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Original Article

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

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

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

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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.

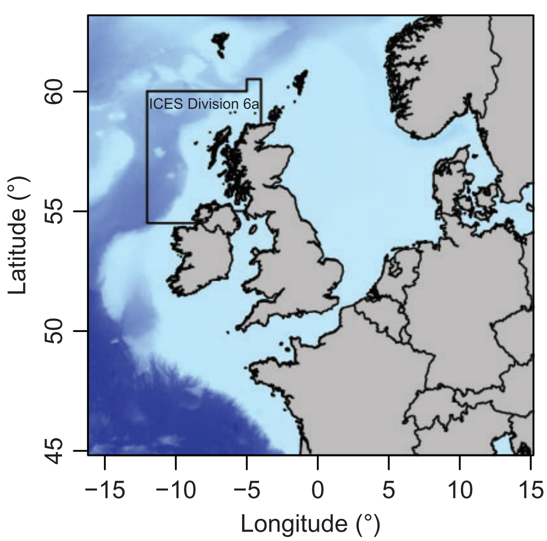

Figure 1. Map showing ICES Division 6a; the study area. Bathymetry data taken from Amante and Eakins (2009).

Material 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 (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 with M. For these other species, only the landings are modelled because the discard rates are low (Heath *et al.*, 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

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	$N_{1,y,i} = \left(\alpha_i SSB_{y-1,i}e^{-\beta_i SSB_{y-1,i}}\right)e^{\epsilon_i}$	Ricker curve with lognormal process errors, $\epsilon_i \sim Normal(0, \sigma^2)$. 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	$R_{y,k} = \sum_i (p_iL_{y,i,k})$	Product of fish landings and price p
(T1.11)	Fleet total cost	$c_{*_k} = \nu(c_{v_k} + c_{f_k})$	Sum of the variable costs c_v and the fixed costs c_f per vessel multiplied by the number of vessels ν. The variable costs are proportional to fleet effort using a constant ρ such as $c_{v_k} = \rho_kE_k$
(T1.12)	Fleet net profit	$\pi_{y,k} = R_{y,k} - c_{*_k}$	

Table 2. Fleets considered in the simulation model and their characteristics.

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	$\geq$120	Demersal whitefish	9	430.5	213.0
TR1>24	Large UK whitefish trawlers	$\geq$24	$\geq$120	Demersal whitefish	10	1250.8	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	1236.3	618.1

The number of vessels and their associated annual costs per vessel are mean values for the years 2007–2011 obtained from Seafish.

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.

Parameterization

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. For saithe, the input values were taken from ICES (2013).

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, 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 10 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 2007–2011 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 summarized in Table 2.

The price of fish in the West of Scotland is dictated by the European market (Scottish Fishermen's Organization, 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 Organization (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.

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

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 maximized 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 equilibrium 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.

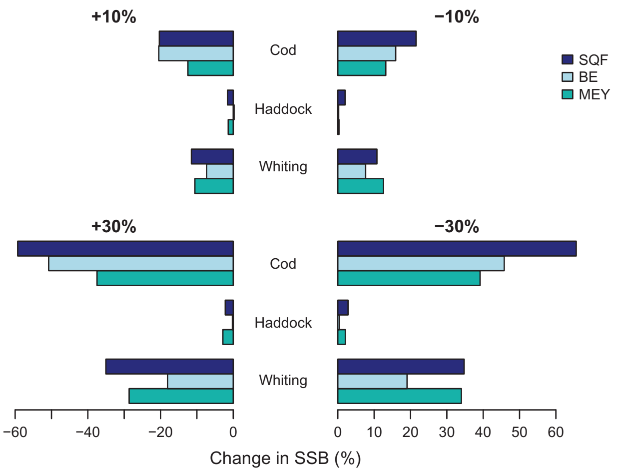

Figure 2. Change in mean equilibrium SSB (%) for cod, haddock, and whiting in the three different scenarios for small (±10%) and large (±30%) changes in seal population.

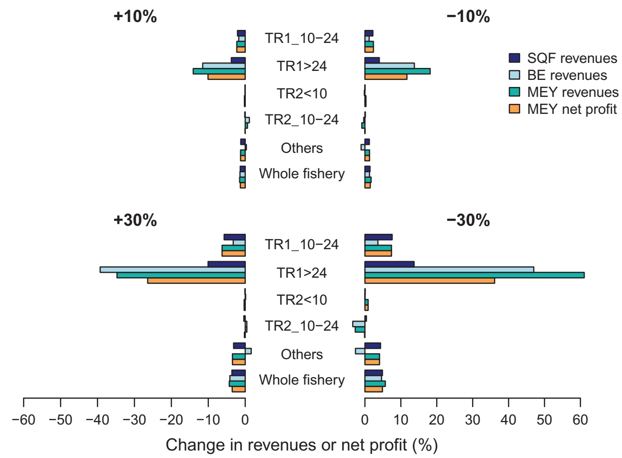

Figure 3. Change in mean equilibrium revenues (%) or net profit (MEY scenario only) by fleet and for the entire fishery in the three different equilibrium scenarios for small (±10%) and large (±30%) changes in seal population.

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 with 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 seal impacts on fishing revenues when the seal predation is increased by 10%, between the initial model set up and when the sensitivity tests 1–5 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 with 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 (<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

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.

(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

The weight of fish consumed by seals is converted to seal "revenue" using fish price.

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% (3204 individuals).

		Fishery			TR1 > 24		
Seal scenario	Equilibrium scenario	Whole	Per vessel	Per seal	Whole	Per vessel	Per seal
+10%	SQF	−1350	−6.13	−0.421	−715	−71.54	−0.223
	BE	−1618	−2.69	−0.505	−1289	−257.83	−0.402
	MEY	−1405	−6.39	−0.439	−903	−90.25	−0.282
−10%	SQF	1414	6.43	0.441	763	76.32	0.238
	BE	1456	2.41	0.454	1541	220.21	0.481
	MEY	1601	7.28	0.500	1165	116.46	0.363

The change is given at the level of the whole fishery or fleet, per vessel and per seal.

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%.

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

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 with a Ricker relationship.

larger than those of the TR2 < 10 fleet, but this arises because the fleet catches mainly *Nephrops* (Supplementary Figure S2). When seal revenues are compared with fleet revenues for all fish species combined (Table 4b), the value of seal predation is negligible since it represents <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.

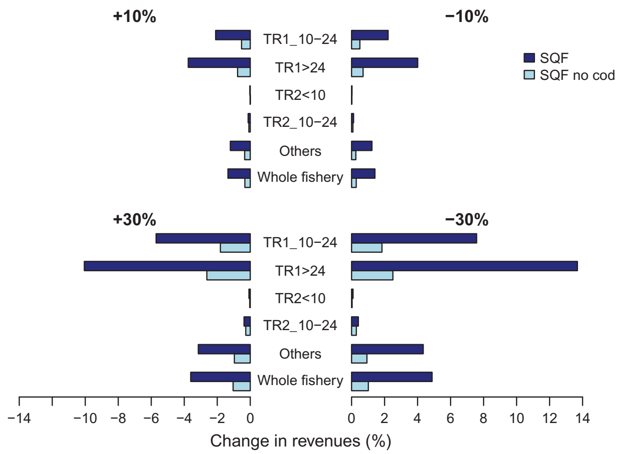

Figure 4. Change in revenues (%) by fleet and for the entire fishery for a small (±10%) and large (±30%) change in seal population in the initial SQF scenario and for the SQF scenario in the absence of cod.

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 <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 with 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 characterize, 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 with SQF and reduces it compared with 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 £4800 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 2 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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