predation on fisheries (Harwood 1984). Recent estimates of the mortality due to seal predation have suggested that it may be of sufficient magnitude to impair stock recovery both in Europe (Cook et al. 2015) and Canada (Fu, Mohn & Fanning 2001; Trzcinski, Mohn & Bowen 2006; O'Boyle & Sinclair 2012; Swain & Mohn, 2013; Swain & Benoit, 2015). By contrast, a report to the European Parliament Committee on Fisheries concluded that the effect of seal predation on fish stocks in Scottish waters was insignificant (Boyd & Hammond 2010).

An impediment to the evaluation of the effects of seals on fish populations is that the estimation of predation rates presents considerable challenges because data on diet and quantities of fish eaten by seals are hard to acquire. Thus the study by Boyd and Hammond (2010) relied on estimates of fishing mortality rates and stock biomass that were made on the basis of fixed natural mortality rates which did not account for seal predation explicitly, making comparisons between fishing and separately estimated seal predation debatable. Similarly, performing stock assessments without accounting for seal predation (where it may be large) can lead to biassed estimates of fishing mortality that give a misleading impression of the ability of managers to influence stock biomass by controlling exploitation in the fishery. In order to avoid this problem it is necessary to estimate stock biomass, fishing mortality and seal predation as part of the same stock assessment so that the respective estimates are calculated on the same basis and are internally consistent.

47   Typically in the ICES area fish stock assessments only account for non-fishing mortality as a constant

48   estimated externally to the assessment itself. This may include estimates of seal predation, as in

49   some North Sea assessments, where natural mortality values used are derived from multispecies

50   models that account for such predation (ICES 2014a). Nevertheless these are treated as fixed values

51   in single species assessments and the resultant estimates of fishing mortality are not necessarily

52   consistent with those derived from the multispecies analysis. In this paper we estimate seal

53   predation and fishing mortality to show the importance of accounting for both these mortalities in a

54   single assessment. We infer a relationship between the seal predation rate and stock biomass, and

55   between stock biomass and subsequent cod recruitment. This allows a full population dynamics

56   model to be constructed which we use to investigate stock trajectories under different scenarios of

57   seal population size, seal predation rate and fishing mortality.

58   The West of Scotland cod is taken as an example of where such an approach is feasible because

59   samples exist of seal diet and cod consumed. Recent assessments by the International Council for

60   the Exploration of the Sea (ICES) show a major decline in spawning stock biomass (ICES 2014b) with

61   high and relatively constant fishing mortality since the 1980s. The decline in biomass reflects similar

62   trends in adjacent cod stocks in the Irish Sea and North Sea. Management advice is effectively to

63   avoid all catches of cod (ICES 2014b). The stock is subject to a "recovery plan" that is intended to

64   reduce fishing mortality and increase the biomass through fishing effort limitation, gear

65   modifications, and landings limits (Kraak et al. 2013). The assessments assume fishing mortality is

66   the principal cause of stock decline, with the implication that reducing fishing mortality will favour

67   stock recovery. Cod may account for approximately 10% of the seal diet on the West of Scotland

68   with an estimated comsumption amounting to three times the official landings in 2002 (Harris 2007),

69   yet ICES assessments do not explicitly consider this mortality. This would suggest that a recovery

70   plan based on assessments which exclude seal predation may be unreliable. The analysis presented

71   here considers how seal predation affects the perception of stock recovery scenarios.

72   **2. Methods**

73   Cook et al's (2015) assessment model is used as the basis of the analysis but is extended to include

74   the period after 2005 and considers the full dynamics of the cod population and the relationship

75   between prey population biomass and seal predation.

76   Our approach involved estimating historical values of the cod stock biomass and mortality rates and

77   then projecting these forward under different assumptions about seal population size and fishing.

78   The projections were done using a stochastic model that takes account of uncertainty in the model

79   parameters and the structural relationship between stock size and recruitment (annual number of

80   cod at age 1).

81   We used standard fishery data reported in ICES (2014b) that comprise fishery catch at age and

82   relative abundance estimates from research vessel surveys, and cover the period 1985-2013 as listed

83   in Table 1. Although there are fisheries data prior to 1985 there are no seal diet data during this

84   earlier period making estimates of seal predation problematic so we restricted the analysis to the

85   more recent period when diet data are available. In order to estimate seal predation rates we used

86   data on cod length compositions in the seal diet, and total cod biomass eaten reported by Harris

87   (2007). Seal population numbers estimated by the UK Sea Mammal Research Unit (SMRU) (SCOS

88   2014) for the Hebrides were used as the population exploiting fish in the West of Scotland as it is

89   predominantly these animals that forage in the area (Harris 2007). Over the time period considered

90   the grey seal population in the area has increased from about 27,000 to 30,000 though in recent

91   years it has remained stable. In contrast seal populations foraging in the North Sea have increased.

92   Data on cod consumption by seals was only available for 1985 and 2002. The data were analysed

93   using an age structured stock assessment model outlined below, which is fully documented in Cook

94   et al (2015). The population of cod N at age a in year y decays exponentially as a result of a total

95   mortality, Z;

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

96 The total mortality is partitioned between fishing mortality F, natural mortality M and seal predation

97 mortality P as:

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

98

99 Fishing mortality is assumed to be the product of an age effect or selectivity, s, and a year effect

100 (fishing effort), f ;

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

101 Where the age and effort component follow an autoregressive process with variances σ^2_f and σ^2_s

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

$$s_{a,y} = s_{a,y-1} \, exp(\varepsilon_{s,a,y}), \qquad \varepsilon_{s,a,y} \sim Normal(0, \sigma^2_S), \; y \neq 1$$

102 Natural mortality M is assumed to be dependent on size and given by the Lorenzen (1996) equation:

$$5 \qquad M_{a,y} = A \bar{w}_{a,y}{}^B$$

103 Where $\bar{w}$ is the mean weight at age and A and B are constants.

104 Seal predation mortality is modelled as the product of a size preference (or selectivity), s_{seal}, and an

105 "effort" component, qG, where q represents the annual *per capita* capacity of seals to prey on cod

106 (the "predation rate"), and G is the abundance of seals. The seal predation mortality is thus:

$$6 \qquad P_{a,y} = s_{seal,a,y} q_y G_y$$

107 The quantity q will depend on the ability of seals to find and catch cod, the time it takes to process

108 prey items and the presence of other prey and may change over time. To avoid any structural

109 assumptions between predation rate and prey abundance q is assumed to follow a simple

110 autoregressive process with variance σ^2_q:

$$7 \qquad q_y = q_{y-1} exp(\varepsilon_y), \qquad \varepsilon_y \sim Normal(0, \sigma^2_q)$$

111

112   Assuming seals prefer a size range of cod, their selectivity is modelled as function of mean fish

113   length at age, $\bar{l}$, using gamma shaped curve with constant parameters α and β (Millar & Fryer 1999):

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

114

115   We also calculated the "partial biomass" (PB) of cod available to seals as the sum of the biomass at

116   age in the stock weighted by the size selectivity of the seals:

9
$$PB_y=\sum_a s_{seal,a,y}\bar{w}_{a,y}N_{a,y}$$

117

118   We fitted the model using the Bayesian statistical package WinBUGS (Lunn et al. 2000) configured as

119   described in Cook et al 2015 but with minor changes to include more recent catch data. Observed

120   landings, discards, survey indices and total consumption of cod by seals were assumed to be

121   lognormally distributed. The numbers of cod at length in the seal diet were assumed to be

122   multinomially distributed. In the original assessment model catch data were split between observed

123   cod landings and discards, with each data component fitted separately in the model with different

124   observation errors. The model assumes fixed discard size selection over time. Catch data beyond

125   2005, however, comprise almost entirely discards with a different pattern of discarding. Hence, in

126   order to extend the model to 2013 we treated the catch data from 2006 onwards as an aggregate of

127   landings and discards and fitted the model to the total catch at age with a new observation error

128   distribution. This circumvents the need to estimate discard selection for this period. In all other

129   respects the model was the same as the original. We saved a random subset of 1000 samples from

130   the Markov Chain Monte Carlo (MCMC) simulation for all model parameters for subsequent use in

131   the projection model described below.

132   Since the ICES cod assessment is the recognised standard for fishery advice we compared our stock

133   biomass and fishing mortality estimates to their most recent assessment (ICES 2014c) as a check of

134   consistency. Since this assessment only gives a time series back to 1981 we also compared the

135   estimates to the 2002 assessment (ICES 2002) as this provides stock estimates back to 1966, giving a

136   longer perspective on changes to the biomass. Each of these assessments uses different values for

137   natural mortality, M, which has the effect of rescaling the biomass estimates. Higher values of M

138   give larger values of biomass. In order to compare trends across assessments we rescaled the

139   biomass from the two ICES assessments to give the same mean biomass for the period 1985-2002 as

140   our assessment. This is the period when all three series overlap.

141   We used equations 1-6 and 8 as the basis for a stochastic forward projection model. The input

142   quantities used are listed in Table 2. Each realisation of the model was based on one of the MCMC

143   samples. For each random draw we fitted Ricker (1954) and Beverton-Holt (1957) stock recruitment

144   models by least squares to the sample time series of stock-recruitment pairs assuming lognormal

145   errors. We estimated both parameters in each model and chose the model with the lowest AIC to

146   forecast recruitment. Annual recruitment variability was then simulated by bootstrapping residuals

147   from the fitted model.

148   It is possible that annual recruitment residuals are correlated as the result, for example, of an

149   environmental trend. We examined the residuals after fitting the Beverton-Holt model to the mean

150   stock and recruitment values from the stock assessment model but found no evidence of a time

151   trend (Figure S1.1, supplementary material) so treated the bootstrapped residuals in the simulation

152   model as independent.

153   In the case of seal predation we fitted a type II functional response (Holling 1959) to model the

154   relationship between seal predation rate (q) and cod partial biomass of the form:

10        $q_y=c/(1+cdPB_y)$

155 where *c* and *d* are constants. This relationship assumes that the biomass of other prey remains

156 constant.

157 Annual variability in q_y was simulated by bootstrapping the residuals from the model fit. We

158 examined the residuals after fitting the model to the mean partial biomass and q_y values from the

159 stock assessment model but found no evidence of a dependence on biomass (Figure S1.2,

160 supplementary material) so treated the bootstrapped residuals in the simulation model as

161 independent.

162 The projection model differs from the stock assessment model in using structural functions to

163 describe stock-recruitment and q-partial biomass relationships. While it is possible to fit these

164 relationships within the assessment model doing so imposes a particular structural form on the

165 model estimates, and in the case of the functional response in particular, there are very few data to

166 adequately inform a parametric relationship. Estimating the recruitment values and q_y values in the

167 assessment model without an assumed functional form allows the exploration of a variety of

168 structural relationships to be investigated in the projection phase.

169 To test that the projection model using a type II response was consistent with the stock assessment

170 trend we ran the projection model from a base population biomass estimated for 1985 forward to

171 2013 and compared the median projected population to the population trajectory derived from the

172 stock assessment model assuming the same historical time series of fishing mortality and seal

173 population size.

174 To investigate the conditions for recovery of the cod stock we projected the population forward for

175 50 years from the base year of 2013 under a range of combinations of fishing mortality and seal

176 population size. For fishing mortality we scaled the 2013 population estimate by values ranging from

177 0.6 to 1.8, in increments of 0.1. This range corresponds to a larger interval compared to the

178 observed range (0.74-1.64) from the stock assessment. In the case of the seal population we scaled

179   the estimated 2013 population by values ranging from 0.8 to 1.2, in increments of 0.1. This narrower

180   range reflects an assumption that the seal population is unlikely to change substantially without

181   human intervention.

182   Since cod stock recovery is considered urgent we considered the probability of the cod spawning

183   stock biomass increasing above the 2013 level by the fifth year of projection. We also assumed that

184   by year 50 the population would be in equilibrium and calculated the median cod spawning biomass

185   under the various scenarios.

186   For comparison to a fixed natural mortality rate projection we ran the model assuming that the seal

187   predation rate was independent of cod biomass by setting $c=mean(q_y)$ and $d=0$ in equation 10 and

188   set the seal population multiplier at 1. This scenario therefore is equivalent to status quo seal

189   numbers and will result in non-fishing mortalities that have a stationary mean over time and most

190   closely resembles current practice when making forward projections for this stock.

191   In order to test the sensitivity of the projections to the assumption of a type II functional response

192   we also ran the model at constant seal population under two additional models for seal predation

193   rate. Firstly q_y values were simply projected forward using the time series model (equation 7) from

194   the base value estimate in 2013. This allows the seal predation rate to vary independently of prey

195   biomass. Secondly we fitted a loess function to capture the relationship between q_y and partial

196   biomass rather than the parametric relationship in equation 10. This allows the MCMC samples to

197   determine the shape the functional response relationship and potentially could allow a type III

198   response to occur.

199   3. **Results**

200   The estimated trend in cod spawning stock biomass from the ICES assessments and the current

201   analysis suggests that the biomass has declined from a value close to 80000 tonnes in the mid-1960s

202   to around 11000 tonnes in recent years (Figure 1a). There is close agreement in the trend between

203 the assessments although the current analysis indicates higher values in recent years compared to

204 the ICES assessment. The two ICES assessments show comparable trends in fishing mortality (Figure

205 1b) though the 2002 assessment shows a sharp decline at the end of the time series. Our analysis

206 shows a lower fishing mortality which declines over most of the period but an increasing trend in

207 recent years. This difference is due to the fact that our model allocates an increasing proportion of

208 the total mortality to seal predation rather than fishing. Both the ICES assessments and our

209 assessment give similar estimates of total mortality and is the reason why the biomass estimates are

210 alike (Cook et al. 2015). Full details showing the model fit to the observations are given in

211 supplementary material (Figures S2.1 to S2.10).

212 Figure 2a shows the relationship between cod spawning stock biomass and recruitment at age 1. The

213 fitted model, based on the mean values from the stock assessment, is a Beverton-Holt relationship

214 which was selected most frequently in the stochastic projections. Figure 2b shows the seal predation

215 rate as a function of cod partial biomass. The predation rate, q, declines with increasing cod biomass

216 and, in effect, results in a type II functional response. The fitted line (solid) is equivalent to the disc

217 equation (Holling 1959). Also shown is the loess smoothed relationship (dashed line) which suggests

218 that q_y may decline at the lowest partial biomass and captures some elements of a type III response.

219 By applying the relationship in Figure 2b it is possible to calculate total mortality, Z, for combinations

220 of partial biomass and fishing mortality. The resulting contour plot is shown in Figure 3 for the type II

221 response (equation 10). Over-plotted in the figure are the observed values from the stock

222 assessment. It can be seen that as the cod partial biomass and fishing mortality have declined over

223 time the total mortality has changed little and followed the contour Z=1.2 throughout the recent

224 history of the stock. It shows that despite reductions in fishing mortality, the simultaneous decline in

225 biomass has meant that seal predation mortality has compensated for this reduction.

226 The functional relationships shown in Figure 2 provide the basis of the forward projection model by

227 forecasting recruitment and reflecting changes in seal predation rate as the biomass develops. The

228 projection model using equation 10 for the functional response is compared to the historical

229 estimates of biomass in Figure 4. The median projected biomass follows the observed values for the

230 first 13 years but thereafter tends to increase while the observed values decline and level off.

231 Although the projected values lie below the median, they remain within the 95% credible interval in

232 the region of the 15th percentile. Other functional response models produced qualitatively similar

233 results and are not plotted.

234 The results of the short term projection which considers the probability of the spawning stock

235 biomass in year 5 falling below the 2013 base value are shown in Figure 5a. At current rates of

236 fishing and seal numbers the probability of further decline is around 0.17. At equilibrium, the

237 probability that the stock is below the base value is higher at about 0.25 (Figure 5b).

238 Figure 6 shows the median cod spawning stock biomass at equilibrium under different combinations

239 of seal populations and fishing mortality. At the current rate of fishing and with the existing seal

240 population, the median equilibrium spawning stock biomass would be close to 40000 tonnes. This

241 represents an increase over the current biomass but is about half the biomass estimated in the mid

242 1960s. To achieve the latter would require a reduction in fishing mortality of about 20% or a very

243 much larger reduction in the seal population.

244 The projections under stationary seal population size are summarised in Figure 7. For a constant seal

245 predation rate the perceived risk of stock decline is lower under this assumption than a type II

246 response both in the short and long term. The projected median biomass is almost identical to the

247 full model for the five year projection but in the long term there are major differences. At low fishing

248 mortality the stationary natural mortality scenario gives lower biomass values while the converse is

249 true for high fishing mortalities. This shows that for a heavily exploited stock, if there is a predator

250 type II functional response, there is a danger of underestimating the risks of stock decline and

251 overestimating future biomass.

252   The sensitivity of the projected biomass to the functional response assumption can be seen in figure

253   7 which shows probability of decline and spawning stock biomass for the time series model of q_y and

254   the loess smoothed q_y-partial biomass relationship. For the five year projection the loess model gives

255   the highest probability of stock decline at intermediate fishing mortality rates. The same model gives

256   almost identical results to the type II response for probability of decline at year 50. The time series

257   model gives a much higher long term risk to the biomass because it assumes the 2013 value (which

258   is high) is propagated forward regardless of stock size. In general, the effects of the different

259   assumptions on seal predation rate are largest at equilibrium due to the cumulative effects of

260   predation, fishing and recruitment. The type II and loess models shows the greatest change in

261   equilibrium spawning stock biomass as a function of fishing mortality as they assume a dynamic

262   relationship between predation rate and prey biomass. The same models also suggest higher

263   probability of stock decline in the short term than the fixed natural mortality model.

264

265   **4. Discussion**

266   Both the ICES and the current analysis, which includes seal predation, estimate a long term

267   reduction in the cod spawning stock biomass. In recent years the decline has halted with perhaps a

268   slight increase. Unlike the ICES assessment our analysis suggests the fall in biomass has occurred in

269   the presence of diminishing fishing mortality but almost constant total mortality (Figure 3) indicating

270   that other mortalities have compensated for reduced fishing. The compensation appears to be a

271   result of the effect illustrated in Figure 2b that the seal predation rate increases as partial cod

272   biomass decreases and is typical of a type II functional response. Such a response has been reported

273   before for grey seals (Middlemas et al. 2006). Smout et al (2013) also estimated functional responses

274   for seals but found evidence of prey switching based on data at a much finer spatial scale. Our

275   analysis offers little evidence of prey avoidance at low biomass values as implied by predator

276   switching, perhaps because the spatial resolution in the assessment data is absent.

277 We were able to incorporate the seal functional response and the stock recruitment relationship

278 into a cod stock projection model that generated biomass trajectories consistent with historically

279 estimated values (Figure 4) and hence supported use of the model to project the stock beyond the

280 current level. The 5 year ahead and long term projections indicate that there remains a risk that the

281 biomass will not increase at current rates of fishing and seal population (Figure 5). However, the

282 biomass is close to the lowest observed and this risk is large compared to the conventional

283 probability of 0.05 used by ICES to determine rates of fishing that ensure the lowest spawning stock

284 biomass is avoided. There is also some indication that the projection model may, if anything, be

285 over-optimistic since the observed cod biomass lies near the lower range of 95% CI of the projected

286 population (Figure 4). This may be the due to model misspecification of the seal functional response

287 or to changes in biological factors such as cod maturation rates and fecundity which would change

288 the estimated stock-recruitment relationship. There may also be a numerical response by predators

289 to local abundance not accounted for in the model or arising from seal herds in the North Sea

290 foraging in the West of Scotland. The latter seems less likely as fish stocks are at higher abundance in

291 the North Sea and seal tracking data do not show this movement (McConnell et al 1999).

292 The divergence between the observed stock biomass and the projected population from the

293 simulation model in more recent years might be the result of an environmental effect on

294 recruitment. In the adjacent North Sea area, for example, there is evidence of a negative

295 temperature effect on cod recruitment (O'Brien et al 2000; Cook & Heath 2005). Rising temperature

296 or a climatic trend could therefore explain weaker than expected recruitment in recent years which

297 would contribute to a decline in the stock biomass. The recruitment residuals for the West of

298 Scotland, however, show no time trend indicating that such an effect is difficult to detect. The

299 relationship between stock size and recruitment appears to be able to explain much of the dynamics

300 but will not capture environmental effects.

301   With *status quo* seal populations and current (2013) fishing mortality prevailing over the long term,

302   median cod spawning stock biomass is projected to be higher than current levels but below the

303   earliest observed values (Figure 6). It suggests that in the long term current fishing rates, which are

304   close to the historical minimum, should allow some stock recovery provided the stock-recruitment

305   relationship holds in the future. However, an increase in the seal population of only 10% could

306   reduce the long term median biomass from 40000 tonnes to little more than 30000 tonnes. Both the

307   equilibrium analysis and the short term projection therefore indicate that the prospects of stock

308   recovery under current conditions are fragile. Our stock assessment suggests that fishing mortality in

309   recent years has tended to increase and, if sustained, would further compromise stock recovery.

310   The SMRU estimates of the size of seal population in the West of Scotland indicate little change for a

311   number of years (SCOS 2014) and if this continues there would be no change to the risk of recovery

312   of the cod stock. Seal populations in Europe have a measure of protection under a variety of

313   European and national legal instruments reflecting a public desire to conserve them. European

314   Union regulations (EU 2009), for example, restrict the trade in seal products effectively outlawing a

315   market in Europe and hence removing any incentive to hunt seals. In the UK, legislation places

316   restrictions on the killing of seals and methods of slaughter while allowing the shooting of seals

317   under certain limited conditions (HMSO 1970). Although the protection is not absolute, no

318   systematic hunting or large scale culling of grey seals in the UK has taken place since 1978 and

319   populations around the British Isles have increased for a number of years (SCOS 2014) though the

320   recent increase has taken place mainly in the North Sea. As human intervention to control seal

321   population size is unlikely it means the cod recovery can only be enhanced by reducing fishing

322   mortality.

323   Our analysis implicitly assumes that the cod stock in the West of Scotland is well mixed and equally

324   available to both seals and the fishery. This may not be the case. Studies in the Celtic Sea and North

325   Sea suggest that seals forage in areas away from areas of high fishing activity (Matthiopoulos et al.

326   2004; Cronin et al. 2012). There are also likely to be areas where seals are able to forage where

327   commercial fishing is not possible. Hence the fishery and seals may exploit different cod populations

328   and avoid competition. If correct this would mean the estimated impact of seal predation in our

329   analysis is too high. While cod are known to exhibit site fidelity many individuals migrate between

330   spawning and feeding grounds or show dispersal behaviour (Robichaud & Rose 2004; Neuenfeld et

331   al. 2013). A comprehensive analysis of genetic material in the Northeast Atlantic indicates that the

332   West of Scotland population is indistinguishable from adjacent stocks (Heath et al. 2014). This

333   suggests the population is well mixed and while seals and the fishery may operate in different areas

334   they are probably not exploiting discrete populations. It seems that sufficient exchange is likely to

335   occur to justify the modelling assumptions.

336   An obvious weakness in the analysis is the paucity of seal consumption data to parameterise the

337   functional response in the projection model. Only two years of data were available for analysis with

338   the most recent observation made in 2002, more than a decade before the base year used for

339   projections. However, the two samples come from years when the cod stock was in very different

340   states providing considerable contrast in the data to inform the model. In both years the

341   consumption of cod by seals was in the region of 6000 tonnes while the spawning stock biomass of

342   cod reduced by approximately 60% over the same period. Sampling of seal diets around the British

343   Isles occurred in 2010 and 2011 and preliminary estimates of consumption appear similar to the

344   earlier years (Hammond, *pers comm*) and this is consistent with the estimated seal consumption for

345   these years from our stock assessment model.

346   Bias may arise in the estimates of seal predation if the scat samples on which the diet is determined

347   do not adequately reflect true seal food intake. The samples themselves may not be truly random

348   since they are collected at accessible haul out sites. Furthermore, if larger fish are only partially

349   consumed, leaving the head uneaten, the otoliths on which the seal diet it determined will be absent

350   leading to bias toward small fish in the estimated size range consumed. If large fish are under-

351   represented in the samples predation on younger fish will be over-estimated (and vice-versa for

352   older fish). It could imply a greater impact on the cod spawning stock because total mortality on

353   larger fish would be proportionately larger than currently estimated. Clearly these are sources of

354   potential bias and uncertainty that merit further investigation.

355   The Lorenzen relationship used to account for other non-fishing mortalities (equation 5) assumes

356   that all non-fishing mortality (including seal predation) is subsumed in the estimate which means

357   that our estimates of seal predation may be biased low. However in fitting the stock assessment

358   model we estimated the constants of the equation which allows the relationship to adjust

359   downward in the presence of seal consumption data. On average, our estimates of natural mortality

360   from the fitted Lorenzen equation were 25% lower than those from calculated the nominal values in

361   Lorenzen (1996) which indicates bias may be accounted for in the model fit.

362   The type II functional response assumed in the projection model implies that the predation rate by

363   seals increases as the partial biomass of cod decreases. This means that for a fixed fishing mortality,

364   if the biomass is in decline, the total mortality rate will increase and accelerate that decline. The

365   converse of this effect is that total mortality will decrease if the cod biomass is increasing and will

366   accelerate any recovery. For the West of Scotland cod, provided fishing mortality can be reduced to

367   a level sufficient to bring about some biomass increase, seal predation should diminish and further

368   aid stock recovery. These effects would be modified in the presence of a numerical response by

369   seals, especially if the distribution of cod became more patchy when total abundance changes.

370   The principal difference between the projection model developed here and those more usually

371   applied to evaluate future stock development is that reductions in fishing mortality rate do not

372   necessarily translate into reduced total mortality acting on the stock. Consequently a random

373   fluctuation producing poor recruitment, for example, could reduce stock biomass and cause an

374   increase in seal predation that negates a reduction in fishing mortality rate. At low stock biomass

375   such effects can increase the risk of further stock decline and predict lower biomass compared to

376   models which assume seal predation rate is constant.

377   The debate about the cod-seal interactions can be polarised with protagonists suggesting that the

378   decline (or lack of recovery) in cod populations is either the result of fishing or that seal predation is

379   responsible. If the "fishing" hypothesis is correct then the obvious solution is to reduce fishing, while

380   if the "seals" hypothesis is true then cod recovery can only occur if predation can be reduced,

381   essentially through a seal cull. From the perspective of the cod, death as a result of fishing or

382   predation is equally unattractive. Its problem is that the total mortality, from whatever source, is

383   high enough to either cause population decline or prevent recovery. Reducing that total mortality

384   can be influenced by human intervention but how that intervention occurs will depend on the

385   relative value of seals, cod and the fishery to society.

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493   Table 1. Fishery data sets used in the assessment model.

Data type	Years
Landings by all fleets	1985-2005
Discards by all fleets	1985-2005
Combined landings and discards (total catch)	2006-2013
Scottish quarter 1 survey	1985-2010
Scottish quarter 4 survey	1996-2009
Irish quarter 1 survey	2003-2013

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496   Table 2. Input quantities for the simulation model drawn from MCMC samples saved after fitting the
497   stock assessment model.

Quantity	Description	Usage
$f_{y,2013}$	Fishing effort multiplier in base year	Reference fishing effort
σ^2_f	Process error on fishing effort	Noise added to fishing effort
$N_{a,2013}$	Population number at age in base year	Base population for projections
N_1,y	Recruitment at age 1 in all years	Estimation of stock-recruitment parameters
SSB_y	Spawning stock biomass in all years	Estimation of stock-recruitment parameters
PB_y	Partial biomass available to seals in all years	Estimation of functional response parameters
$s_{a,2013}$	Fishery selectivity at age in base year	Fixed fishery selectivity for projection
$q_{seal,y}$	Seal predation rate in all years	Estimation of functional response parameters
α, β	Parameters of the seal selectivity curve	Calculation of seal selectivity
A,B	Parameters of the Lorenzen equation	Estimation of natural mortality

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503   **Figure legends**

504   Figure 1. Stock trends in (a) cod spawning stock biomass and (b) fishing mortality from three stock

505   assessments. The solid line is the estimated trend from the most recent ICES assessment in 2014.

506   The dotted line shows the ICES assessment conducted in 2002 and the filled points are the estimates

507   from the current analysis which includes seal predation. Open circles in (a) show the partial biomass

508   available to seals estimated from the model.

509   Figure 2. Relationships for SSB and recruitment, and seal predation rate and partial biomass. (a) The

510   relationship between recruitment and spawning stock with a fitted Beverton-Holt model. (b) The

511   relationship between seal predation rate and cod partial biomass with fitted functional response

512   models. The grey dots are the MCMC samples. The black dots are the mean values of the MCMC

513   samples and the solid line is the type II model fitted to the means to illustrate the form of the

514   function used. The dashed line shows the loess model used in the sensitivity runs.

515   Figure 3. The total mortality (Z) for combinations of fishing mortality (F) and cod partial biomass

516   (PB). The solid lines are contours of equal Z. Over-plotted are the values of Z from the historical

517   estimates of fishing mortality and partial biomass from the stock assessment model joined as a time

518   series with a dotted line. Earlier years are in the top right and recent years in the lower left.

519   Figure 4. The spawning stock biomass projected from 1985 using a type II functional response

520   compared to the observed quantities from the stock assessment model. Lines show the percentiles

521   ranging from 5 to 95% (dashed) from the projection model and points show the estimates from the

522   stock assessment model.

523   Figure 5. The probability that the cod spawning stock biomass is lower than the baseline value in (a)

524   year 5, and (b) year 50, for relative changes in fishing effort and seal population size. Contours show

525   the probability levels. The dot in position (1,1) shows the 2013 state.

526   Figure 6. The median cod spawning stock biomass at equilibrium for relative changes in fishing effort

527   and seal population size. The dot in position (1,1) shows the 2013 state and implies an SSB of around

528   40000 tonnes, higher than the 2013 estimate of about 11000 tonnes as estimated from the current

529   analysis.

530   Figure 7. Comparison of short and long term projections made with a type II functional response

531   (solid line), constant seal predation rate (dashed line), auto-correlated predation rate (dotted line)

532   and "loess" functional response (dots and line) on the probability of stock decline and median SBB.

533   Projections were performed assuming a constant seal population corresponding to the most recent
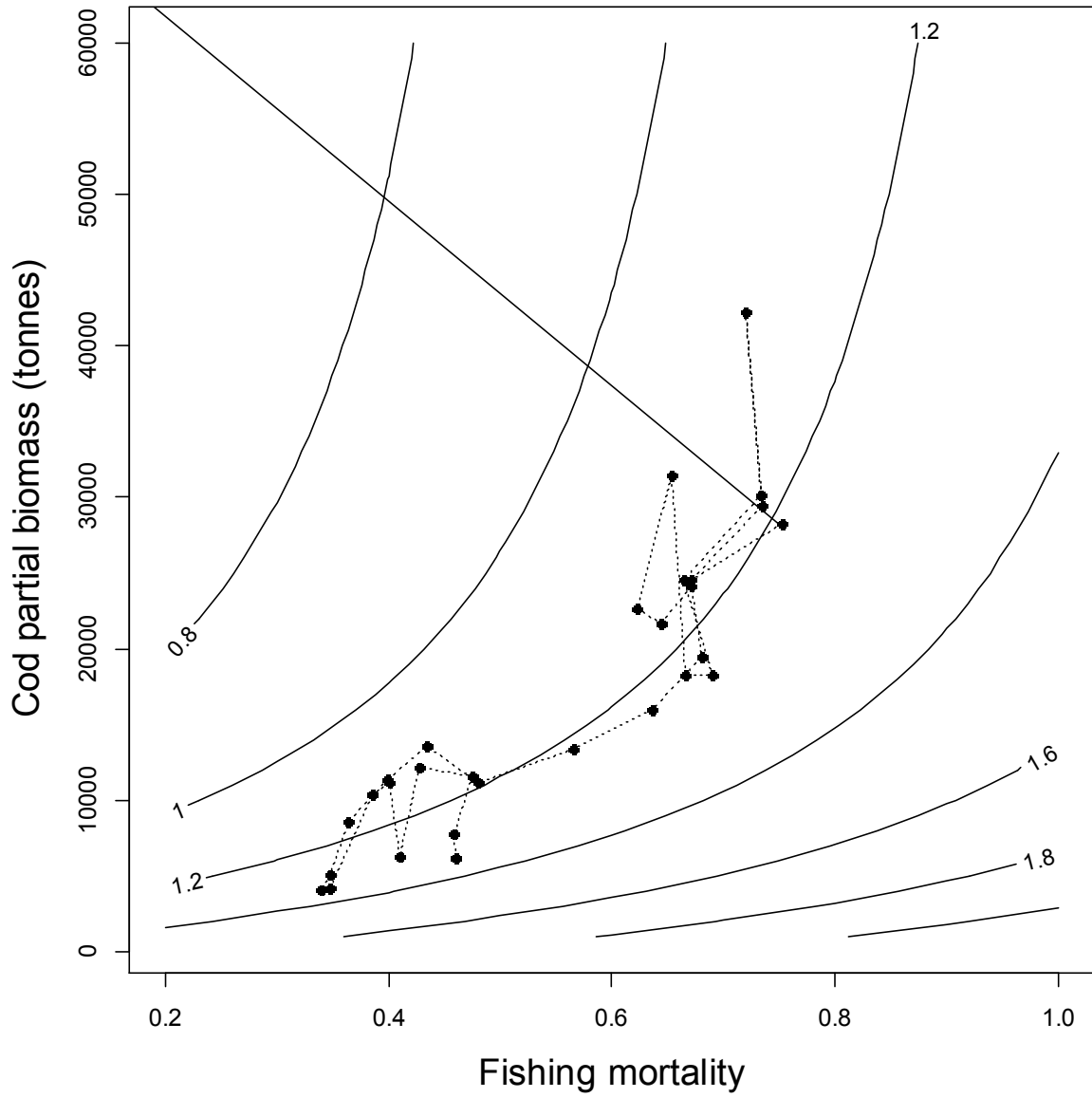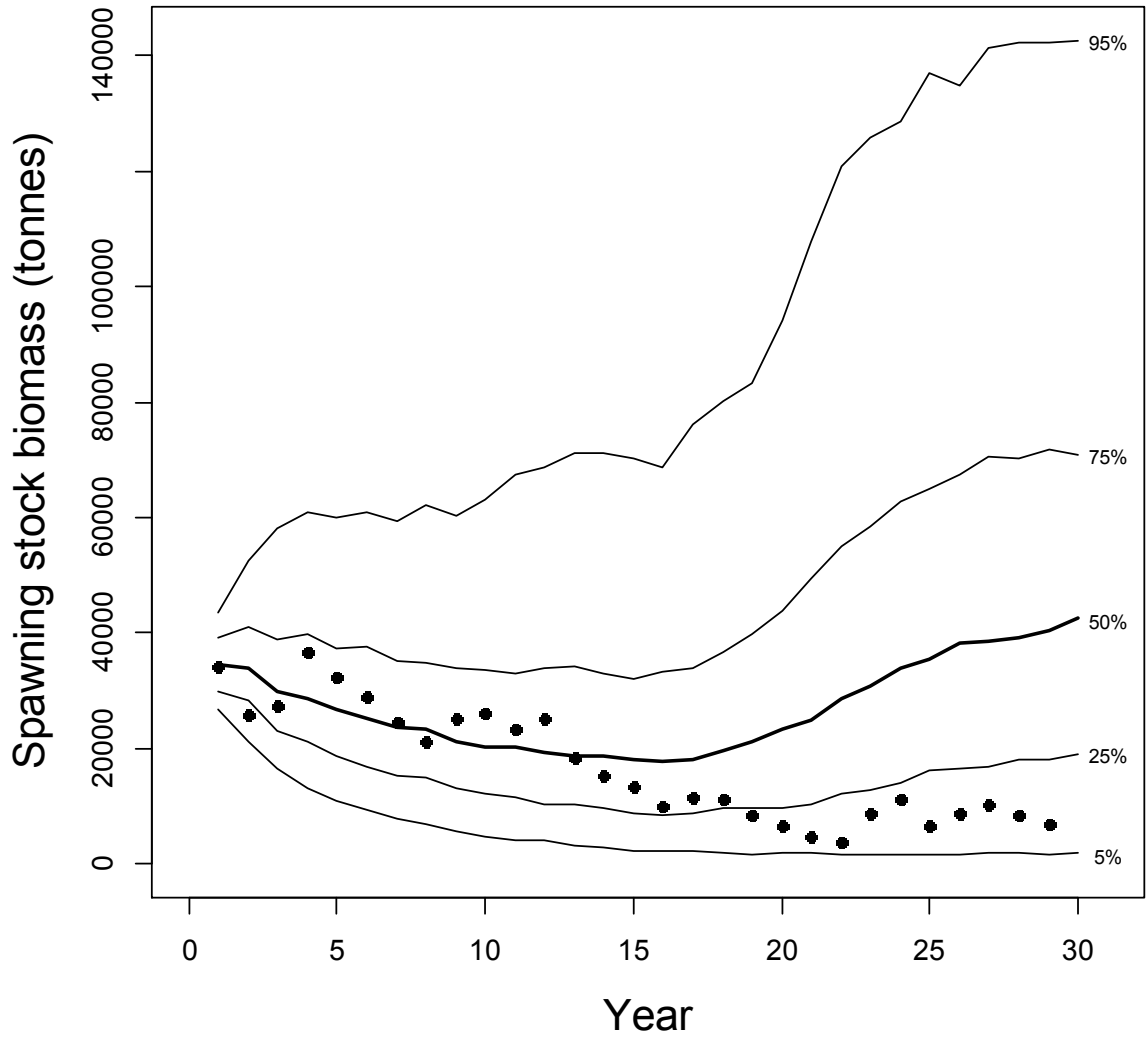
534   population size.

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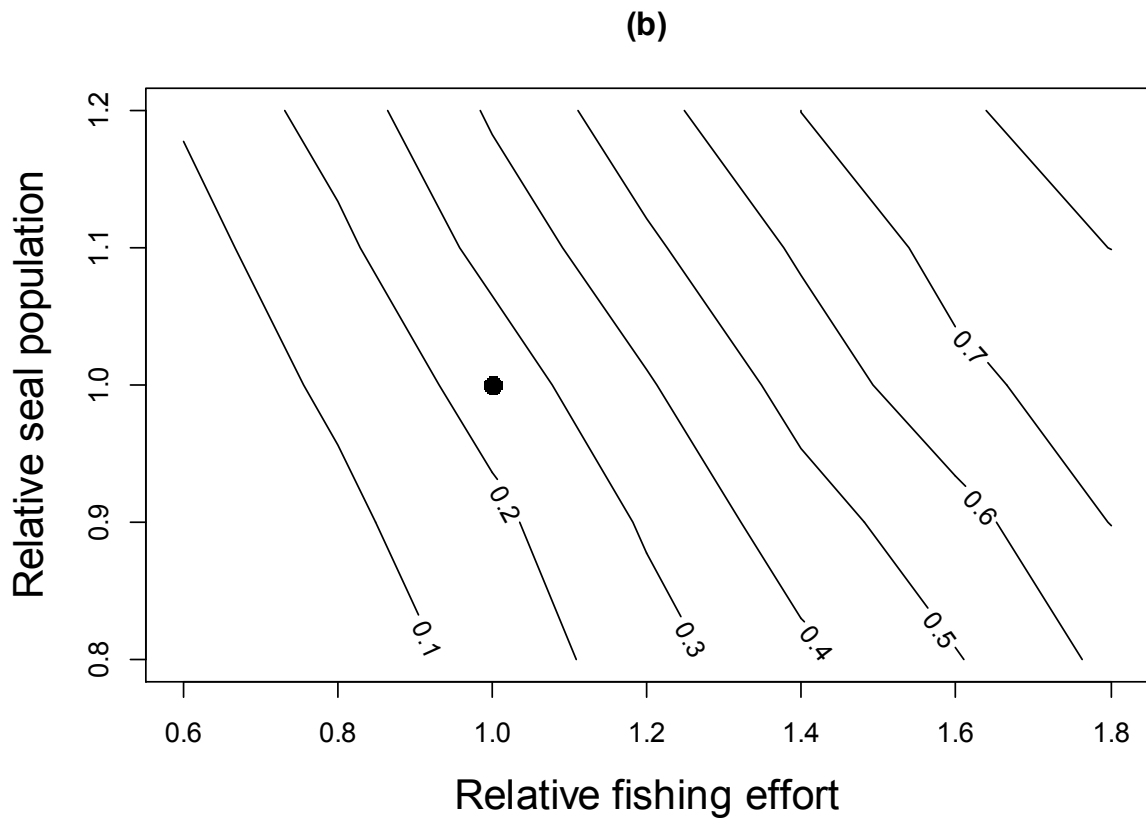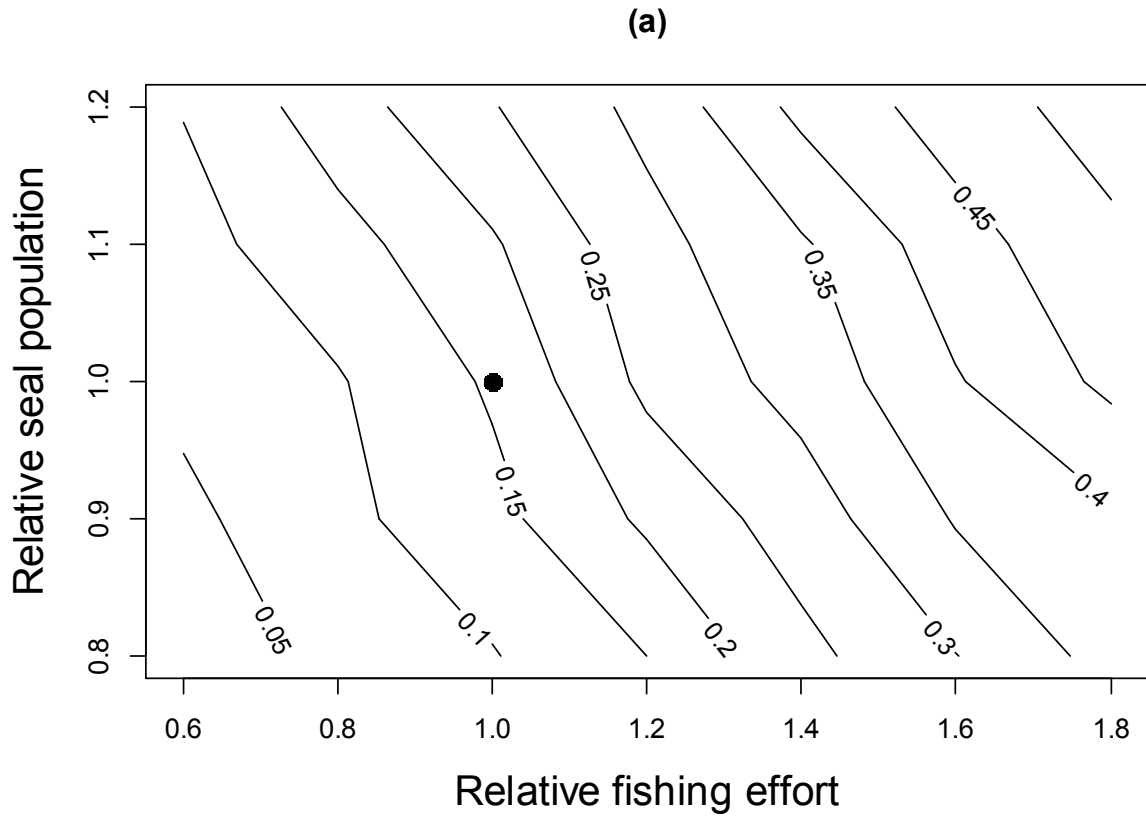537   Figure 1

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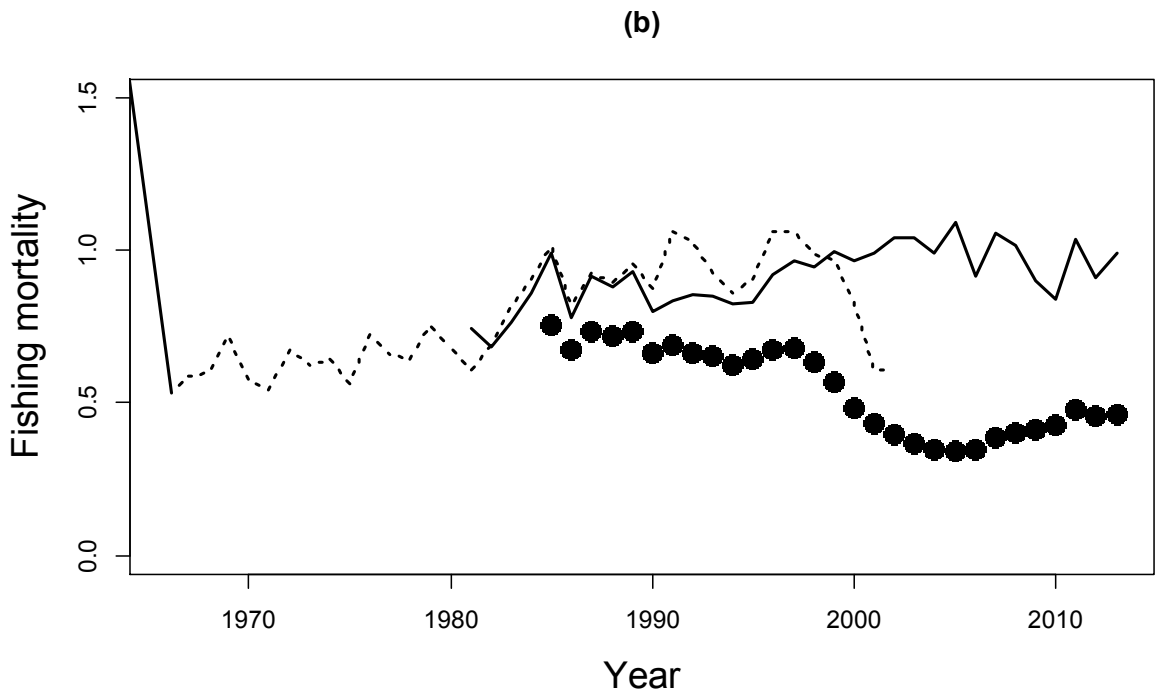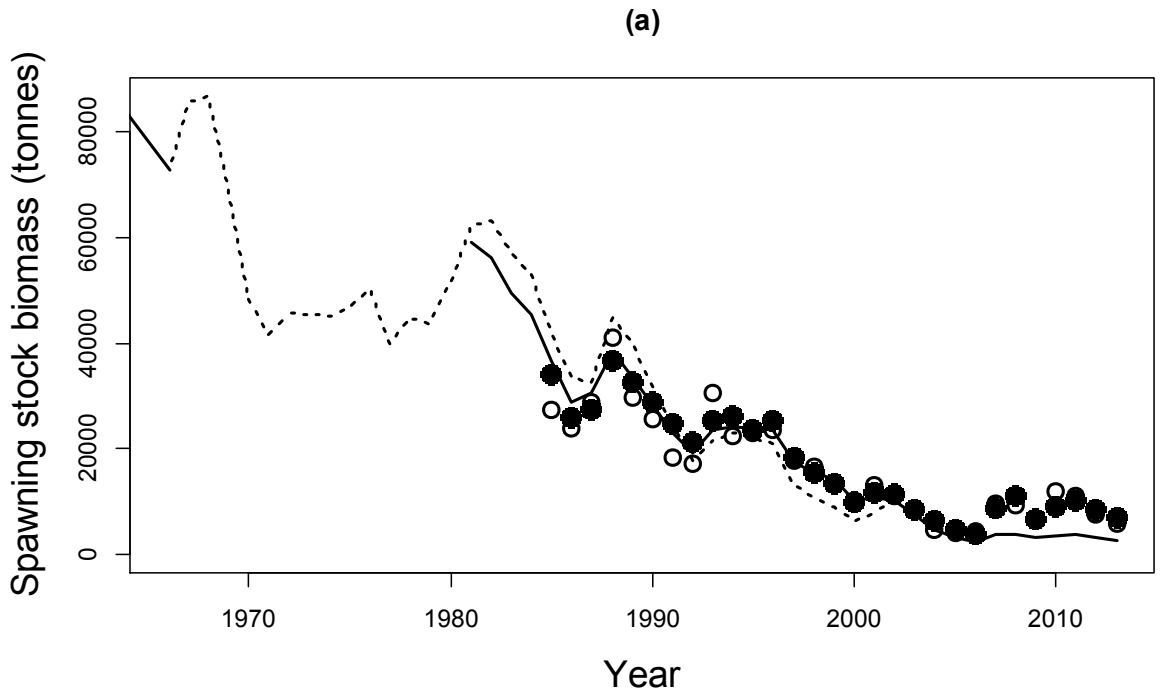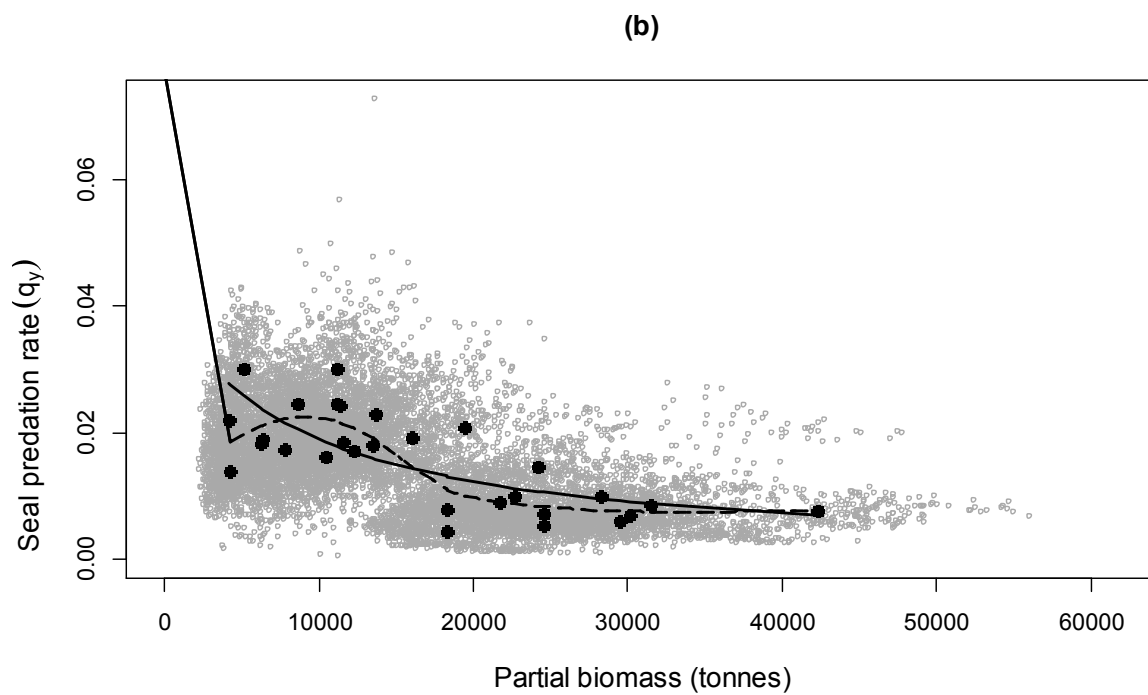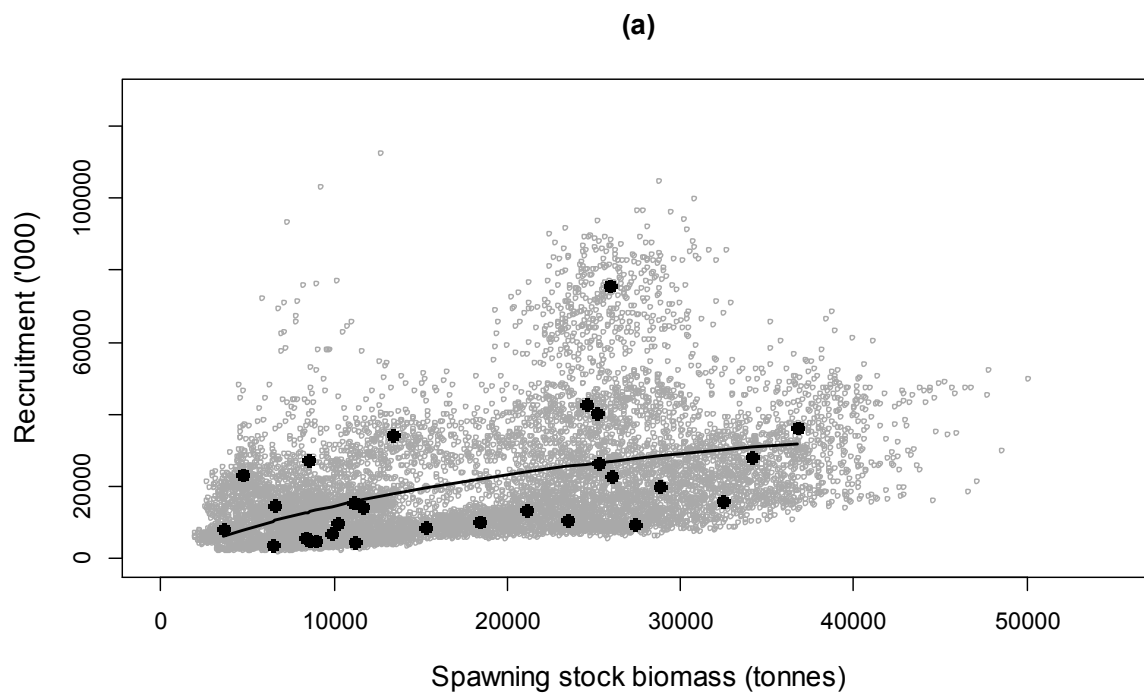
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545   Figure 4

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(a)

(b)

Year 5 Year 50