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Bioeconomic modelling of grey seal predation impacts on the West of Scotland demersal fisheries

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Abstract

The role grey seals have played in the performance of fisheries is controversial and a cause of much debate between fishers and conservationists. Most studies focus on the effects of seal damage to gears or fish and on prey population abundance but little attention is given to the consequences of the latter for the fisheries. We develop a model that quantifies the economic impact of grey seal predation on the West of Scotland demersal fisheries that traditionally targeted cod, haddock and whiting. Three contrasting fishing strategy scenarios are examined to assess impacts on equilibrium fleet revenues under different levels of seal predation. These include status quo fishing mortality (SQF, steady state with constant fishing mortality), open access fishing (bioeconomic equilibrium, BE) and the maximum economic yield (MEY). In all scenarios, cod emerges as the key stock. Large whitefish trawlers are most sensitive to seal predation due to their higher cod revenues but seal impacts are minor at the aggregate fishery level. Scenarios that consider dynamic fleet behaviour also show the greatest effects of seal predation. Results are sensitive to the choice of seal foraging model where a type II functional response increases sensitivity to seal predation. The cost to the fishery for each seal is estimated.

Keywords: seal predation, bioeconomic model, multifleet, mixed species fishery, cod, haddock, whiting, West of Scotland

Introduction

There has long been controversy concerning the potential impact seals have on commercial fisheries (Lambert, 2001; Lavigne, 2003; Read, 2008), especially those where traditionally cod (*Gadus morhua*) formed a large portion of catches or revenues. The precipitous decline of cod stocks in the Northwest Atlantic (Hutchings and Myers, 1994) and the poor state of many cod stocks in the Northeast Atlantic (Fernandes and Cook, 2013) has fuelled arguments that seals have had a detrimental effect on these stocks (Butler et al., 2011; Gruber, 2014). A number of studies have evaluated the predation mortality rate of seal populations on cod both off the Canadian coast (Mohn and Bowen, 1996; Trzcinski et al., 2006; O'Boyle and Sinclair, 2012) and in European waters (Alexander et al., 2015; Cook et al., 2015). These studies primarily consider the dynamics of the resource and the role seal predation may have played in the decline of cod stocks or their failure to recover. Most analyses have concluded that fishing has been the principal cause for stock decline but that seal predation may be an important factor in limiting their recovery.

Regardless of any role seal predation has had on the decline in fish stocks, there is a widely held perception that seals represent direct competition with commercial fisheries and are therefore detrimental to both total revenues and profitability even if the fish stocks themselves are in a sustainable state. An important question that arises is the extent to which fish consumed by seals affects commercial fisheries not only in terms of resource abundance but also on the economic performance of the fisheries. Studies quantifying the economics of depredation, the direct seal-induced damage, on fisheries are numerous but focus on losses due to damage to gears or fish (Bosetti and Pearce, 2003; Cronin et al., 2014; Holma et al., 2014). The economic impacts of grey seal predation on fisheries have rarely been fully examined. Here we focus on the economic impact on the fisheries as a result of changes to the resource dynamics driven by seal predation rather than the issue of the possible role of seals in stock decline or lack of recovery.

The West of Scotland area, which corresponds to ICES (International Council for the Exploration of the Sea) Division 6a (Figure 1), offers an opportunity to investigate the economic impact of grey seal predation using data from seal diet studies carried out in 1985 and 2002 (Hammond et al., 2006; Harris, 2007). These studies have documented the importance of a number of commercially important demersal species in grey seal diets including cod, haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) which are the traditional target species in the mixed demersal fishery. Since the 1980s, the grey seal population has increased in the West of Scotland but has stabilized in recent years at around 30 thousand individuals (Thomas, 2015). Grey seal predation mortality on cod has been estimated for this area (Holmes, 2008; Holmes and Fryer, 2011; Cook et al., 2015; Cook and Trijoulet, 2016) and more recently also on haddock and whiting (Trijoulet et al., 2017). However, these studies only consider the biological impacts of seal predation.

In this study we consider the bioeconomic impact of grey seal predation on the West of Scotland demersal trawl fishery, and in particular UK vessels, as these are responsible for the majority of the whitefish catch in this area taking on average 75% of the combined cod, haddock and whiting landings between 2008 and 2012 (ICES, 2013). There are two principal components to the fisheries: one directed at whitefish with haddock as the main target species and a second directed at Norway lobster, *Nephrops norvegicus,* which takes a bycatch of cod, haddock and whiting (ICES, 2016a). We use an age-structured mixed species multifleet model to evaluate the potential impacts of seal predation on fishing revenues and net profits under various levels of seal predation. Three equilibrium scenarios are considered that enable a comparison of grey seal impacts under alternative fishing strategies or regulations.

Materials and methods

The simulation model

The principal equations governing the resource dynamics and the costs and revenues in the model are presented in Table 1. For stocks with sufficient data, the populations are modelled using conventional age-structured methods (Hilborn and Walters, 1992). Each cohort is subject to a mortality comprising the sum of the fishing (F), natural (M) and seal predation (P) mortalities (equations T1.1 and T1.2). New recruits to the stock are given by a Ricker stock recruitment function (Ricker, 1954) and subject to stochastic process error (equation T1.3). Fishing mortality is decomposed into an age effect representing selectivity (s) and a year/effort effect (E) (Pope and Shepherd, 1982) and is further partitioned by fleet (k) (equation T1.4). Following Cook et al. (2015), seal predation mortality is assumed to be the product of seal selectivity for each age class (sel), seal predation rate (ability of seals to catch fish, q) and the total number of seals (G) (equation T1.5).

For the other fish species with no age-structured data available, a Schaefer surplus production function is used (Schaefer, 1954) following the formulation of Fletcher (1978) (equation T1.6). This describes the stock biomass dynamics in terms of carrying capacity (K) and maximum sustainable yield (msy).

Catches for age-structured stocks are calculated from the Baranov (Baranov, 1918) equation (T1.7) and partitioned into landings and discards (T1.8) while, for other species, landings are approximated directly from the biomass using equation T1.9. This equation corresponds to the Baranov catch equation for biomass assuming $F = Z$ and provides an adequate approximation when F is large compared to M. For these other species, only the landings are modelled because the discard rates are low (Heath and Cook, 2015).

Fleet revenues are obtained by multiplying landings by fish price (T1.10). Fleet costs are estimated following a cost function (T1.11). Variable costs are assumed proportional to fishing effort. Both the variable costs per vessel (c_v) and the fixed costs (c_f) are held constant in the model. The fleet net profits are calculated by taking the difference between fleet revenues and costs (T1.12).

Modelled species and fleets

For simplicity, species, in rank order by value that, along with cod, haddock and whiting, represent over 95% of the revenues of the UK demersal trawlers fishing in Division 6a (STECF, 2016a) were considered in the simulation model. These are saithe (*Pollachius virens*), anglerfish (*Lophius* sp.), megrim (*Lepidorhombus* spp.), European hake (*Merluccius merluccius*), ling (*Molva molva*) and *Nephrops*. Of these species, cod, haddock, whiting, ling and saithe account for the greatest proportion of the grey seal diet (Harris, 2007). However, although the saithe biomass consumed by seals is of a comparable scale to whiting, it is a very small fraction of the saithe stock biomass (ICES, 2015b), while ling accounts for a very small part of the UK commercial catch (ICES, 2016b). Hence seal predation is considered only for cod, haddock and whiting. No trophic interaction is considered between fish species.

Five fleets were selected based on definitions used by ICES (2015a) and are shown in Table 2. The fleets are identified by mesh size and by vessel length class. The "Others" fleet corresponds to all other gears used in UK fisheries in Division 6a and all foreign vessels catching cod, haddock and whiting.

Parameterisation

Age-structured stock dynamics

For cod, haddock and whiting, we used the age-structured stock assessment model described by Trijoulet et al. (2017) to provide estimates of the main input parameters. The model was fitted to the ICES stock assessment data (ICES, 2013) augmented with age compositions in seal diet derived from Harris (2007) and seal population size from Thomas (2013). Outputs from these analyses include a time series of fishing mortality, natural mortality, seal selectivity, seal predation rate, recruitment and spawning stock biomass (SSB) that are provided in Supplementary material.

Other species dynamics

For the other species, those without a full age-based assessment, the Schaefer surplus production model was fitted by least squares to the biomass data from ICES reports (ICES, 2013; ICES, 2014) to obtain values for msy and K (equation T1.6). The landings were treated as known, error free, values. The status quo fishing mortality for these species was estimated using the average biomass and landings between 2007 and 2011 using equation T1.9. No biomass estimates are available for ling and the landings were almost constant over the past ten years. For simplicity we assumed that ling landings scaled linearly with effort. Average landings between 2007 and 2011 were partitioned by fleet and assumed to correspond to an effort index of $E = 1$. Input values for the other species are given in Supplementary material.

Fishing selectivity by fleet

Fleet specific catch data were used to partition the fishing mortality at age by fleet for the age-structured stocks. Total fishing mortality for the other species was partitioned down to fleet level by using the proportion of the fleet catch in the total catch. This is described in more detail in the Supplementary material.

Economic parameters

Cost and revenue data for the years 2007 to 2011 for the four UK fleets were made available by the UK agency Seafish, and were corrected for inflation using the gross domestic product deflator with 2012 as the reference year. Economic data are usually aggregated for the North Sea and the West of Scotland (Anderson et al., 2013), so for this study, the West of Scotland data have been extracted by identifying the vessels that spend the majority of their time in Division 6a. Here, it is assumed that costs incurred due to fuel, crew share and other fishing costs are variable and that total vessel outlay, depreciation, interest and other financing expenses are fixed costs. Variable and fixed costs values used in the simulation model were averages over 2007-2011 to be consistent with the reference period used for the fish stock values.

No cost data are available for the "Others" fleet. We assumed that this fleet was operating at the break-even point during the reference period 2007-2011 and used the revenues to estimate the costs. Within the UK fleets, average fixed costs per vessel are typically around half of the average variable costs. The total aggregated costs for "Others" was scaled to the number of vessels (all assumed foreign vessels), and partitioned using this ratio. The costs and the number of vessels for all fleets are summarised in Table 2.

The price of fish in the West of Scotland is dictated by the European market (Scottish Fishermen's Organisation, 2016) which means a change in the quantity of local landings has little effect on fish prices. As a result, the fish prices are assumed to be constant for each species in the simulation model. They correspond to fixed average real prices between 2007 and 2011 taken from Marine Management Organisation (2012) and are shown in Table 3 .

Equilibrium fishing scenarios

Modelling regulations and fisher choices in the West of Scotland is complex. For simplicity we chose to run the simulation model under equilibrium scenarios which correspond to three different fishing or regulation strategies. This allows the comparison of grey seal impacts in contrasting scenarios to test the sensitivity of the results. The three scenarios "status quo F (SQF)", "bioeconomic equilibrium (BE)" and "maximum economic yield (MEY)" are outlined below. All the scenarios consider the impact of seal predation on fishing revenues and profitability under biological equilibrium conditions when the nine species considered show no change in mean SSB. The results presented are averages from the process error around recruitment over 50 years when SSB is at equilibrium.

The SQF scenario keeps the fishing mortality at the base level constant (i.e. $E = 1$). It results in a biological equilibrium that assumes fleet behaviour does not respond to economic incentives. This scenario serves as a reference case for comparison with the other scenarios where fleet behaviour is dynamic and varies with the fleet net profit.

The BE scenario assesses the impact of seal predation in the extreme open-access case where no regulation exists and vessels can enter or exit the fishery freely. Classical economic theory shows that, in this environment, fishers act independently and try to maximise their individual profit so that, in the long-term, the fishery tends to the bioeconomic equilibrium where total revenues equal total costs (Knowler, 2002). In this scenario, each UK fleet can invest or disinvest in effort or number of vessels following the value of its net profit. Given the value of the fleet net profit at the initial biological equilibrium (equation T1.12), fishing effort is adjusted and the model run to the new biological equilibrium. This process is then repeated until the BE is reached. It is assumed that higher net profit will lead to larger investment in the number of vessels and effort per fleet.

The MEY scenario represents the economic equilibrium assuming the fishery is closed to new entrants and the fleet composition is fixed. The fleets are assumed to collaborate to obtain a sustainable fishery where the aggregated fishery net profit is maximised at the equilibrium

(Guillen et al., 2013). The goal is to determine the level of effort per fleet which maximises the total fishery net profit.

Because the cost function for the "Others" fleet is uncertain due to the lack of economic data for this fleet, its effort is kept constant in both the BE and MEY models so the fleet cannot modify its fishing behaviour with its net profit. Additional information on scenarios is given in Supplementary material.

Seal predation scenarios

Fleet revenues were compared at different levels of seal predation mortality (P). Scaling factors of 0.7-1.3 in steps of 0.1 were applied to the equation for P (equation T1.5) in the three equilibrium scenarios. The scale range is limited to ±30% to avoid unrealistic departures from the current state. Assuming seal selectivity (sel) and predation rate (q) are more or less constant, applying a scaling factor to P corresponds to a change in seal population (G). In this study, the predation rate is assumed constant by default for all scenarios. However, q may be time varying especially if it is related to prey abundance such as in a functional response (Holling, 1959) and this is considered in the sensitivity analysis described below.

In order to quantify the impact of a single seal on the fishery and on the fleet most affected by seal predation, we calculated the change in revenue per seal and the change in revenue per vessel when seal predation is changed by 10%. The change in revenue per seal is calculated as the difference between fishing revenues at the baseline number of seals and at increased/decreased seal predation, divided by the number of seals that represents 10% of the population.

In order to allow comparison with fleet revenues, the weight of fish consumed by seals was converted to equivalent "revenues" by multiplying it with fish prices.

Consistency check and sensitivity analysis

The main parameters of the model are derived from the average state of the fishery between 2007 and 2011. As a check for consistency, the landings for this period were estimated by the model using mean population sizes from stock assessments for the same period. The estimated landings were then compared to observed values and shown to be consistent (Supplementary material).

Sensitivity to the different assumptions in the simulation model was tested as follows:

1. The model was run for two other commonly used stock-recruitment relationships to test robustness to the choice of curve. These were Beverton and Holt (1957) and the smooth hockey-stick (Froese, 2008).
2. The parameter estimates of the Schaefer surplus production function msy and K (equation T1.6) were increased separately by 10% for all species to investigate estimation errors.
3. A type II functional response of seals to cod biomass was applied as an alternative foraging model to the constant predation rate assumption. This was based on the cod partial biomass as described in Cook and Trijoulet (2016). This response is not considered for haddock and whiting due to difficulties fitting a type II functional response (Trijoulet, 2016).
4. The BE and MEY scenarios are run allowing the fleet "Others" to vary its effort at each iteration with its net profit to test the assumption of constant effort.
5. A SQF scenario was run in the absence of cod to examine the sensitivity of the results to the species composition in the fishery in the event of a cod stock collapse (Cook and Trijoulet, 2016).

The sensitivity of the simulation model to seal predation was analysed by calculating the difference in change in fishing revenues when the seal population is increased by 10% between the initial model set up and when the sensitivity tests 1 to 5 are applied. For simplicity, results for sensitivity tests 1-4 are shown for the fleet most affected by seal predation only.

Results

Bioeconomic results

Changes to SSB in the three scenarios resulting from different levels of seal predation are shown in Figure 2. Cod is the most sensitive to a change in grey seal numbers followed by whiting. The estimated equilibrium haddock SSB is little changed in all three scenarios even for large changes in seal population.

The change in revenues and net profit at different levels of seal population is shown in Figure 3. Larger whitefish vessels (TR1>24) are most affected by a change in grey seal population in all scenarios. For this fleet, in the dynamic scenarios (BE and MEY), the percentage change in revenues is much larger than the change in seal population. The smaller whitefish fleet (TR1_10-24) and the "Others" fleet are less affected. As expected, the *Nephrops* trawlers show little change since cod, haddock and whiting represent a very low proportion of their revenues. Although individual fleets show large changes in revenues, when the whole fishery is considered, changes in seal predation of ±30% result in about 5% changes in revenue. This arises because *Nephrops* have a high value relative to other stocks and are unaffected by seal predation in the model.

The MEY equilibrium is the only scenario where profits respond to seal predation. Here, the changes in net profit with seal predation are similar to the changes in revenues for all fleets except TR1>24, where the impact on the net profit is less than on the revenues (Figure 3).

The value of the quantity of fish eaten by seals was compared to fleet revenues for the current number of seals in the Division 6a (Table 4). When revenues from cod, haddock and whiting are compared (Table 4a), seal ”revenues” only represent a small proportion (less than 0.5 %) of the total revenues and this proportion is considerably smaller than the proportion for the whitefish fleets. Note that seal revenues of cod, haddock and whiting can be larger than those of the TR2<10 fleet, but this arises because the fleet catches mainly *Nephrops* (Figure S.2). When seal revenues are compared to fleet revenues for all fish species combined (Table 4b), the value of seal predation is negligible since it represents less than 2% of each fleet revenue.

Table 5 shows the change in annual fishing revenues for a 10% change in seal population for the entire fishery and the TR1>24 fleet. Also shown is the “cost” per seal to the fishery or fleet. The results are of the same order of magnitude for all scenarios. For the TR1>24 fleet, the cost per seal is less than that for the fishery in all but one case but the cost per vessel is large as the losses are distributed among few vessels. For the whole fishery, the costs per vessel are lowest in the BE scenario because the *Nephrops* fleets expand to dissipate the profits. In contrast, for TR1>24, the costs per vessel are highest under this scenario (BE) because some vessels exit the fishery.

Sensitivity analysis

Table 6 shows the changes in grey seal impacts on TR1>24 for the different sensitivity scenarios. The three fishery scenarios show little change for all sensitivity tests except for the seal foraging model. Here a type II functional response for cod has a large effect. Overall, the dynamic scenarios show greater sensitivity than the SQF scenario.

The impact of grey seals on all fleet revenues and therefore the whole fishery is substantially reduced if the cod stock collapses (Figure 4). Even reducing the seal population by 30% only increases the revenues of TR1>24, the most affected fleet, by less than 3%.

Discussion

In the model, an increase in grey seal predation resulted in a clear decrease in the cod and whiting stocks. However, even large changes in grey seal predation have little impact on the haddock biomass. This is partly because the predation mortality on haddock is low compared to fishing mortality and also because seals show very low selectivity on the younger ages which contribute most to the stock biomass. This study suggests that the impact of seal predation on the haddock stock is likely to be low.

Cod is the key stock in evaluating the impacts of seal predation on the demersal fishery. Seal predation mortalities are much greater on cod than haddock and whiting (Trijoulet et al., 2017) so seal predation effects are more substantial for this stock. In addition, the price per tonne of cod is roughly twice that of haddock and whiting, so cod make a proportionately larger contribution to the revenues.

The three scenarios, SQF, BE and MEY, represent very different fishing strategies but a clear pattern emerges that the larger whitefish trawlers (TR1>24) are most sensitive to the effects of seal predation (mainly on revenues, less so on profits) and that this is largely due to revenues accruing from cod. In the scenario where the cod stock has collapsed, although the TR1>24 fleet still shows the greatest effects of seal predation, the impact is substantially reduced.

For the TR1_10-24 fleet, whitefish are a principal target, yet *Nephrops* makes a significant contribution to the catches. As *Nephrops* is nearly twice as valuable as cod, the revenues of this fleet are less sensitive to cod biomass and any seal predation on it. Not surprisingly, the TR2 fleets that target *Nephrops* are little affected by seal predation. Overall, the value of fish caught by seals is low in comparison to the fleet revenues and seal predation impacts are relatively small at the level of the whole fishery because *Nephrops* dominates the value of the total landings.

We chose a number of fishing scenarios to explore whether seal predation effects were sensitive to contrasting fleet behaviour. While none represent the current fishery accurately they show similar effects that may characterise, qualitatively, what may occur in reality. The SQF scenario shows the smallest effects of predation while both the BE and MEY scenarios show substantially greater sensitivity to seals. Both of these scenarios allow vessels to adapt their fishing strategy in response to economic incentives and such behaviour appears to magnify the effects of seal predation. Current estimates of the economic performance of the fleets suggest that they are operating close to BE (Lawrence et al., 2016), a scenario which heightens sensitivity to seal predation compared to SQF and reduces it compared to MEY. However, the magnitude of the change in revenues due to increased seal predation is much more sensitive to the population model assumptions (stock recruitment function, seal functional response, etc.) in the dynamic fishing scenarios. The results of the BE and MEY scenarios should therefore be treated as more uncertain than when fishing at SQF.

For all scenarios, a small change in grey seal population of ±10% did not show substantial variations in fleet revenues and the results appear relatively robust to most model assumptions, with the possible exception of seal functional response to cod biomass. The type II functional response results show that an alternative seal foraging model may alter the results significantly. The effect of the response is to accelerate decline when stocks are already declining and similarly accelerate increase when stock are increasing. Inevitably this will contribute to greater sensitivity to seal predation as the effect is inversely density dependent. This highlights the need for a more realistic seal foraging model.

Depredation and seal-induced infections are a different source of impact that would need to be added to predation effects to get a more complete estimate of the economic effects of seals. There have been a number of studies estimating the cost of seal-induced infections and depredation. These give an annual cost between £300 and £4,800 per fisher or processor (Bjørge et al., 1981; Bosetti and Pearce, 2003; Butler et al., 2011) and a corresponding cost per seal between £15 and £290. Given the estimates of cost of seal predation in the West of Scotland from this study, it would suggest the costs including depredation could be as high as £700 per seal.

Although seals may represent a cost to the fishery, they may support positive benefits to the economy from activities such as ecotourism. Grey seals are the third most popular wildlife attraction in Scotland after cetaceans and seabirds (Woods-Ballard et al., 2003). In the West of Scotland, tourism gains from whale and seal-watching have been estimated at around £1.8 million in 2001 and the indirect income from other tourism attractions during the visitor stay can reach £7.8 million per year (Warburton et al., 2001). Consequently it can be argued that even if grey seals represent only a portion of these gains, grey seal presence may be more beneficial than harmful to the Scottish economy. However, these gains do not benefit the fishers that suffer the costs.

Our model does not consider predatory interactions other than that of seals on three major species. Seabirds and cetaceans are also responsible for removal of large quantities of commercial fish (Overholtz and Link, 2007) and the largest predation on demersal fish comes from predatory fish themselves (Sparholt, 1994; Engelhard et al., 2014). Incorporating trophic interactions is likely to have a minor effect on the estimated direction of change seen from the model given that this study investigates the sensitivity to seal predation under average conditions. The results describe the relative impacts of seal predation on the different fleets under various exploitation scenarios rather than predict actual revenues and profit in the long-term.

There are a number of additional reasons for treating the results presented here with caution. Seal predation mortality was estimated using only two years of seal diet data (Harris, 2007) that are themselves highly uncertain. This should not have a major impact on the qualitative impact of seals on the different fleets and fish stocks but may cause uncertainty in its magnitude. In addition, this study also makes the assumption that the fish population is homogeneous and equally available to seals and fishers which are in direct competition with each other. Currently the majority of cod landings are taken in the far north of Division 6.a and along the continental shelf edge (STECF, 2016b) while seal foraging mostly occurs on the continental shelf (Jones et al., 2015) including areas considered unsuitable for trawl fishing (Marine Environmental Mapping Programme, 2015). Seals may therefore predate on fish which are not directly available to fishers and although the absence of overlap between fishing and foraging zones does not mean the absence of competition, the interaction between seals and fishers is likely to be more complex than assumed here. This has potential to bias resulting model estimates and is an issue that requires further investigation.

Conclusion

Overall, seal predation effects on revenues are small at the whole fishery scale. The TR1>24 fleet is the most sensitive to seal predation, and this is primarily due to the importance of cod in its catch. It seems, therefore that the importance of the seal-fishery interaction in the West of Scotland is limited to one major fleet and stock. However, assessing the significance of this interaction is heavily dependent on the assumption of the seal foraging model and is an area in need of further research.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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Tables

Table 1: Equations used in the simulation model.

Number	Name	Equation	Comments
(T1.1)	Fish abundance at age a and year y for species i	$N_{a,y,i} = N_{a-1,y-1,i}e^{-Z_{a-1,i}}$	Exponential decay for cod, haddock, whiting and saithe
(T1.2)	Total mortality	$Z_{a,i} = M_{a,i} + F_{a,i} + P_{a,i}$	M is the natural mortality. $P = 0$ for saithe
(T1.3)	Recruitment at age 1	$N_{1,y,i} = \left(\alpha_i SSB_{y-1,i}e^{-\beta_i SSB_{y-1,i}}\right)e^{\varepsilon_i}$	Ricker curve with lognormal process errors, $\varepsilon_i \sim Normal(0, \sigma^2)$. The SSB is given by $SSB_{y,i} = \sum_a \left(N_{a,y,i}m_{a,i}w_{a,i}\right)$, where m is the proportion of mature fish and w the fish weight.
(T1.4)	Fishing mortality for fleet k	$F_{a,i,k} = s_{a,i,k}E_k$	Product of fleet selectivity s and effort index E
(T1.5)	Seal predation mortality	$P_{a,i} = sel_{a,i}q_iG$	Product of seal selectivity sel, seal predation rate q and seal number G
(T1.6)	Biomass for the other fish species	$B_{y+1,i} = B_{y,i} + \frac{4msy_i}{K_i}B_{y,i}\left(1 - \frac{B_{y,i}}{K_i}\right) - L_{y,i}$	Schaefer model where msy is the maximum sustainable yield and K the carrying capacity
(T1.7)	Fishing catches	$C_{a,y,i,k} = \frac{F_{a,i,k}}{Z_{a,i}}N_{a,y,i}(1 - e^{-Z_{a,i}})$	Baranov equation. Catches by seals are calculated by replacing F by P in T1.7

(T1.8)	Landings for age-structured stocks	$L_{y,i,k} = \sum_a \lambda_{a,i,k} C_{a,y,i,k}$	λ is the proportion of landings in the total catch
(T1.9)	Landings for the other species	$L_{y,i,k} = (1 - e^{-F_{i,k}}) B_{y,i}$	Baranov equation for biomass assuming $F = Z$
(T1.10)	Fishing revenues	$R_{y,k} = \sum_i (p_i \, L_{y,i,k})$	Product of fish landings and price p
(T1.11)	Fleet total cost c_*	$c_{*_k} = v(c_{v_k} + c_{f_k})$	Sum of the variable costs c_v and the fixed costs c_f per vessel multiplied by the number of vessels v. The variable costs are proportional to fleet effort using a constant ρ such as $c_{v_k} = \rho_k E_k$
(T1.12)	Fleet net profit	$\pi_{y,k} = R_{y,k} - c_{*_k}$	

Table 2: Fleets considered in the simulation model and their characteristics. The number of vessels and their associated annual costs per vessel are mean values for the years 2007-2011 obtained from Seafish.

Fleet code	Definition	Vessel length (m)	Net mesh size (mm)	Target species	Number of vessels	Variable costs (£'000)	Fixed costs (£'000)
TR1_10-24	Small UK whitefish trawlers	10-24	≥120	Demersal whitefish	9	430.5	213.0
TR1>24	Large UK whitefish trawlers	≥24	≥120	Demersal whitefish	10	1,250.8	467.3
TR2<10	Small UK *Nephrops* trawlers	<10	70-99	*Nephrops*	31	47.6	27.0
TR2_10-24	Large UK *Nephrops* trawlers	10-24	70-99	*Nephrops*	151	137.7	73.0
Others	Other gear and foreign vessels	All	All	Demersal whitefish, *Nephrops*	19	1,236.3	618.1

Table 3. Average fish price (p) per tonne (2007-2011) for the nine fish species considered in the simulation model and proportion of the total catch made by the UK vessels for indication.

Species	p (£'000)	% of total catch by UK vessels
Cod	2.1	53
Haddock	1.2	76
Whiting	1.1	74
Saithe	0.8	43
Anglerfish	3.2	33
Megrim	3.0	54
Hake	1.9	26
Ling	1.4	32
Nephrops	2.9	99

Table 4: Comparison of fleet and seal revenues from cod, haddock and whiting with that for seals under the three scenarios and at the baseline number of seals. The weight of fish consumed by seals is converted to seal "revenue" using fish price.

a. Revenue of cod, haddock and whiting by fleet expressed as a proportion (%) of the total cod, haddock and whiting revenue from all fleets including revenue from consumption by seals.

Scenario	TR1_10-24	TR1>24	TR2<10	TR2_10-24	Others	Seals
SQF	12.90	54.81	0.07	5.23	26.70	0.29
BE	50.24	26.78	0.91	0.87	20.99	0.21
MEY	20.99	23.60	0.10	7.07	47.79	0.45

b. Revenue of cod, haddock and whiting taken by seals expressed as a proportion (%) of the total fleet revenue including all species.

Scenario	TR1_10-24	TR1>24	TR2<10	TR2_10-24	Others
SQF	0.46	0.19	1.22	0.10	0.10
BE	0.12	0.29	0.08	0.55	0.10
MEY	0.56	0.80	1.72	0.15	0.13

Table 5: Change in annual fishing revenues (£'000) for the fishery and for TR1>24 following an increase or decrease in seal population of 10% (3,204 individuals). The change is given at the level of the whole fishery or fleet, per vessel and per seal.

Seal scenario	Equilibrium scenario	Fishery			TR1>24		
		Whole	Per vessel	Per seal	Whole	Per vessel	Per seal
+10%	SQF	-1,350	-6.13	-0.421	-715	-71.54	-0.223
	BE	-1,618	-2.69	-0.505	-1,289	-257.83	-0.402
	MEY	-1,405	-6.39	-0.439	-903	-90.25	-0.282
-10%	SQF	1,414	6.43	0.441	763	76.32	0.238
	BE	1,456	2.41	0.454	1,541	220.21	0.481
	MEY	1,601	7.28	0.500	1,165	116.46	0.363

Table 6: Sensitivity of the three scenarios expressed as the change in seal impacts on TR1>24 revenues (%) for an increase in seal population of 10%. The change in impacts is calculated by taking the difference between changes in revenues for the initial simulation results and changes in revenues for the sensitivity test results. For instance, a value of 4.1 (BE scenario, sensitivity test 1) means that seal impacts on the fleet revenues are increased by 4.1% when a Beverton-Holt stock recruitment relationship is used compared to a Ricker relationship.

Sensitivity test	Sensitivity to the	Change considered	SQF	BE	MEY
1	Ricker stock-recruitment model	Beverton-Holt	0.0	4.1	0.0
		Hockey-stick	-0.1	2.5	3.5
2	Schaefer parameters	$msy + 10\%$	-0.2	-0.1	-6.2
		$K + 10\%$	0.0	5.0	0.6
3	Constant seal predation rate	Type II seal functional response to cod biomass	10.7	23.7	10.7
4	Constant effort for "Others"	Effort can vary with fleet net profit	None	-0.6	-2.5

Figures

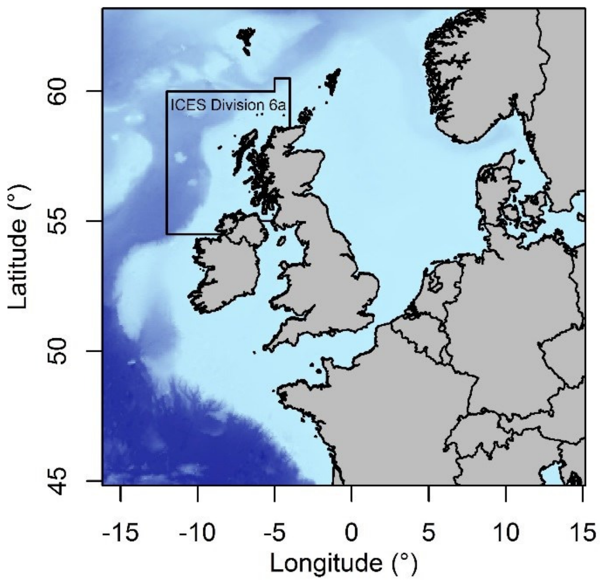
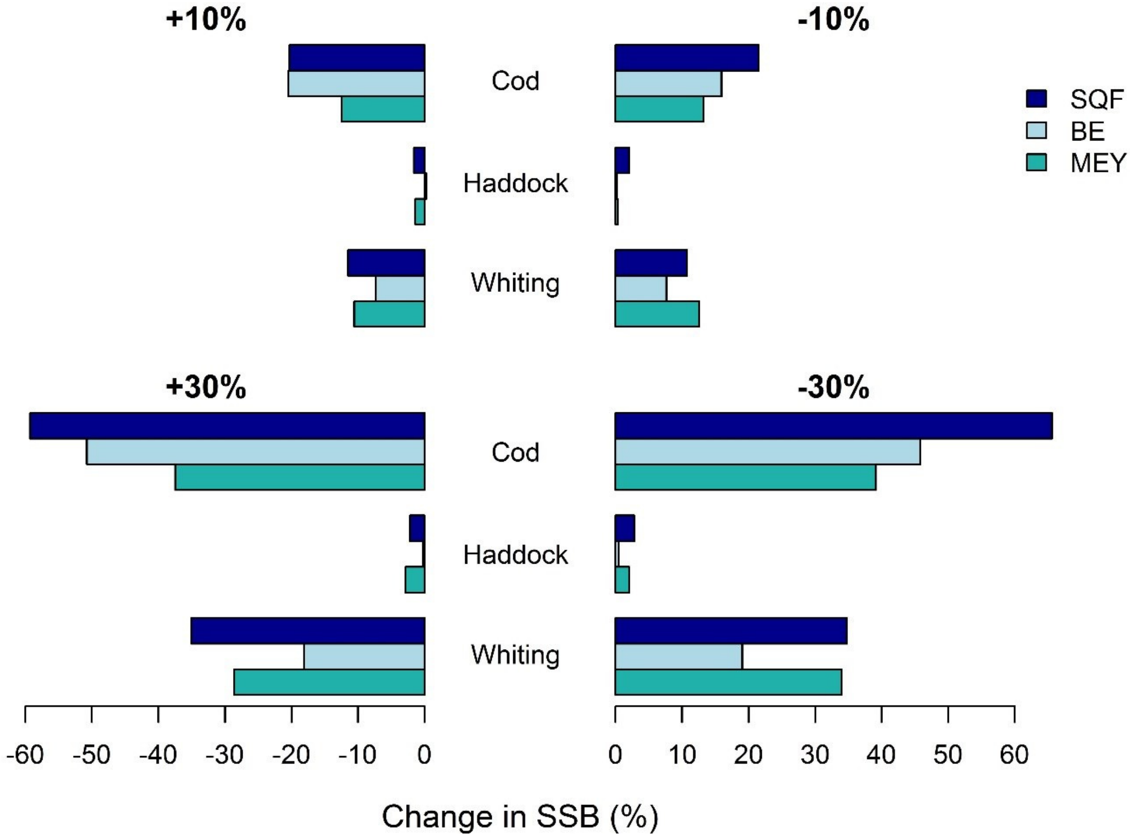


Figure 1: Map showing ICES Division 6a; the study area. Bathymetry data taken from Amante and Eakins (2009).



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547 Figure 2: Change in mean equilibrium SSB (%) for cod, haddock and whiting in the three
548 different scenarios for small (±10%) and large (±30%) changes in seal population.

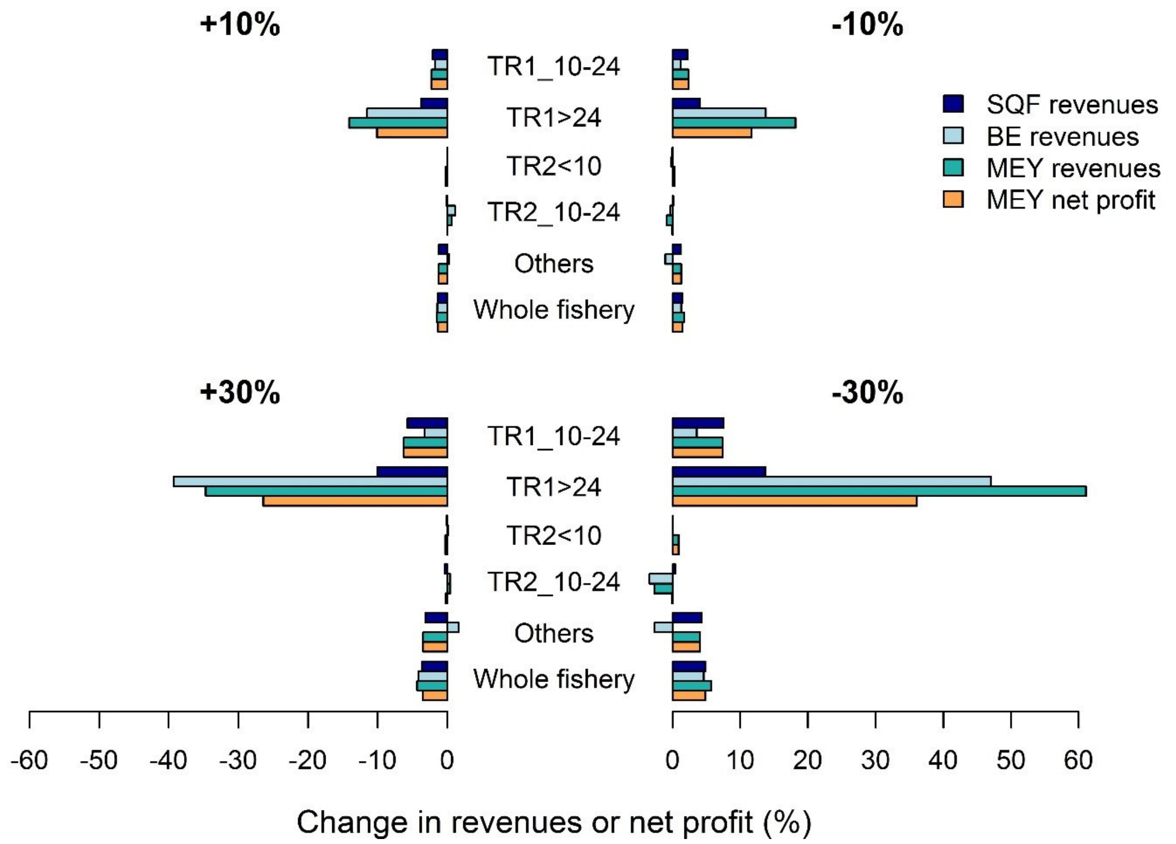

Figure 3: Change in mean equilibrium revenues (%) or net profit (MEY scenario only) by fleet and for the entire fishery in the three different equilibrium scenarios for small (±10%) and large (±30%) changes in seal population.

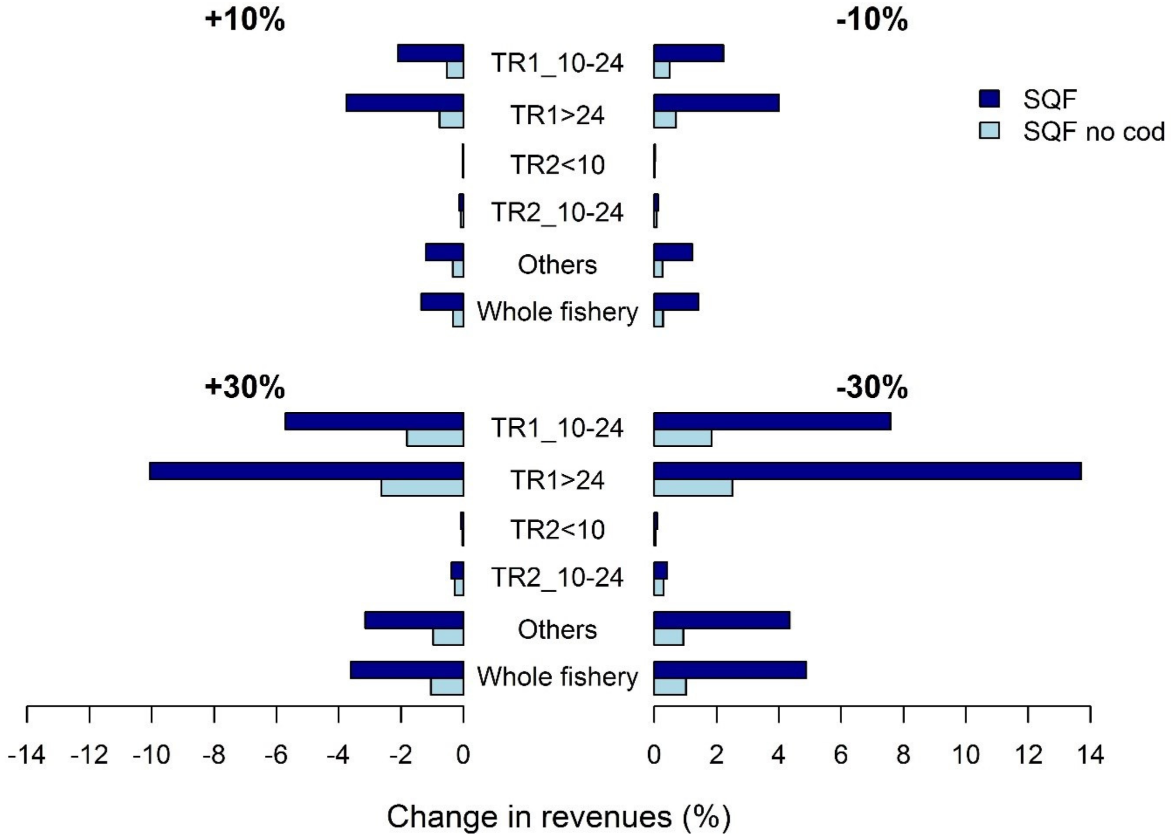

Figure 4: Change in revenues (%) by fleet and for the entire fishery for a small (10%) and large (30%) change in seal population in the initial SQF scenario and for the SQF scenario in the absence of cod.

Supplementary material: Inputs of the simulation model, methods used to partition fishing mortality into fleets, characteristics of the equilibrium scenarios and model consistency check

A. Inputs of the simulation model

For the age-structured stocks (cod, haddock, whiting and saithe), age specific fishing mortality, averaged over the years 2007-2011, was used as an estimate of status quo F with an assumed relative effort index, $E = 1$. This value of F at age effectively defines selectivity at age (s) (Table S.1). It was partitioned into fleets using the ratio of the fleet catch to the total catch (see part B). Natural mortality and seal selectivity were obtained directly from the stock assessment outputs. For seal predation rate (q), an average of the values estimated for the two years 1985 and 2002 when seal diet data were available was used (Table S.2). Ricker stock recruitment parameters were obtained by fitting the function to the log recruitment and SSB values by least squares. The residual variance after fitting the model was used to characterise recruitment process error. In the case of saithe, input parameter values were taken from the ICES assessment (ICES, 2013c).

For the other fish species, data from the literature were used to estimate the Schaefer parameters given in Table S.2. The landings from Division 6a, when not available in the reports, were taken from the ICES online databases (ICES, 2011; ICES, 2015a). For megrim and hake, ICES estimates of biomass are available only for a larger management area (ICES, 2013a; ICES, 2014), so for these species the biomass for the entire stock was scaled to the biomass in Division 6a by applying the proportion of the landings in 6a to the total landings for the area. For *Nephrops*, the biomass was estimated for each functional unit by multiplying population abundance by the mean weight of an individual in the landings and was then summed over all the functional units (ICES, 2013a).

Table S.1: Age-structured inputs for the simulation model.

Species	Age	Natural mortality (M)	Seal selectivity (sel)	Fleet selectivity (s)				
				TR1_10-24	TR1>24	TR2<10	TR2_10-24	Others
Cod	1	0.595	0.101	0.000	0.002	0.003	0.077	0.002
	2	0.341	0.917	0.019	0.089	0.004	0.115	0.022
	3	0.275	0.873	0.066	0.309	0.000	0.013	0.028
	4	0.235	0.483	0.066	0.311	0.000	0.002	0.100
	5	0.203	0.234	0.037	0.173	0.000	0.002	0.126
	6	0.197	0.129	0.021	0.099	0.000	0.000	0.083
	7+	0.181	0.069	0.021	0.098	0.000	0.000	0.083
Haddock	1	0.643	0.010	0.000	0.001	0.001	0.076	0.005
	2	0.397	0.076	0.007	0.029	0.000	0.033	0.008
	3	0.350	0.171	0.010	0.044	0.000	0.021	0.017
	4	0.314	0.241	0.014	0.064	0.000	0.006	0.026
	5	0.327	0.293	0.022	0.099	0.000	0.002	0.029
	6	0.280	0.397	0.017	0.075	0.000	0.001	0.051
	7	0.276	0.455	0.024	0.107	0.000	0.006	0.011
	8+	0.256	0.599	0.012	0.055	0.000	0.045	0.035
Whiting	1	1.250	0.259	0.000	0.000	0.001	0.076	0.005
	2	0.819	0.635	0.001	0.002	0.001	0.053	0.010
	3	0.651	0.803	0.006	0.015	0.000	0.039	0.028
	4	0.582	0.881	0.017	0.042	0.000	0.038	0.043
	5	0.559	0.918	0.022	0.053	0.000	0.016	0.059
	6	0.547	0.926	0.026	0.064	0.000	0.009	0.070
	7+	0.559	0.945	0.041	0.101	0.000	0.001	0.025
Saithe	3	0.405	NA	0.004	0.094	0.000	0.000	0.065
	4	0.372	NA	0.008	0.182	0.000	0.001	0.127
	5	0.347	NA	0.011	0.232	0.000	0.001	0.161
	6	0.313	NA	0.010	0.228	0.000	0.001	0.158
	7	0.293	NA	0.011	0.229	0.000	0.001	0.159
	8	0.282	NA	0.010	0.226	0.000	0.001	0.157
	9	0.274	NA	0.009	0.197	0.000	0.001	0.137
	10+	0.264	NA	0.009	0.197	0.000	0.001	0.137

Table S.2: Other inputs of the simulation model. Standard errors are shown in parentheses for the parameters estimated by regression. For the recruitment parameters the standard errors are on the log-transformed scale.

Species	Seal predation rate q	Ricker parameters			Maximum sustainable yield msy (tonnes)	Carrying capacity K (tonnes)	Fishing mortality (F) or landings (tonnes, ling only)				
		α	β	σ			TR1_10-24	TR1>24	TR2<10	TR2_10-24	Others
Cod	0.019	1,250 (±0.248)	0.011 (±1.064)	0.646	-	-	-	-	-	-	-
Haddock	0.011	8,796 (±0.659)	0.021 (±0.527)	1.016	-	-	-	-	-	-	-
Whiting	0.003	8,880 (±0.198)	0.002 (±1.824)	0.544	-	-	-	-	-	-	-
Saithe	-	1,486 (±0.203)	0.066 (±0.240)	0.547	-	-	-	-	-	-	-
Anglerfish	-	-	-	-	2,678 (±659)	18,251 (±4,806)	0.030	0.070	0.000	0.011	0.227
Megrim	-	-	-	-	1,464 (±291)	21,345 (±4,916)	0.045	0.019	0.000	0.000	0.036
Hake	-	-	-	-	16,910 (±3,197)	32,998 (±6,896)	0.040	0.129	0.000	0.032	0.363
Nephrops	-	-	-	-	21,383 (±2,450)	132,276 (±9,961)	0.005	0.000	0.010	0.115	0.019
Ling	-	-	-	-	-	-	137	918	0.000	0.000	1,875

B. Partition of the fishing mortality into fleets

B.1. Age-structured stocks

To partition the fishing mortality by fleet, catch at age data for UK vessels from Marine Scotland for cod, haddock and whiting were used in conjunction with catch at age data from ICES reports (ICES, 2013a; ICES, 2013c). Marine Scotland data were available for the years 2012-2014, however, from 2014 onward, ICES merged data for haddock in ICES Division 6a and the North Sea to perform a single northern stock assessment and no separate assessment for 6a is available after 2013 for this species. Consequently, for spatial consistency with seal diet data, ICES reports for 2013 were used to partition the fishing mortality into fleets for the three species and only the 2012-2013 data from Marine Scotland were used. For saithe, no catch at age data by mesh size is available but the 2012 total landings by mesh size were recorded. These are therefore used to partition the fishing mortality into fleets.

The number of fish of species i caught at age a by the fleet called "Others" ($C_{a,i,Others}$) was estimated following Equation (S.1).

$$C_{a,i,Others} = C_{a,i,ICES} - (C_{a,i,TR1} + C_{a,i,TR2}) \tag{S.1}$$

The "Others" fleet represents the foreign vessels and UK vessels using gears other than the whitefish (TR1) and *Nephrops* (TR2) trawls. Its catch at age could be estimated by deducting the catches at age of the UK fleets (TR1+TR2) from the total catch at age recorded by ICES ($C_{a,i,ICES}$). For saithe the catch at age by mesh size was obtained by scaling the total ICES catches at age in ICES Division 6a by the proportion of each fleet in the total landings in 2012.

Having now the catch at age values for the three fleet groups (subscript "gr") (i.e. TR1, TR2 and "Others"), it was possible to estimate the proportion ($\varphi_{a,i,gr}$) that each group represents in the total catch at age for the four species. The average (2007-2011) total fishing mortality at age ($\bar{F}_{a,i}$) obtained from the stock assessment model (Trijoulet et al., 2017) for cod, haddock and whiting and the average 2007-2011 from ICES (2013c) for saithe were used to calculate the fishing mortality at age for the three fleet groups ($F_{a,i,gr}$) by multiplying $\bar{F}$ by the proportion of each fleet in the total catch at age.

$$F_{a,i,gr} = \varphi_{a,i,gr}\bar{F}_{a,i} \tag{S.2}$$

Finally, it was necessary to partition the resulting fishing mortality for the TR1 and TR2 mesh size groups into the fleets TR1_10-24, TR1>24, TR2<10 and TR2_10-24. To do so, the Marine Scotland data on landings per fleet were used to estimate the proportion of TR1 and TR2 total landings for each fleet k (ψ_k) (Table S.3).

Table S.3: Estimated proportion of catch by mesh size group taken by each fleet (mesh size and vessel length combination).

Species	**TR1_10-24**	**TR1>24**	**TR2<10**	**TR2_10-24**
Cod	0.176	0.824	0.037	0.963
Haddock	0.184	0.816	0.010	0.990
Whiting	0.290	0.710	0.010	0.990
Saithe	0.044	0.956	0.000	1.000

This enabled the calculation of the partial fishing mortality at age for the four fleets (Rijnsdorp et al., 2006).

$$F_{a,i,k} = \psi_k F_{a,i,gr} \tag{S1.3}$$

This partial fishing mortality was used to determine the values of the selectivity at age (s) used in equation T1.4 of the simulation model. It was assumed that the effort index for each fleet (E_k) was 1. Consequently, the values of fishing mortality at age ($F_{a,i,k}$) derived were used as the values of selectivity at age for each fleet (s) and were kept constant in the simulation model.

To partition the catches into landings and discards, landings and discards at age data (2012-2014) made available by Marine Scotland was used to estimate the proportion of fish retained in the total catch (λ) (Table S.4). The data give the partition only by mesh size not by vessel length, so it was assumed that the proportion of fish retained only depends on the mesh size as is currently assumed in ICES (2015b). Also, no data exist for the foreign vessels but because most of the foreign vessels are whitefish trawlers (only 1% of total catch of *Nephrops* in 6a comes from foreign vessels (ICES, 2015a)), it is assumed that the proportion of fish retained at age for the "Others" fleet is the same as the UK TR1 fleets.

Some age classes are not represented in the data making it difficult to know if it is because these classes are not caught or if it is due to sampling error. As a result, a regression model was fitted to the three years of data to estimate the missing data assuming a linear relationship between the logit of the proportion of fish retained and the fish age. Within the simulation model, the mean proportion of fish retained in 2012-2014 was used to partition catches into landings and discards following equation T1.8. Following ICES (2013c), the simulation model assumed there are no discards of saithe.

Table S.4: Proportion of landings in the total catch (λ) used in the simulation model

Species	**Age**	**TR1 and Others fleets**	**TR2 fleets**
Cod	1	0.034	0.000
	2	0.008	0.004
	3	0.090	0.125
	4	0.293	0.996
	5	0.474	1
	6	0.806	1
	7+	0.943	1
Haddock	1	0.235	0.025
	2	0.669	0.069
	3	0.848	0.289
	4	0.956	0.513
	5	0.954	0.487
	6	0.988	0.703
	7	0.679	0.512
	8+	0.996	0.839
Whiting	1	0.168	0.003
	2	0.169	0.014
	3	0.567	0.095
	4	0.730	0.270
	5	0.839	0.701
	6	0.761	0.879
	7+	0.804	0.972
Saithe	3	1	1
	4	1	1
	5	1	1
	6	1	1
	7	1	1
	8	1	1
	9	1	1
	10+	1	1

B.2. Other species

Data extracted from ICES databases have been used to partition the landings into UK and foreign fleets for each species (ICES, 2011; ICES, 2015a) by taking averages between 2007 and 2011.

The partition inside the UK fleets is more difficult due to the lack of empirical data and the fact that the economic data (STECF, 2015) do not assume the same fleet partition as ICES and this study. Different data sources were used by species.

TR2<10 fleet

Except for *Nephrops*, the Marine Scotland database reports the landings of species other than cod, haddock, whiting and saithe for the TR2<10 fleet as very small such that they were considered insignificant. Consequently, within the model, the TR2<10 fleet only fish on *Nephrops*.

Anglerfish

ICES (2013a) states that 10% of the UK anglerfish landings come from the *Nephrops* trawlers. Also, the STECF data annex tables for the years 2008-2011 records that on average 63% of the UK landings are caught by vessels larger than 24 meters and 37% by vessels between 10 and 24 meters (STECF, 2013). Consequently it has been concluded that 63% of the UK landings should be attributed to TR1>24, 10% to TR2_10-24 and 27% to TR1_10-24 (Figure S.1).

Megrim

According to ICES (2013a), only TR1 fleets fish on megrim in ICES Division 6a. STECF data enabled us to conclude that 70% of the UK megrim are caught by vessels between 10 and 24 meters (STECF, 2013).

Hake

Of the UK landings for hake, 64% correspond to vessels larger than 24 m while 36% corresponds to vessels between 10 and 24 m (STECF, 2013). Also, hake is caught by mixed gear trawlers (ICES, 2014). The 20% and 16% caught by TR1_10-24 and TR2_10-24 respectively were allocated to be consistent with the total landings of other species (except *Nephrops*) recorded in the Marine Scotland database.

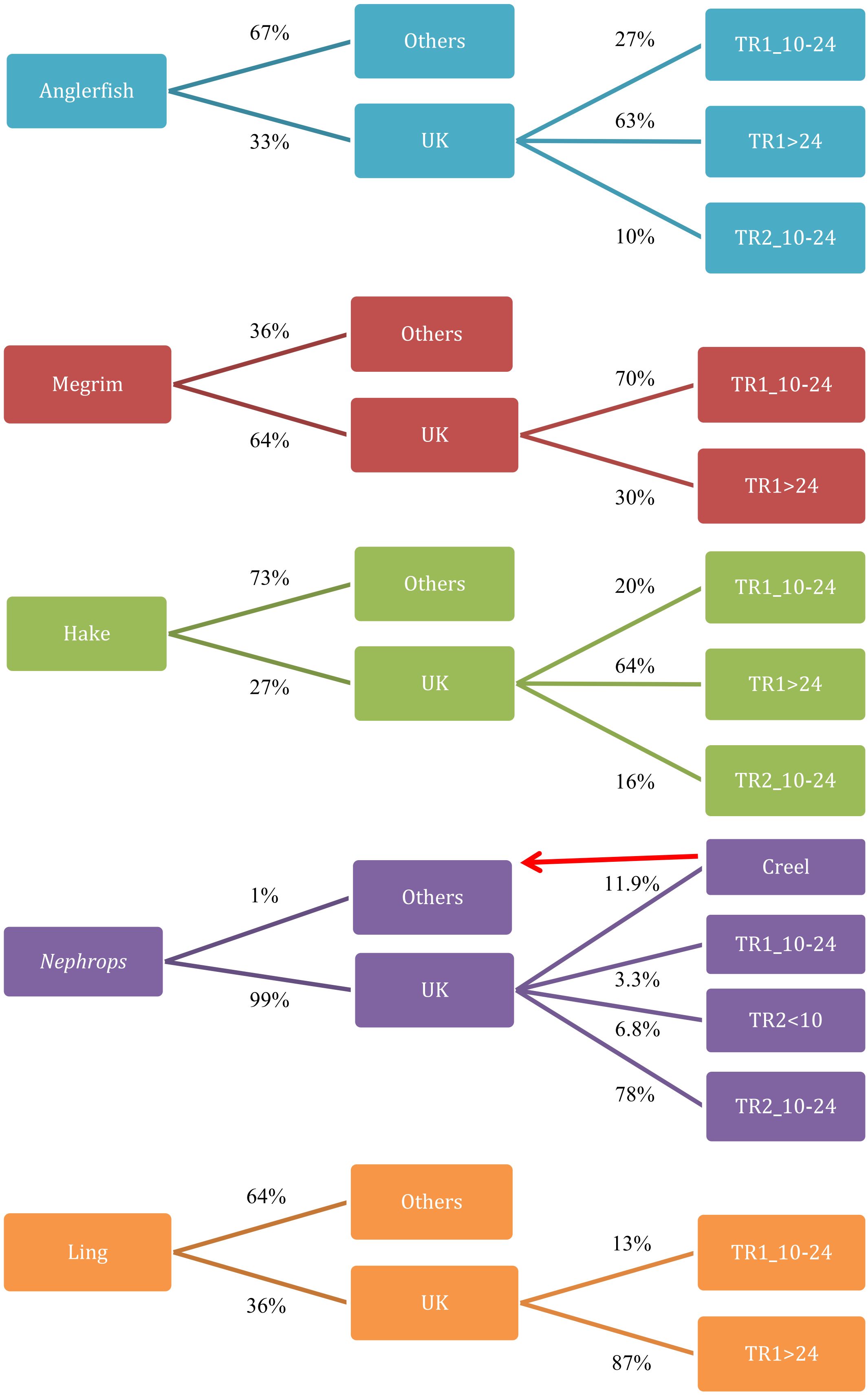

Figure S.1: Partition of landings into fleets for species other than cod, haddock, whiting and saithe.

Nephrops

ICES (2013a) gives the *Nephrops* landings in Division 6a for the different gear types and enables the partition into TR1, TR2 and creel fleets. The creel landings are allocated to the "Others" fleet since this fleet corresponds to the foreign vessels plus non demersal trawl UK vessels. The Marine Scotland database which gives effort and landings by vessel length and mesh size for the years 2000-2012 also records the landings for *Nephrops*. The 2007-2011 data were used to partition the landings between fleets for this species.

Ling

The lack of empirical data on ling increases the uncertainty around the partition for this species. 87% of the UK landings come from vessels larger than 24 m (STECF, 2013). This corresponds to the TR1>24 fleet. The remaining 13% corresponds to vessels between 10 and 24 m and there is no information on a possible bycatch by the *Nephrops* trawlers in ICES (2013b). Consequently these landings have been allocated to the TR1_10-24 fleet.

This partition is believed to be a good approximation of the current fleet specific landings for species other than cod, haddock, whiting and saithe. It is used to calculate the baseline landings for ling and the baseline fishing mortality for anglerfish, megrim, hake and *Nephrops* used in the bioeconomic models (Table S.2).

C. Characteristics of the dynamic equilibrium scenarios

In the bioeconomic equilibrium (BE) scenario, the change in effort index for each iteration was modelled using a sigmoid curve which is bounded by a maximum (Δ_{max}) change in effort and a minimum effort (here zero). The fleet effort index is scaled by a factor Δ_k at each iteration (n) such as:

$$\Delta_{k,n+1} = \frac{\Delta_{max}\pi_{k,n}}{\tau c_{*,k,n} + |\pi_{k,n}|} + 1 \qquad \text{(S1)}$$

The parameter τ is the steepness of the curve. When the net profit (π) is zero, $\Delta_{k,n+1}$ is equal to 1 and there is no change in effort. If the net profit is negative, $\Delta_{k,n+1}$ is less than 1 and the effort at the next iteration is reduced, inversely effort increases if the net profit is positive. We set Δ_{max}= 1.5 and $\tau = 0.2$. This means that, at each iteration, the fleet effort can only change by a maximum of 50%. Exploratory runs with alternative values in equation (S1) only changed the number of iterations required to reach the BE but otherwise gave the same result.

In this scenario it is assumed that the fleet investment or disinvestment impacts the fleet total costs such that there is no requirement to partition the costs into variable and fixed costs. The vessels within a fleet are assumed identical and the marginal cost constant so a change in fishing mortality produces a linear change in costs and can be interpreted as a change in effort and/or vessel number. Total fleet costs are therefore expressed as:

$$c_{*_k} = E_k c_k \tag{S2}$$

The term c_k is the initial costs per fleet when $E_k = 1$. The entire fishery is assumed to be at the BE when each fleet net profit is dissipated at the steady state.

In the maximum economic yield (MEY) scenario, as the fishery is closed to new entrants, fishers can only modify their effort and cannot invest/disinvest in vessel number so the number of vessels remains the same. As a result, a change in effort only impacts the variable costs and the fixed costs stay constant (T1.11). The fishery reaches the MEY when the total fishery net profit (π) is maximised:

$$\pi = max\left(\sum_k \pi_k\right) \tag{S3}$$

The model is solved for the level of effort per fleet which satisfies this economically optimal fishery at the steady state. The optimizer in the package DEoptim (Mullen et al., 2011) was used in the statistical software R (R Core Team, 2016) to perform the maximisation. Alternative global optimizers such as simulated annealing gave similar results indicating that the results were not sensitive to the optimizing algorithm. As an upper bound on effort, we assumed that the fleets are currently operating at their maximum effort allocation so fleet effort index can only remain the same or decrease compared to the baseline.

D. Consistency check: composition of landings per fleet

The model estimates landings in the first year of simulation similar to the observed values (Figure S.2) indicating that the model parameterisation is consistent with fishery data. There are clearly some differences which will arise from the averaging process used to derive the model inputs.

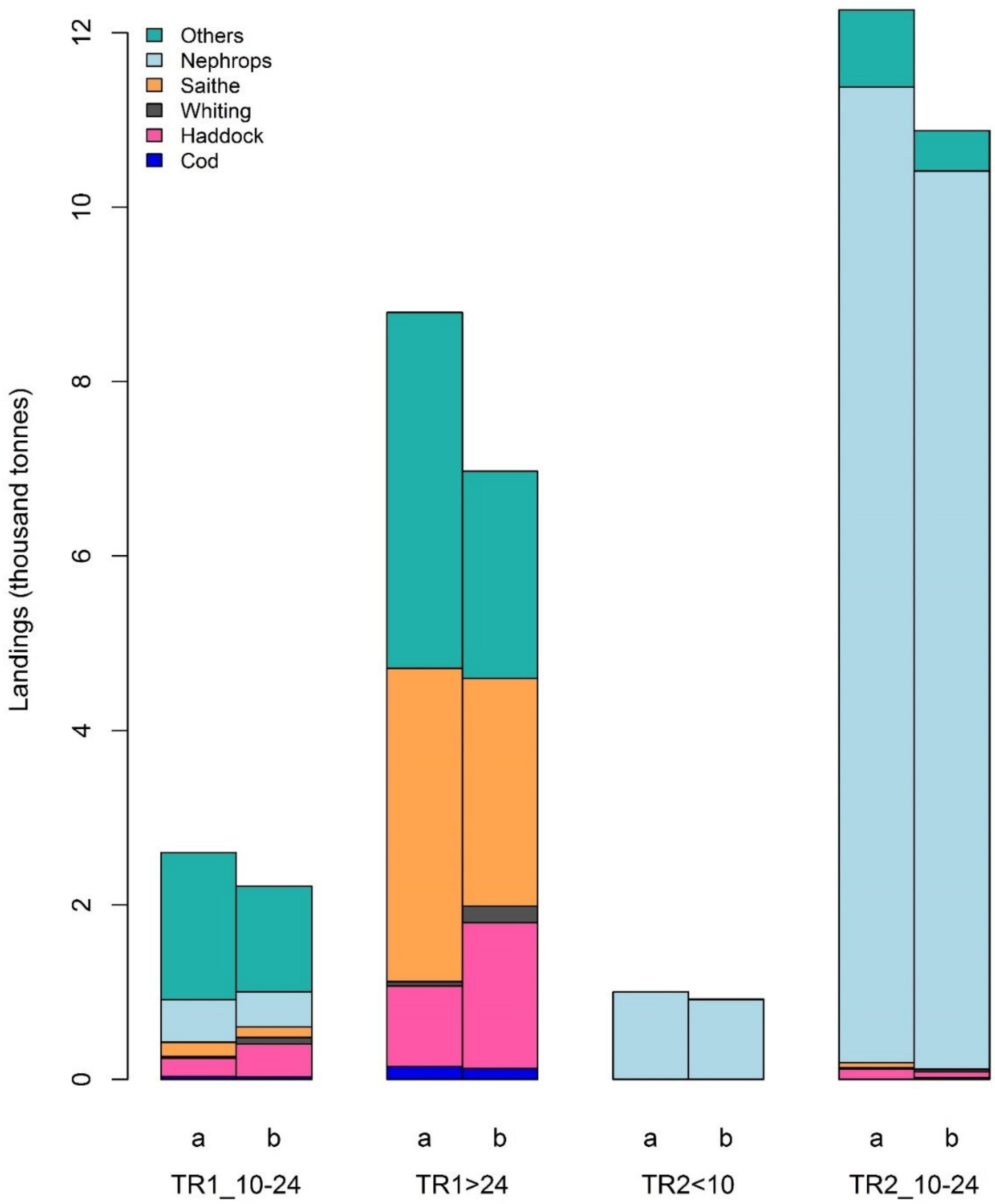

Figure S.2: Landings ('000 tonnes) by UK fleet and species estimated in the first year of simulation (a) and the mean observed values over 2007-2011 reported by Marine Scotland (b).

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