



Bioeconomic modelling of seal impacts on West of Scotland fisheries

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Abstract

It has been several decades that groundfish stocks have decreased around the UK. Meanwhile, grey seal population has increased. This has created a controversy between fishers and conservationists as regards to the role grey seals have played in the stock depletion. Currently, opinions are still divided, and further studies need to be done to mitigate these conflicts.

A bioeconomic model able to quantify the economic impact of grey seal predation on West of Scotland demersal fisheries for cod, haddock and whiting was developed. The biological part of the model accounts for seal predation and fishing catches and is linked to an economic model accounting for fleet revenues and costs.

Three scenarios are tested. The “status quo F” model assesses seal predation impacts on fleet revenues at the biological equilibrium. Two dynamic models are also studied to determine seal impacts when fleet behaviour is considered: the maximum economic yield scenario (MEY) where the fishery net profit is maximised and the bioeconomic equilibrium (BE) model where the profits are dissipated in the long-run.

Cod is the fish the most impacted by grey seal predation so is the key stock in evaluating fishery effects. While the biological impacts can be important, seal predation is not economically important at the fishery level but some fleets are more sensitive than others. The large whitefish trawlers are likely to be the only fleet that could benefit from a reduction in grey seal predation. The following increase in its revenues would be certainly improved by fishery regulations.

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Chapter 1

Introduction

1.1. The seal and fishery controversy

The late 20th century has been marked by a decrease in the commercial groundfish stocks in the North Atlantic. The fisheries have profoundly changed to adapt to the modification in fish stocks resulting primarily from overfishing. Many fish stocks are even considered as outside safe biological limits (FAO, 2011). This is notably the case for the Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) which are listed as “vulnerable” by the International Union for Conservation of Nature (The IUCN Red List of Threatened Species, 2015).

Cod is a good example of the decline in the demersal stocks in the North Atlantic. Cod landings have substantially decreased since the 1970s (Figure 1.1) (FAO FishStatJ, 2014). In the UK, the landings have decreased by 90% since the 1980s (ICES, 2014c) and the stock is depleted in the Baltic Sea (Isomaa et al., 2013; ICES, 2014a). On the eastern Canadian coast the stocks have collapsed in the 1990s and currently only one stock shows some evidence of recovery since the 13 years of moratorium on fishing (Bundy, 2005; Bundy and Fanning, 2005; Swain and Chouinard, 2008; Bundy et al., 2009; Frank et al., 2011). The recovery of the other stocks is believed to be long and difficult (Neubauer et al., 2013; Swain et al., 2013; Bousquet et al., 2014; Sinclair et al., 2015; Swain and Benoit, 2015) despite an increase in the cod abundance recently (Hutchings and Rangeley, 2011; Swain and Mohn, 2012). This decline in fish stock is not yet completely understood. Most studies agree that climate change (Rose, 2004; Brander, 2005; Cook and Heath, 2005; Pershing et al., 2015) and high level of fishing

(Hutchings and Myers, 1994; Myers et al., 1996) are responsible for this decline. This has often resulted in regime shifts (Frank et al., 2005; Bundy et al., 2009; Frank et al., 2011) where the depleted fish stocks cannot compete against the growing communities (Bundy and Fanning, 2005). The decline in the demersal stocks became a subject of controversy dividing opinions among fishers and scientists (Harwood, 1984; Lambert, 2001).

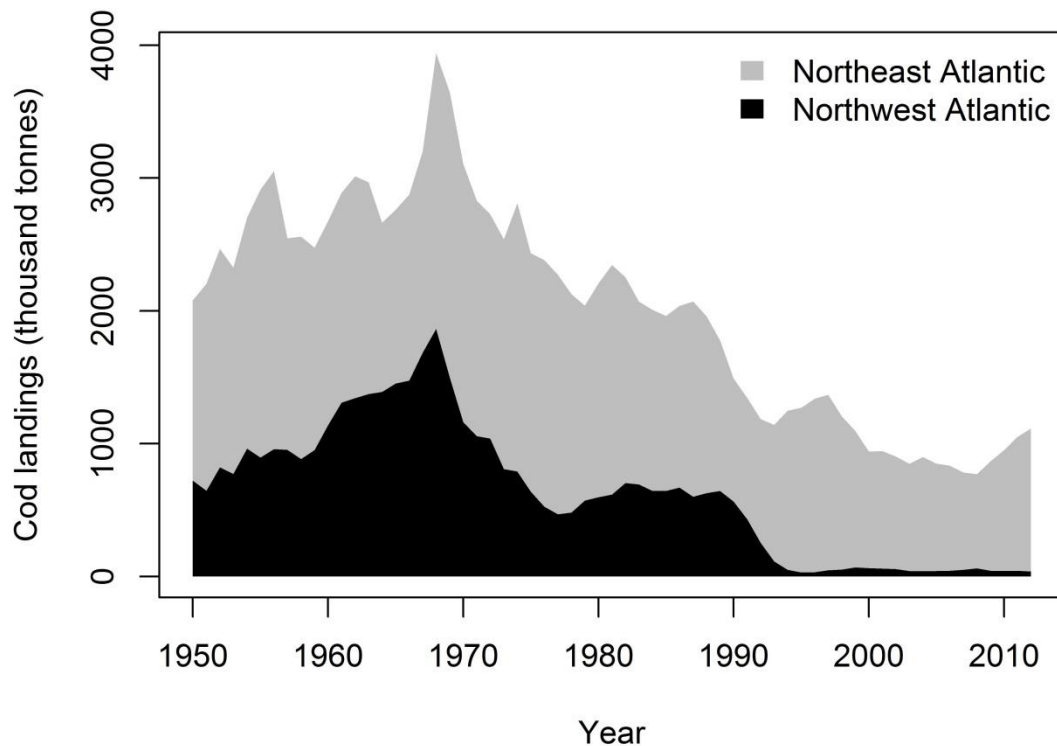


Figure 1.1: Landings of cod in the North Atlantic from 1950 to 2012 (FAO FishStatJ, 2014).

While the fish stocks were declining in the North Atlantic, the grey seal (*Halichoerus grypus*) population was increasing (Figure 1.2) (Ministry of Agriculture and Forestry, 2007; Thomas et al., 2011; Thomas, 2012; Finnish Game and Fisheries Research Institute, 2015). The grey seal is a marine mammal whose range goes from the Northwest to the Northeast Atlantic and which is subject to removal by only killer whales (*Orcinus orca*) and humans. The three main regions where grey seals breed in the North Atlantic are the UK, the east coast of Canada and the Baltic Sea. While in the 1980s the number of grey seals in Canada and the UK were similar, the Canadian population has increased exponentially in a few decades (Bowen et al., 2003) to present

currently the largest grey seal colonies of almost 350,000 individuals (Thomas et al., 2011).

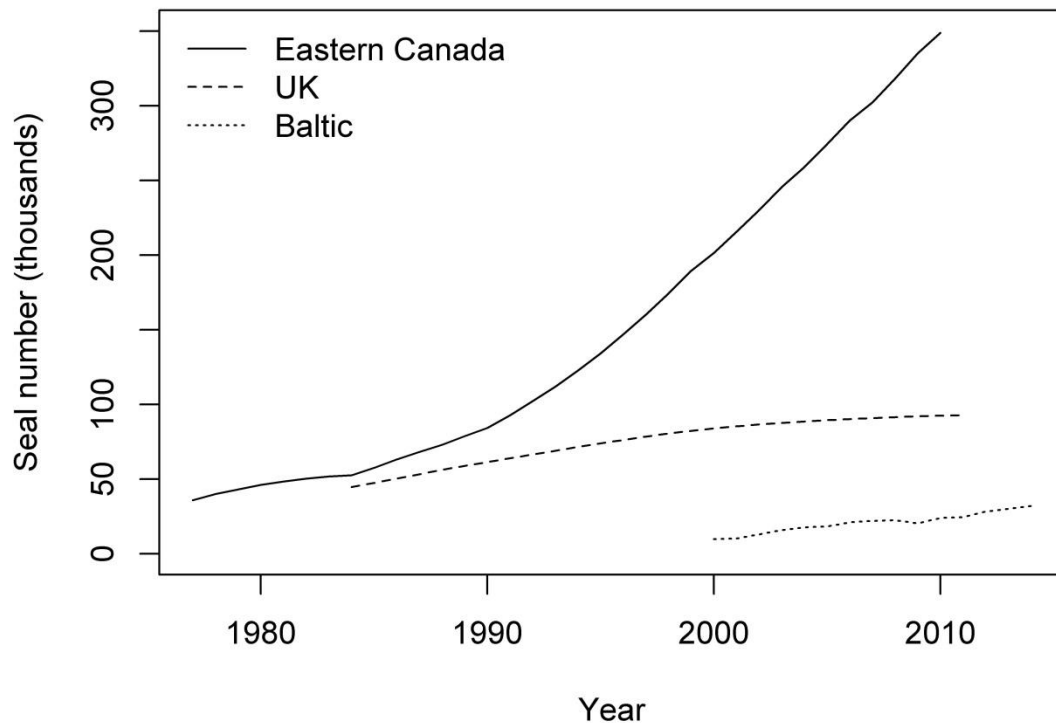


Figure 1.2: Estimates of grey seal numbers in the North Atlantic (Ministry of Agriculture and Forestry, 2007; Thomas et al., 2011; Thomas, 2012; Finnish Game and Fisheries Research Institute, 2015).

The implementation of different protection acts in the North Atlantic seems to have contributed to the expansion of the grey seal populations. Around the UK, the grey seal population was estimated to be 500 individuals at the beginning of the 20th century (Lambert, 2001). Thinking that they were rare, the Grey Seal (Protection) Act was then created in 1914, establishing a closed season for seal hunting. The closed season was also extended in 1932. The population of grey seals then started to increase. In parallel, fishers saw a decrease in fishing catches and were subject to seal damage to gear and fish at the netting stations (Bjørge et al., 1981; Bjørge et al., 2002; Bosetti and Pearce, 2003; Königson et al., 2007; Bruckmeier et al., 2013; Cronin et al., 2014; Gruber, 2014). The salmon fishery is particularly concerned by these impacts (Butler et al., 2011). Fishers sought a seal cull to control the population. Seal culls occurred in 1960s and in addition, the UK Conservation of Seals Act (CoSA) created in 1970 allowed seal shooting during close seasons by anybody at the netting stations to prevent fish and net

damages (section 9.-(1)(c)) and by hunting licence holders (section 10.-(1)) (HM Government, 1970). Pressure from conservationists and the media against culling meant that the last grey seal culls occurred in 1970s. In 1992, grey seals and harbour seals appeared in Annex II of the European Habitats Directive, and Special Areas of Conservation were created in the Moray Firth for Atlantic salmon in 1999 and for harbour or common seals (*Phoca vitulina*) in 2000. But seals can still be killed under the CoSA. The Moray Firth Seal Management Plan was then implemented in 2005 to enable protection of fisheries while protecting seal conservation and tourism (Butler et al., 2008). The plan establishes a limit for the number of seals (grey and harbour seals) that can be killed each year and seems to provide an adaptive co-management framework for balancing seal and fisheries conservation in the area. In 2010, the Marine (Scotland) Act was established, giving the ability to kill seals under certain conditions only by licensed fishers who can prove that seals are detrimental to their living (Part 6, section 110, (Scottish Parliament, 2010)). In 2013, 98,800 (95% confidence interval: 81,400-122,000) grey seals were present around the UK (Thomas, 2014).

On the Canadian east coast, in 1971, a quota management system was instituted for seal hunting, because of a concern for population depletion (Fisheries and Oceans Canada DFO). Sealing occurred following total allowable catches in the Gulf of St Lawrence and the eastern Scotian Shelf but is prohibited in protected areas such as the offshore breeding zone of Sable Island. A licensing system is also possible for fishers who can prove that seal predation is harmful to their livelihood. A commercial market exists in Canada for commercial use of seal pelts for clothing, oils, health supplements and meat. Seals most impacted with the sealing market are the harp seals (*Pagophilus groenlandicus*) and the hooded seals (*Cystophora cristata*). Harvests never exceed 5,000 individuals for grey seals and none are currently killed for commercial use. However, because of the collapse of cod and its non-recovery despite the closure of the fishery in 1993, the government continues to propose large scale seal culls to reduce the predation pressure on the fish stocks (Fisheries Resource Conservation Council, 2011; Standing Senate Committee on Fisheries and Oceans, 2012).

In the Baltic Sea, seals are fully protected with the exception of grey seals in Finland and Sweden. Seals started to be a concern in the Baltic Sea after the different

international conventions giving high priority to all Baltic seal species (Bonn Convention 1979, Bern Convention 1979, HELCOM 1992, EU Habitats Directive 1992). In 1993, the “Mainland Finland: Hunting Act and Hunting Decree” allowed grey seals to be killed during hunting seasons with a hunting licence and following quota restrictions (Ministry of Agriculture and Forestry, 2007). In certain areas, grey seals are protected and can only be shot if they are found causing damage inside nets. These mainly concern fixed nets, pots and traps (Königson et al., 2007; Königson et al., 2013; Königson et al., 2015). Besides seal hunting, a fishery insurance system exists since 1958 allowing compensation when seal damage occurs. Also, since 2002, European and national funds enable fishers to get compensation for seal damage and funds for fishing technology development (Lunneryd et al., 2003; Lehtonen and Suuronen, 2004; Fjälling et al., 2006; Suuronen et al., 2006).

The decrease in fish stocks coupled with the increase in seal population has created a controversy between fishers and conservationists (Lambert, 2001; Lavigne, 2003; Read, 2008). Fishers argue that the depletion in fish stocks is due to seal predation and ask for a return of seal culls while the conservationists seek to protect the grey seal population and stress the economic benefit it offers (i.e. seal-watching and ecotourism). The seal and fishery controversy has become a political, economic, social and environmental issue with the media and public opinion often supporting the conservationist’s position.

1.2. The gap in the literature and the choice of the West of Scotland as case study

Research has been pursued, and still is, to understand the cause of fish stock depletion and the possible responsibility of seals in this decline. The first concern is to understand grey seal diet. Much research focusing on seal diet data collection and analysis exists (Bowen and Harrison, 1994; Hammond and Grellier, 2006; Hammond et al., 2006; Harris, 2007; Lundström et al., 2007; Gosch et al., 2014). However, looking at how much commercial fish grey seals eat is not enough to conclude on their impacts on

the fisheries. Fishing being an economic activity, it is necessary to study the impact of grey seal predation on fish stocks and the consequences on fishing revenues and net profits. The literature quantifying the economics of seal damage impacts on fisheries is large (Bjørge et al., 1981; Bosetti and Pearce, 2003; Bruckmeier et al., 2013; Cronin et al., 2014; Gruber, 2014). However, the bioeconomic impacts of grey seal predation on fisheries have never been fully examined.

The West of Scotland area represents an opportunity to investigate grey seal predation following seal diet studies carried out in 1985 and 2002 (Hammond et al. 2006, Harris 2007). This corresponds to the ICES (International Council for the Exploration of the Sea) Division VIa. The 2002 seal diet data were used to estimate total consumption of cod in VIa (Harris, 2007) and suggested it exceeded the ICES estimated cod spawning stock biomass (SSB) (ICES, 2014c). This means seals may consume more fish than can actually be produced every year. This may be due to the fact that the seal consumption and/or SSB estimates are incorrect. Both estimations present limitations. Seal consumption estimates suffer from the uncertainty around grey seal numbers and the assumption regarding the estimation itself. SSB estimates are sensitive to the assumption of stock-recruitment but mainly on the assumption of natural mortality which affects the estimates of fishing mortality and therefore the perception of the stocks. Yet, these estimates may be evidence that grey seal predation on cod is large in this area. The fishery that is the most in competition with seals in VIa is therefore the mixed demersal fishery for whitefish. Cod, haddock and whiting (*Merlangius merlangus*) were the main targeted species in the past but the decline of cod and whiting has reduced the quantities landed today and Norway lobster (*Nephrops norvegicus*), anglerfish (*Lophius* sp.), saithe (*Pollachius virens*) and haddock are now the fish with the greatest landings (ICES, 2014c).

Since the 1980s, the grey seal population has increased in the West of Scotland but has stabilized in the recent years (Thomas, 2014). Grey seal predation mortality on cod has already been estimated in this area (Holmes, 2008; Holmes and Fryer, 2011; Cook et al., 2015; Cook and Trijoulet, 2016). However, cod is not the only commercial demersal species that appears in grey seal diet, haddock and whiting are also present (Hammond et al., 2006; Harris, 2007). The weight of haddock consumed by grey seals in VIa is notably slightly larger than the weight of cod consumed. Whiting is also one of the fish

the most numerous in grey seal diet. It can therefore be argued that if grey seal predation is large on cod that may also be the case for haddock and whiting. This highlights the necessity of estimating grey seal predation on the three species in the West of Scotland and to study its impacts on the fishery.

Fishery managers need to address biological as well as economic problems when dealing with fisheries because they need to protect the fish stocks without serious detriment to the livelihood of fishers. Bioeconomic modelling offers one approach to addressing this question and Table 1.1 illustrates many of the typical issues that have been addressed. Bioeconomic models are often developed to answer specific questions and for specific areas (Prellezo et al., 2012). Bioeconomic models such as FISHRENT (Salz et al., 2011) and FLR (Kell et al., 2007) are notably interesting to perform simulation or optimization studies focusing on fisheries management scenarios. They were both applied to trawl fisheries in the North Sea (Hoff and Frost, 2008; Simons et al., 2014) but the model FLR was also used in the Mediterranean Sea (Maravelias et al., 2012). The model TEMAS (Ulrich et al., 2002b; Ulrich et al., 2007) was created to study fleet behaviour and enables complex economic modelling where fishers can change their effort in the short or long-term using discrete choice random utility models and entry-exit modelling respectively (Marchal, 2005; Vermard et al., 2005; Kronbak et al., 2009; Andersen et al., 2010). However, while these bioeconomic models created by economists present really complex economic components, the fish stock dynamics is often modelled superficially and some bioeconomic models do not present any biological modules (Prellezo et al., 2012). Numerous complex biological models, where prey-predator interactions are considered, currently exist (Harvey et al., 2003; Speirs et al., 2010; Alexander et al., 2014). Nevertheless, this level of complexity in the biological part of the model is not often encountered in fisheries bioeconomics and models created by biologists show often a biological part with a complex multispecies model but where the economic part is less developed (Beattie et al., 2002). The challenge in fisheries bioeconomics is to have a complete model where the fish stock dynamics is as developed as the economic part. This motivated the choice of creating a specific bioeconomic simulation model in this study. This also brings more flexibility in the conception of the model depending on the data available for the fishery and area of interest.

Table 1.1: Summary of the principal literature topics and goals in fisheries bioeconomics.

Topics	Principal goals	References
Effect of marine reserve on fishery and fish stock	<ul style="list-style-type: none"> - Biological and economic performances of a marine reserve creation - Effect of dispersal on management outside a marine reserve 	<ul style="list-style-type: none"> - Hannesson (1998); Pezzey et al. (2000); Sanchirico and Wilen (2001); Beattie et al. (2002); Boncoeur et al. (2002); Armstrong (2007); Kar and Matsuda (2008); Chakraborty and Kar (2012) - Armstrong and Skonhoft (2006)
Optimal management policy	<ul style="list-style-type: none"> - Determine the optimal harvest or effort policy - Estimation of the optimal long-run surpluses - Determine the optimal fishing season - Fisheries regulation policies and management 	<ul style="list-style-type: none"> - Laukkanen (2001); Ulrich et al. (2002a); Bjørndal et al. (2004); Puga et al. (2005); Hritonenko and Yatsenko (2006); Pal et al. (2012); Guillen et al. (2013); Simons et al. (2014) - Gilbert (1988) - Kellogg et al. (1988); Önal et al. (1991); Larkin and Sylvia (1999) - Matulich et al. (1996); Brasao et al. (2000); Ulrich et al. (2002b); Clark (2006); Kell et al. (2007); Ulrich et al. (2007); Hoff and Frost (2008); Kronbak et al. (2009); Cissé et al. (2013)
Modelling fishing behaviour	<ul style="list-style-type: none"> - Location choice - Change in effort and/or capacity 	<ul style="list-style-type: none"> - Holland and Sutinen (1999); Wilen et al. (2002); Marchal (2005); van Putten et al. (2012) - Hilborn (1985); Bjørndal and Conrad (1987); Hilborn and Walters (1987); Kronbak (2005); Vermard et al. (2005); Ulrich et al. (2007); Andersen et al. (2010); Nøstbakken et al. (2011); van Putten et al. (2012)
Modelling fish prices	As a function of supply or demand	Barten and Bettendorf (1989); Herrmann (1996); Delgado et al. (2003)
The different equilibria in a fishery system	<ul style="list-style-type: none"> - Equilibria for seasonal fisheries, marine reserves or patches - Equilibria for age-structured or multispecies models 	<ul style="list-style-type: none"> - Ardito et al. (1993); Sanchirico and Wilen (1999); Kar and Matsuda (2008) - Tahvonen (2009); Kar and Chakraborty (2010); Pal et al. (2012); Sana et al. (2012)
The impact of species interactions on fisheries	<ul style="list-style-type: none"> - Effect of competing species on fishermen's profits - Effect of prey-predator interactions on fisheries 	<ul style="list-style-type: none"> - Chaudhuri (1986); Flaaten (1991); Kar and Chaudhuri (2004) - Flaaten (1998); Boncoeur et al. (2002); Kar and Chakraborty (2010); Chakraborty and Kar (2012); Pal et al. (2012)
The impact of environmental quality on fisheries	<ul style="list-style-type: none"> - Effect of water quality - Effect of fish quality - Include environmental quality 	<ul style="list-style-type: none"> - McConnell and Strand (1989); Massey et al. (2006) - Larkin and Sylvia (1999) - Knowler (2002)
Fish stock recovery	<ul style="list-style-type: none"> - Fishermen behaviour and stock collapse - Optimal management for stock recovery 	<ul style="list-style-type: none"> - Pitcher (1995); Mackinson et al. (1997) - Lleonart et al. (2003); Da Rocha et al. (2010); Hutniczak (2012)

This thesis studies the bioeconomic impacts of grey seal predation on the mixed demersal fishery for cod, haddock and whiting in VIa. It is comprised of two main modelling studies. First, a parameter estimation analysis was realised to estimate the seal (notably grey seal predation mortality for the three fish species of interest) and fish stock parameters necessary for the bioeconomic model using Bayesian techniques. For this, the state-space stock assessment model previously used for cod in Cook et al. (2015) and Cook and Trijoulet (2016) was developed for haddock and whiting. It provides therefore updated estimates for cod and new estimates for haddock and whiting. Then, a simulation study was carried out. The estimates were used in an age-structured multifleet bioeconomic model which studies the impacts of seal predation on fishing revenues and net profits.

Nine fish species are considered within the simulation model: cod, haddock, whiting, saithe, anglerfish, European hake (*Merluccius merluccius*), megrim (*Lepidorhombus whiffiagonis*), ling (*Molva molva*) and Norway lobster (*Nephrops norvegicus*) since they represent most of the fishing revenues in VIa (STECF, 2013). Three equilibria are compared and enable the investigation of grey seal impacts for different fisheries scenarios. The first scenario studies the impacts of seal predation at the steady state keeping the current fishing mortality constant. Grey seal predation impacts are also considered in two dynamic scenarios accounting for fleet behaviour. The bioeconomic equilibrium corresponds to the unregulated fishery scenario where the fleet net profits are dissipated in the long-run. The maximum economic yield equilibrium (MEY) represents the conventional equilibrium considered in the fisheries economics and assumes the total fishery net profit is maximised at the equilibrium.

This study is the first attempt to estimate grey seal predation mortality for haddock and whiting in VIa. To our knowledge, it represents also the first study considering grey seal predation within a multifleet bioeconomic model which investigates not only the impact of grey seal predation on the fish stocks but also on fleet revenues.

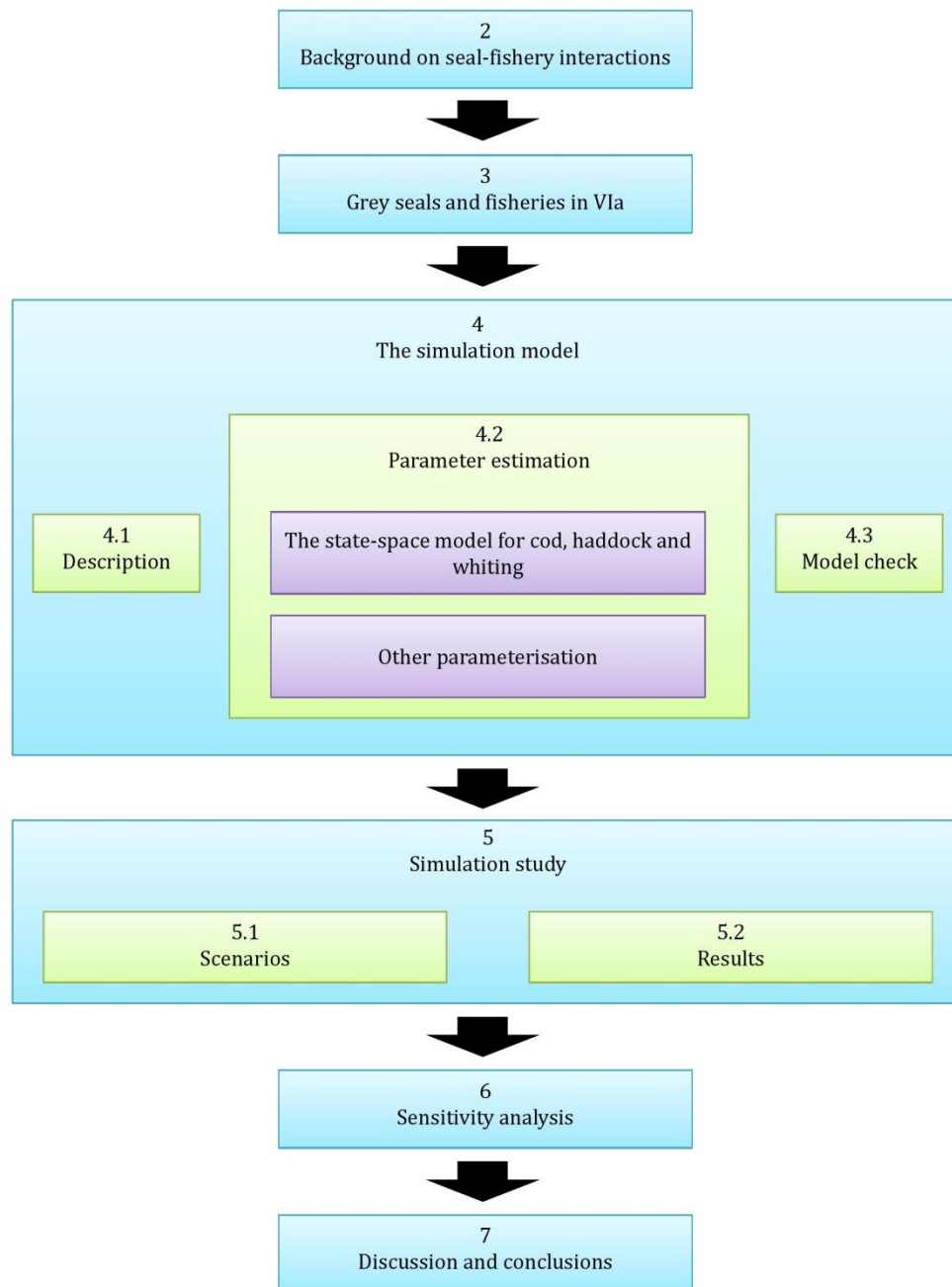


Figure 1.3: Structure of the thesis highlighting the main components of the chapters.

The study is divided into six additional chapters (Figure 1.3). Chapter 2 introduces the background on seal impacts on fisheries. It assesses grey seal diet in the three main breeding zones in the North Atlantic and identifies what we currently know about grey seal impacts on the commercial fish stocks as well as the gaps in the literature. Chapter 3 presents the situation for grey seals and the fisheries in the West of Scotland, the area

of interest. It gives an overview of the fisheries present in the area and explains the choice to concentrate on the impact of seal predation on the demersal fishery. The dynamics of the grey seal population since the 1980s is also presented. Chapter 4 is the main chapter describing the modelling studies. It defines the bioeconomic simulation model but presents also the state-space model developed for cod, haddock and whiting necessary to the parameterisation of the simulation model. Finally this chapter studies the consistency of the simulation results. Chapter 5 presents the three different simulation scenarios and their results. Chapter 6 explores the sensitivity of the bioeconomic results to the assumptions taken in the study. Finally, the last chapter discusses the results and concludes on the impacts of grey seal predation on the West of Scotland fisheries.

Chapter 2

Background on grey seal predation and interactions with fisheries in the North Atlantic

The aim of this chapter is to give an overview of what has been done to attempt to quantify the interactions between seals and fisheries in the North Atlantic (Canada, UK and Baltic Sea). In order to reach this purpose, the grey seal diet is first analysed. Some studies quantify the impact of seals on fish stocks without relating the consequences for fisheries. Consequently, the impacts that seals can have on fish stocks are deliberately differentiated with their impacts on the fisheries. These latter effects can be direct and is called depredation impacts (e.g. damage to gear or fish) or indirect (predation on fish stocks, propagation of diseases). The impact of grey seal predation on fisheries is rarely considered and there is a gap in our understanding of the economic consequences for the fisheries due to seal damage or predation. This chapter highlights the necessity to develop bioeconomic modelling to fully assess the effect of grey seal predation on fisheries in the North Atlantic so the relevance of this study.

2.1. Grey seal diet

2.1.1. Methods used to assess grey seal diet

There exist different methods to study seal diet, each of them having their own advantages and limitations. The most common methods are presented below. Other more recent methods exist such as the use of stable isotopes and DNA analysis but are not considered here since not broadly used yet (Bowen and Iverson, 2013).

2.1.1.1. Scat sampling

Scat analysis is the most common method used to determine seal diet. This consists of the collection of faecal samples on seal haul-out sites and on their analysis to extract fish remains such as otoliths and any other hard part (e.g. cephalopod beaks, bones). In the UK, this method has been used in 1985 and 2002 by the Sea Mammal Research Unit (SMRU, University of St Andrews) to assess grey seal diet in the North Sea and the West of Scotland (Hammond et al., 2006; Harris, 2007) but also more recently in 2010/2011 (unpublished data). Some studies have based their estimates of cod consumption by grey seals on this method in the West of Scotland (Holmes, 2008; Holmes and Fryer, 2011; Cook et al., 2015; Cook and Trijoulet, 2016), and this technique has also been used to analyse the impact of harbour seals on fish stocks in the North Sea (Bjørge et al., 2002).

The advantage of the scat sampling method is that it is simple and non-intrusive but it only reflects recent seal feeding and foraging close to shore. For these reasons, most studies assume that the inshore and the offshore diets of grey seals are the same. However, this method has been used to study the offshore diet of grey seals using samples collected on Sable Island (Canada), an offshore haul-out site (Bowen and Harrison, 1994; Beck et al., 2007). Furthermore, this method is limited when the otoliths are partially or completely digested so cannot be related to an identified fish species because the otoliths are too damaged. These are often discarded during the analysis and can induce important bias in the results. Often, a digestion factor is used to

account for partial digestion. Some improvements have been also done to account for complete digestion using feeding experiments on captive individuals. The factors applied are called number correction factors (NCFs) and began to be commonly used when dealing with seal diet (Tollit et al., 1997; Bowen, 2000; Grellier and Hammond, 2006; Hammond and Grellier, 2006; Hammond et al., 2006; Harris, 2007; Lundström et al., 2007; Gosch et al., 2014; Hammill et al., 2014). Even if it is believed that seal diet estimates corrected for partial and complete digestion are reliable, these processes can vary with individual seals but also with prey and NCFs may not be available for some fish species in certain geographic areas (Tollit et al., 1997; Grellier and Hammond, 2006; Bowen and Iverson, 2013). This adds to uncertainty in seal diet estimates. Moreover, the scat sampling method assumes that grey seals eat the head of all prey. However, this approach is subjected to limitation due to head rejection and belly-biting behaviours which appear to be observed in grey seals notably by fishers (Moore, 2003). In these cases, the head and then the otoliths of the fish are not consumed. This seems to occur mainly when grey seals forage on large fish and can underestimate the proportion of large fish in grey seal diet (Bowen and Harrison, 1994; Harris, 2007; O'Boyle and Sinclair, 2012). Also, some fish such as cartilaginous fish do not have otoliths and may be underestimated in the sample. This highlights the advantage of using all the hard parts found in seal scats. Finally, studies using the scat sampling method assume that all otoliths found in the samples correspond to fish consumed by grey seals. The presence of otoliths in the samples can also result on predation of small fish by piscivorous fish (Arnett and Whelan, 2001). In that case, otoliths found in the sample are not fully representative of grey seal diet but rather what other fish have eaten.

2.1.1.2. Stomach and intestines contents

The second possible method to study grey seal diet is the analysis of hard prey remains in stomach and/or intestine contents. This technique has been used to determine seal diet mainly in Canada and the Baltic Sea (Bjørge et al., 1981; Andersen et al., 2007; Lundström et al., 2007; Lundström et al., 2010; Benoît et al., 2011a; Kauhala et al., 2011; Suuronen and Lehtonen, 2012; Hammill et al., 2014) but also cetacean (Bjørge et al., 1981), bird (Andersen et al., 2007) and fish diets (Bundy, 2005; Bundy and Fanning, 2005).

Beside digested otoliths analysis limitations, this technique requires dead animals from hunting, bycatch or stranding so the number of samples is often limited. As with the scat method, this approach only accounts for recent feeding. This could be a serious problem notably when grey seals are caught at the netting stations. Indeed, the grey seal diet possibly reflects in that case the species caught by the fishery and can bias grey seal diet composition (Lundström et al., 2007; Lundström et al., 2010).

2.1.1.3. Quantitative Fatty Acid Signature Analysis (QFASA)

This method, less often used in the UK, consists on the analysis of seal blubber assuming that the acid signature of the prey is accumulated in fatty tissues. This technique has been used in Canada to assess the impact of seal predation on cod (Trzcinski et al., 2006) and sex differences in grey seal diet (Beck et al., 2007). More recently, Lundström (2012) applied this method to assess the diet of Baltic grey seals.

This process has the advantage of giving a broad idea of seal diet from weeks to months so it can be used to assess offshore diet as it is not limited to recent feeding. A recent publication also concluded it may be possible to detect changes in the diet using fatty acid signature analysis (Stewart et al., 2014), which could permit the investigation of switching in seal diets. However the composition of lipids can be modified during the seal's metabolism, prey lipid composition can vary with seasons and age, and the acid signature is often given for taxonomic groups rather than exact species (O'Boyle and Sinclair, 2012). If the acid signature of a prey is unknown because it has been modified by grey seal metabolism or because its signature model is unknown, the prey will be unidentified and underestimated in the diet. However, the acid signature library for grey seal diet is well documented (see discussion in Trzcinski et al. (2006)).

2.1.1.4. Summary

As discussed above, each method has advantages, disadvantages and bias (Table 2.1). In this thesis, seal diet data obtained from scat sampling is used to estimate grey seal inputs for the bioeconomic models because this is the method to assess grey seal diet in the West of Scotland. Seal diet estimates have large confidence intervals which

highlight the limits of this method (Harris, 2007). The biases induced by the scat sampling method may add limitations to the simulation results. This is something that needs to be kept in mind when analysing the results of the bioeconomic models.

2.1.2. Variations in grey seal diet

2.1.2.1. Spatial and temporal variations

Spatial variation in the seal diet has been demonstrated (Bowen et al., 1993; Kauhala et al., 2011; Brown et al., 2012). At a large scale such as in the North Atlantic, grey seal diets differ between the Canadian coast, the UK and the Baltic Sea (Bowen and Harrison, 1994; Hammond et al., 2006; Harris, 2007; Lundström, 2012). This is mainly due to the availability of fish stocks. Indeed, grey seals are believed to be opportunistic predators which prey on what is available in their foraging ground (Brown et al., 2012; Gosch et al., 2014). They may be also able to switch from low abundant prey to most abundant ones (Smout et al., 2013). However in the West of Scotland, despite the decrease in cod stock from 1985 to 2002, the consumption of cod by grey seals has not changed (Hammond et al., 2006; Harris, 2007) and this contrasts with the idea of switching. Some researchers have demonstrated that grey seals movements follow fish distribution or aggregations (Harvey et al., 2012; Hammill et al., 2014); this could be an evidence of a certain diet preference. Grey seal diet varies spatially also at a small spatial scale (Lundström et al., 2007; Lundström et al., 2010; Brown et al., 2012; Lundström, 2012).

Table 2.1: Summary of method, advantages, disadvantages and possible bias for the three methods to assess seal diet.

	Scat sampling	Stomach and intestines contents	QFASA
Method	Collection of faecal samples on seal haul-out sites and extraction of fish remains (otoliths, beaks, etc.)	Extraction of fish remains from seal's stomach or intestines	Analysis of the acid signature of prey accumulated in the seal blubber
Advantages	Simple and inexpensive Large number of available samples Non-intrusive	Remains may be found less digested than for the scat method Differentiation by sex possible if genital parts collected also	Long-term diet (weeks to months) May be used to assess offshore diet Possible to test changes in seal diet
Disadvantages	Only recent feeding Only foraging close to shore The partial and complete digestion factors must be available for all fish species	Only recent feeding Only foraging close to shore The partial and complete digestion factors must be available for all fish species Number of samples limited by the acquisition of dead animals	Lipid composition can be modified during seal's metabolism Lipid composition may vary with prey age and with seasons Lipid composition often known for taxonomic groups rather than species Location of feeding area less defined
Possible bias	Need to assume that the inshore and the offshore diets are the same Otoliths limitations: <ul style="list-style-type: none"> - Need to assume that seals eat the head of all preys, possible underestimation if head rejection or belly-biting behaviours - Underestimation for partially digested otoliths which are discarded - Underestimation of fish without otoliths - Need to assume that all otoliths found in the sample come from fish eaten by seals and not from fish eaten by piscivorous fish 	Need to assume that the inshore and the offshore diets are the same Otoliths limitations Diet may reflect the fishery target if seal found at a netting stations	Underestimation if the acid signature of a prey is unknown

Grey seal diet shows also temporal variations. On a yearly basis (Brown et al., 2012), this could be due to a change in fish stocks or fish and grey seal movements; but variation in seal diet also occurs seasonally (Bowen and Harrison, 1994; Ministry of Agriculture and Forestry, 2007; Cronin et al., 2013). This latter variation is mainly due to the change in energetic requirements for grey seals during the year as they favour high quality prey to increase their metabolism (Beck et al., 2007). Indeed, grey seals need to prepare their energetic reserves before they fast. This happens during the moulting season, as more time is spent on land and less time is allocated to hunting and eating compared to the rest of the year. Also during the breeding season, grey seals fast when mating and during the lactation for female seals.

2.1.2.2. Sexual variations

Sexual variation in grey seal diet can be associated with diving behaviour and with body size dimorphism (Beck et al., 2007). Cronin et al. (2013) have demonstrated that body size and mass have an impact on female grey seals trip distance and duration. It is fair to believe that the difference in body size and mass between males and females could also influence diet composition. Moreover, female seal diet composition is more selective than male diet during breeding season to prepare for pregnancy and milking (Beck et al., 2007; Kauhala et al., 2011). This can be related to seasonal change in grey seal diet.

2.1.2.3. Age variations

Variation in grey seal diet according to age arises from a difference in fish selectivity between young and older seals (Bowen et al., 1993). Juvenile grey seals are believed to be less selective than adult grey seals (Kauhala et al., 2011; Lundström, 2012). This could be explained by a lack of diet preference but also by a broader niche breadth which provides them with more diverse fish species (Beck et al., 2007).

2.1.3. Grey seal diet composition

As previously mentioned grey seals are considered as generalist predators (Hammond and Grellier, 2006; Brown et al., 2012; Gosch et al., 2014). They consume prey present in their environment and are able to switch to more abundant prey when a particular food type becomes rare (Smout et al., 2013). However it is still not clear why the consumption rate of cod by grey seals in the UK has not decreased since 1985 (Hammond et al., 2006; Harris, 2007) while the cod stocks have declined substantially (ICES, 2015c; 2016b). The same observation occurred in Canada, where cod is an important component in grey seal diet even when its abundance is low (O'Boyle and Sinclair, 2012; Hammill et al., 2014). This could be evidence for a preference for cod in grey seal diet but can also be explained by different hypotheses. First, it could be interpreted as an indication that cod has not reached levels low enough to induce switching in the grey seal diet, which seems surprising giving the severe decline of the stocks in the past decades (ICES, 2014c). Modelling work by Matthiopoulos et al. (2003) concluded there was an absence of switching behaviour for the UK grey seals using seal diet in the 1980s. However a more recent study, considering also the most recent 2002 seal diet data, found evidence for switching behaviour in the North Sea grey seals (Smout et al., 2013). This may be due to the spatial scale considered but these conflicting results demonstrate the necessity of acquiring more seal diet data in the future to investigate grey seal foraging behaviour. The importance of cod in grey seal diet may also be due to the fact that grey seals predate on fish not directly available to fishers. This is a valid assumption since the VIa breeding haul-out site is notably close to a rocky untrawlable shelf (Marine Environmental Mapping Programme, 2015). However, the absence of overlap between fishing and foraging zones does not mean the absence of competition since the fish stocks in VIa are considered as a single well-mixed population over the entire area. The entire system is dynamic, seals and fish move and some studies have demonstrated that the cod stock in VIa may even not be differentiable from the stocks in the North Sea (Wright et al., 2006; Holmes et al., 2008; Heath et al., 2014b). Also this could depend on cod migrations and aggregations. Grey seals in Canada have been responsible for predation on cod aggregations during the winter (Harvey et al., 2012; Hammill et al., 2014). The proportion of cod in their diet increases therefore during the winter and decreases during the spring and summer

(Bowen et al., 1993), maybe also in relation to the choice of fatty fish to prepare for the moult and breeding months (Beck et al., 2007). Cod may also be locally abundant around subsurface features such as man-made structures that seals may target (Russell et al., 2014).

2.1.3.1. Around the UK

In the North Sea and the West of Scotland, seal diet composition has been studied following scat sample collections in 1985, 2002 by the SMRU (University of St Andrews). The new seal diet data (2010-2011) being not published yet, it is not presented here. In terms of seal selectivity at age, this data is similar to what was observed in 1985 for cod and haddock and the proportion of whiting eaten at age 1 has decreased compared to 1985 and 2002. While the consumption of cod per grey seal increased since 2002, it has decreased for haddock and whiting.

In the West of Scotland, some changes in grey seal diet occurred between 1985 and 2002 mostly in the importance of sandeel (*Ammodytes* sp.) and Atlantic herring (*Clupea harengus*) in the diet (Figure 2.1). The most abundant prey for both samples is sandeel, gadoids and herring (Hammond et al., 2006; Harris, 2007). Cod and haddock are important in grey seal diet representing each 10% of the diet in 2002. Whiting represents only 3% of grey seal diet in weight but is one of the most numerous fish in the faecal samples (Harris, 2007).

In the North Sea, grey seal diet is different, notably in terms of the importance of herring and sandeel (Hammond and Grellier, 2006; Hammond et al., 2006). Indeed, herring is barely consumed (378 tonnes in 2002 while 9,789 tonnes of herring are consumed in the West of Scotland). This is surprising because the herring stock is larger in the North Sea than in the West of Scotland (ICES, 2015b). However there is no assessment for sandeel in VIa so the relative abundance of both species cannot be compared between both regions. Grey seals prey mainly on sandeel which represents 75% and 59% of the diet in 1985 and 2002 respectively and makes it a key species for the predator. After sandeel, cod and haddock are the most important fish in the grey seal diet (7% and 6% of the diet respectively in 2002).

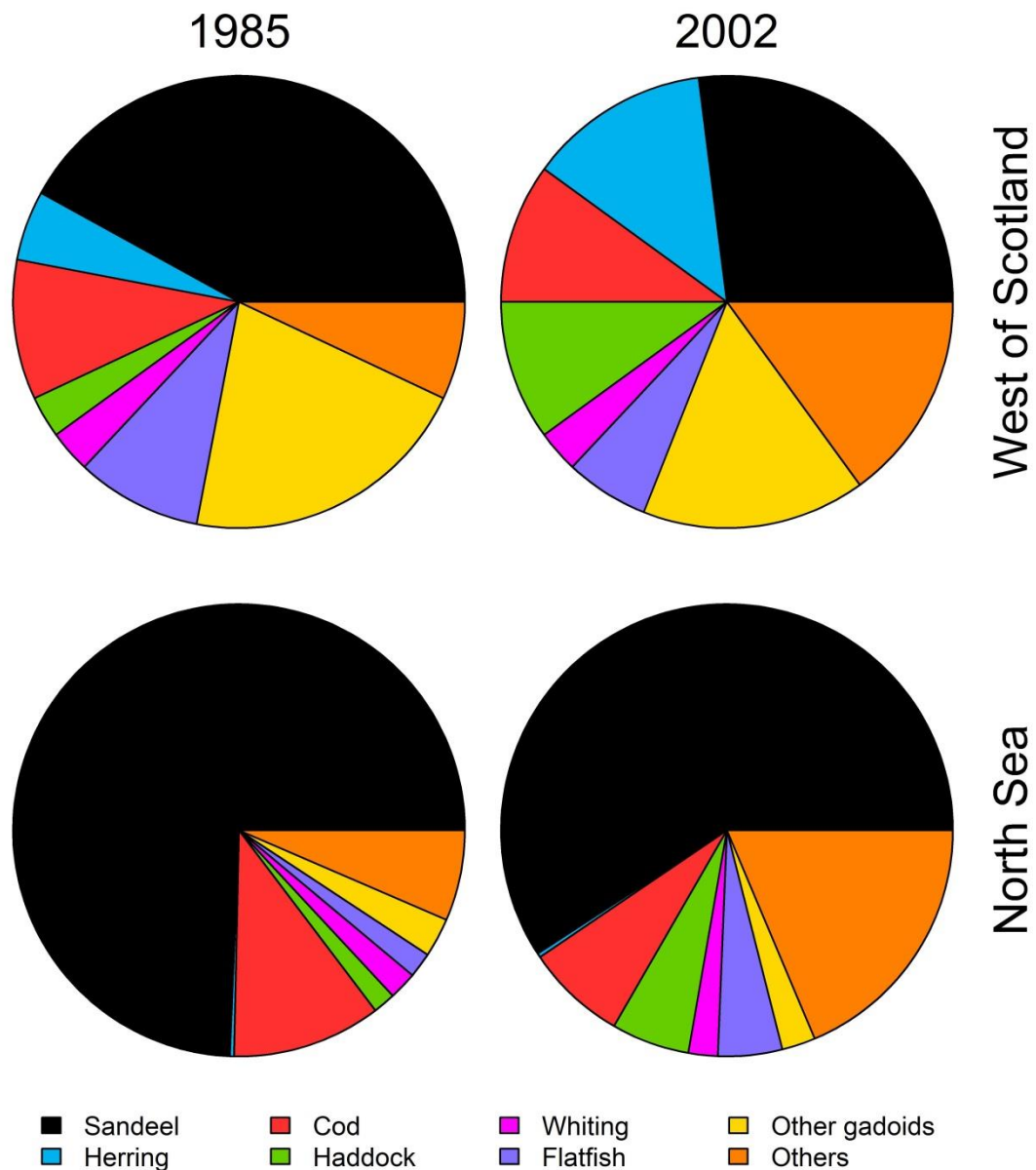


Figure 2.1: Grey seal diet composition (in weight) in the West of Scotland (Harris, 2007) and North Sea (Hammond and Grellier, 2006). In the West of Scotland, the 1985 “Other gadoids” group comprises ling, saithe, pollock (*Pollachius pollachius*) and Norway pout (*Trisopterus esmarkii*) and the “Flatfish” group comprises megrim and plaice (*Pleuronectes platessa*). The 2002 “Other gadoids” group includes also rockling (*Gaidropsarus* sp.), dragonet (*Callionnymus lyra*), poor cod (*Trisopterus minutus*) and blue whiting (*Micromesistius poutassou*) and the “Flatfish” group includes also lemon sole (*Microstomus kitt*). In the North Sea, the 1985 “Other gadoids” group includes ling, saithe and Norway pout and the 2002 group only include saithe and Norway pout. The 1985 and 2002 “Flatfish” groups comprise plaice and sole (*Solea solea*).

In conclusion, around the UK, sandeel, herring and gadoids are the most important species in grey seal diet. While sandeel is not a commercial species for human consumption but a major target for the industrial fisheries making fish meal (ICES,

2015b), the other preys are commercially important. Herring is an important forage fish which is abundant around the UK (ICES, 2015b) and which produces large fishing revenues despite its low commercial value (Marine Management Organisation, 2012). Cod, haddock and whiting are species of higher trophic levels whose density has substantially decreased since the 1980s. They are caught together in demersal mixed fisheries in both regions (ICES, 2014c; 2015c). Despite their decrease, their importance in grey seal diet has not decreased between 1985 and 2002 which seems at first glance in contradiction with the assumption of opportunistic diet for this predator. The importance of the three demersal species in grey seal diet may be evidence of possible competition between seals and the demersal fisheries in the area. Sandeel abundance has decreased since the early 2000s in the northwest North Sea (Heath et al., 2012b; ICES, 2015b), where grey seals are found (Jones et al., 2013). This may be why there is a decline in the proportion of sandeel in grey seal diet between 1985 and 2002. Sandeels have also declined in length (Wanless et al., 2004; van Deurs et al., 2013) and may therefore be less valuable. A decrease in the size of maximum selectivity also appears in grey seal diet between 1985 and 2002 (Hammond and Grellier, 2006). This decline in sandeel abundance and length has strongly affected seabirds (Furness, 2002; Wanless et al., 2005) and we may wonder what is the impact on grey seals. A hypothesis would be that because sandeels have declined in abundance and energetic value, it may be more valuable for seals to catch larger fish such as cod despite their low abundance.

2.1.3.2. In the Baltic Sea

In the Baltic Sea, grey seal diet varies in space in accordance with fish availability (Lundström et al., 2010). As a result, the grey seal diet in the northern Baltic Sea (Gulf of Bothnia, ICES Sub-divisions 30-31) differs with the grey seal diet in the Baltic Proper (Figure 2.2). Atlantic herring is the main prey for all age groups and for both geographic zones (Lundström et al., 2007; Ministry of Agriculture and Forestry, 2007; Lundström et al., 2010; Kauhala et al., 2011; Lundström, 2012) due to its presence in both areas (ICES, 2014a). When the European sprat (*Sprattus sprattus*) is significant in the Baltic Proper diet, it almost does not appear in the Bothnian diet. Inversely, the common whitefish (*Coregonus lavaretus*) plays an important role in the Gulf of Bothnia since undertaking anadromous migrations and does not appear in the Baltic Proper diet. Cod

and cyprinids (Cyprinidae) represent an important part of grey seal diet in the Proper while salmonids and common whitefish are important in the Gulf of Bothnia. This can be related to the presence of cod mainly in the Baltic Proper (ICES, 2014a) and the numerous salmon (*Salmo salar*) aquaculture stations in the Gulf of Bothnia but also to their aggregations during the period of return to the rivers (Suuronen and Lehtonen, 2012).

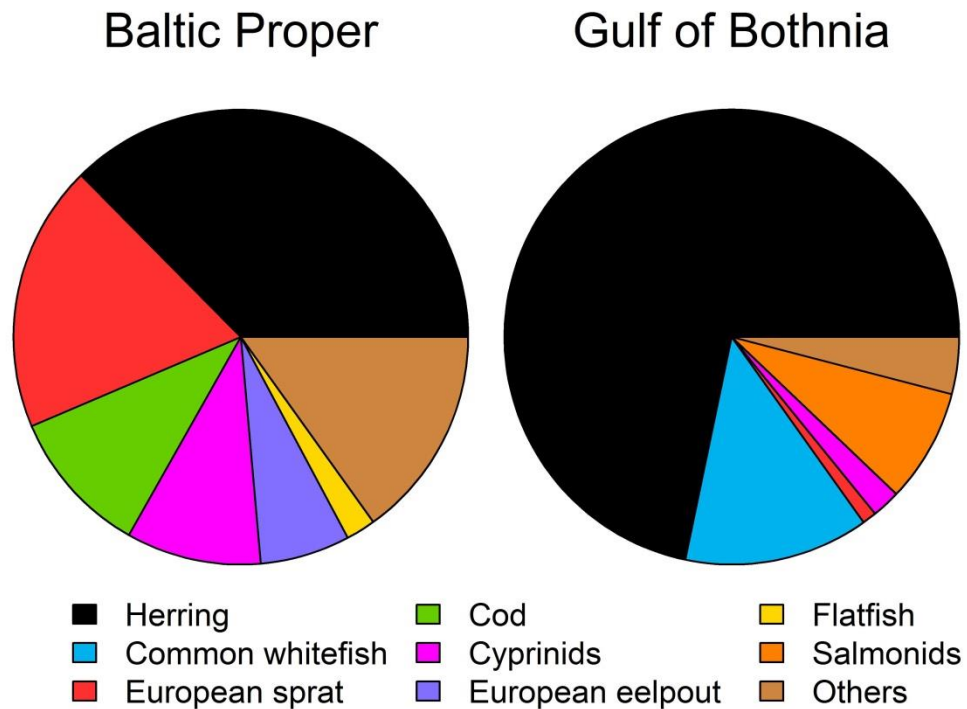


Figure 2.2: Baltic grey seal diet in the Baltic Proper and the Gulf of Bothnia (ICES Sub-divisions 30-31) as fractions of total biomass consumed between 2001 and 2005 reconstructed from stomach and intestine contents (Lundström et al., 2010).

In conclusion, Baltic grey seals eat commercially important fish species such as cod, herring, sprat, salmon and common whitefish (ICES, 2014a). The diet in the Baltic Sea is a good illustration of the opportunist diet of grey seals which eat what is available in the area.

2.1.3.3. Along the Canadian coast

Different inshore grey seal haul-out sites are present on the eastern coast of Canada. Grey seal diet in Cape Breton and Cabot Strait was obtained from the analysis of stomach contents (Hammill et al., 2014) (Figure 2.3). Despite both areas being geographically close, grey seal diet differs. Sandeel and white hake (*Urophycis tenuis*) are important prey in Cape Breton while cod is the most important prey in Cabot Strait. White hake and cod are species that collapsed in 1990s (Myers et al., 1997) and have not yet recovered despite the closure of the fisheries (Fu et al., 2001; Bundy and Fanning, 2005; Hutchings and Rangeley, 2011; Swain and Mohn, 2012; Sinclair et al., 2015) but which are still present in grey seal diet. This can be related to the fact that grey seals follow fish movements and feed on cod overwintering aggregations in the area (Harvey et al., 2012) so consume these species when there are present.

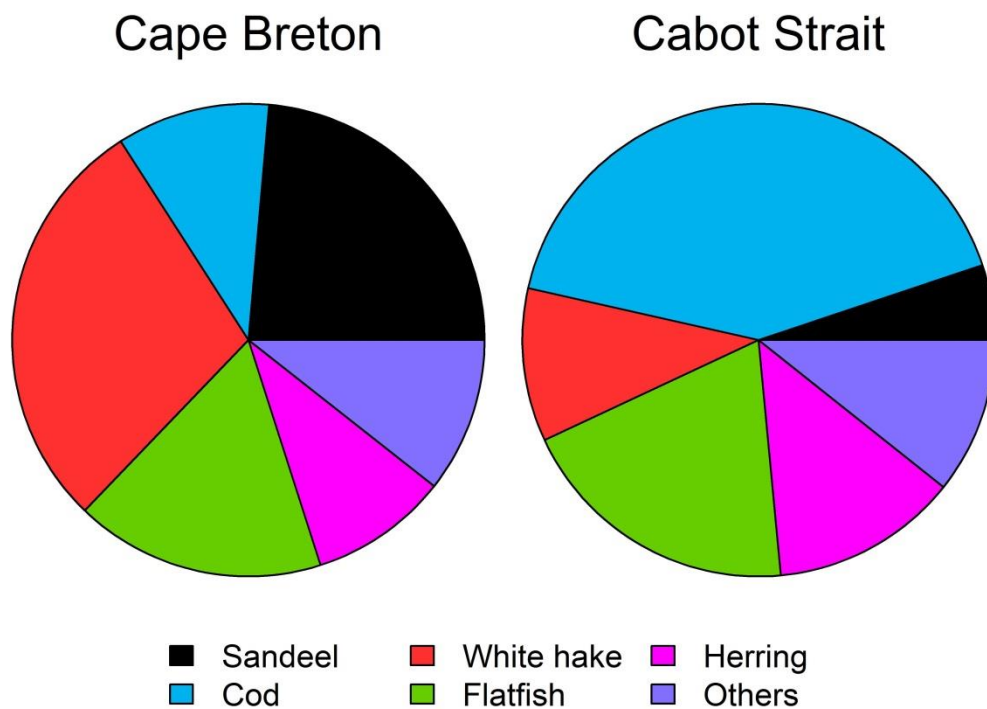


Figure 2.3: Canadian inshore grey seal diet as a fraction of total biomass between 1999 and 2011 reconstructed from stomach contents (Hammill et al., 2014).

A limitation to the methods used to assess grey seal diet is that they often only describe diet close to shore (Bowen and Iverson, 2013). Offshore grey seal diet has been

investigated in the 1990s considering faecal samples (Bowen and Harrison, 1994) and fatty samples (Beck et al., 2007) from a remote haul-out site, Sable Island (Figure 2.4). Grey seal diet varies over time with a decrease in the importance of sandeel more recently. It is also clear that the proportion of cod in the diet has declined after 1993 in accordance with the collapse of the stocks (Myers et al., 1997; Rose, 2004). The most recent diet shows a contribution of redfish (*Sebastes* sp.) in the diet which represents the most important prey after sandeel.

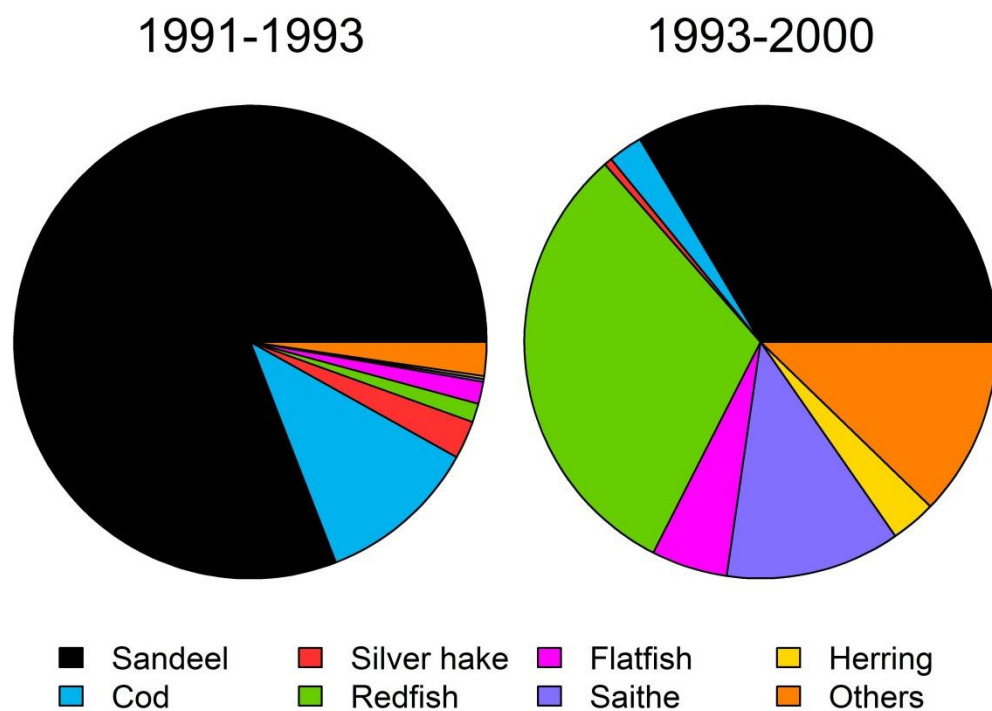


Figure 2.4: Canadian offshore (Sable Island) grey seal diet as a fraction of weight of fish consumed reconstructed from faecal samples (Bowen and Harrison, 1994) and fatty acid analysis (Beck et al., 2007).

2.1.3.4. Summary

Whether it is in Canada, around the UK or in the Baltic Sea, grey seals consume mainly fish of low trophic levels (sandeel, herring, benthic species, etc.) but some commercial demersal species still represent an important proportion of the diet. Despite the decline in cod stocks around the UK, this high trophic level fish still accounts for 10% of the West of Scotland grey seal diet (Harris, 2007) and 6% of the North Sea grey seal diet in 2002 (Hammond and Grellier, 2006; Hammond et al., 2006). There is evidence of a

decrease of cod in grey seal diet in the Baltic Sea and off the eastern Canada where a number of the cod stocks have collapsed (Bowen and Harrison, 1994; Beck et al., 2007; Lundström et al., 2007; Swain and Chouinard, 2008; Lundström et al., 2010; Isomaa et al., 2013). However, recent studies seem to conclude cod is still present in the Canadian grey seal diet (Hammill et al., 2014). Sandeel is a key species in Canadian and British grey seal diet and its variation may affect the consumption of other species. However, the absence of sandeel assessment in Canada, where no fishery exists for this species, does not permit verification of this assumption.

2.1.4. Size composition

The otoliths provide information about the size of prey consumed. Grey seals predate mainly on fish smaller than 50 cm. For example, Harris (2007) has concluded that in 2002 grey seals in the West of Scotland eat mainly cod between 35 and 40 cm, haddock between 24 and 36 cm, whiting between 20 and 28 cm, sandeel between 16 and 24 cm and herring between 24 and 45 cm. Other studies convert the prey size into age and conclude that grey seals eat mainly 2 to 3 years old cod (Holmes, 2008; Holmes and Fryer, 2011; Cook et al., 2015; Cook and Trijoulet, 2016).

In the Baltic Sea, 70% of prey in the grey seal diet have a size comprised between 15 and 25 cm (Lundström et al., 2007) and it seems that the proportion of larger species in the diet increases with seal age (Ministry of Agriculture and Forestry, 2007).

Bowen and Harrison (1994) have shown that Canadian grey seals on Sable Island eat fish with a mean size comprised between 10 and 25 cm. Whereas Beck et al. (2007) showed grey seals prey principally on large cod (>35 cm), herring (>20 cm) and sandeel but any size of redfish. More recently, Hammill et al. (2014) concluded that inshore grey seal consumed cod of an average size between 28 and 39 cm and white hake between 29 and 35 cm.

This size-selectivity may reflect the more abundant sizes of fish available in the ocean instead of a real size-selectivity for fish. However, this selection in prey length, expressed as size, age or maturity, is often used in the literature and has to be taken

into account when modelling trophic interactions. It is important when the concern is to compare seal predation to another type of fish removal (other predators, fishing activities, etc.). Indeed, two predators can consume the same size of prey. In this case, there exists a “scramble” competition where the predators compete for the same fish. If one predator eats younger fish than the second the competition is sequential and the first predator may remove fish before they can be eaten by the second predator. The change in predation with fish length or age is consequently an important feature to consider in competition studies, such as where a fishery and seals exploit the same resource.

2.2. Fish consumption by grey seals

2.2.1. Methods used to estimate fish consumption by grey seals

Papers publishing data on seal diet using the different methods mentioned in part 2.1.1 often give an estimate of total weight of fish consumed by grey seals. To estimate consumption, studies convert the weight of fish consumed by grey seals to energy (Harris, 2007). They then assumed that grey seals fulfil their energy requirements and estimate a gross energy intake per seal. This intake depends on different parameters and some are assumed to be known constant from the literature (Mohn and Bowen, 1996; Benoît et al., 2011a; O’Boyle and Sinclair, 2012). This means that the consumption estimates are uncertain. The consumption is converted back to fish weight to obtain per capita consumption rates (weight of fish consumed per seal per year) and multiplied by the number of seals in the area to obtain total consumption estimates. Since grey seal population estimates change over time with model improvements, it is therefore important to understand that the fish consumption estimated in each study depends on the seal population estimates used. The estimates are therefore also sensitive to the seal numbers estimates. This uncertainty has to be kept in mind in modelling studies using these estimates.

Because of the limited amount of data on seal diet, many studies assess seal predation using prey-predator models. This has been applied using single species models (Holmes, 2008; Holmes and Fryer, 2011), multispecies models (Matthiopoulos et al., 2003; Bundy, 2005; Bundy and Fanning, 2005; Bundy et al., 2009) and using different techniques such as Bayesian methods (Cook et al., 2015; Cook and Trijoulet, 2016), mass-balanced models in Ecopath with Ecosim (Christensen et al., 2005), or the ADAPT framework (Gavaris, 1988).

2.2.2. Fish consumption estimates

2.2.2.1. Around the UK

In the West of Scotland, estimates of fish consumption by grey seals were 53,000 t and 77,000 t in 1985 and 2002 respectively, consisting mainly of sandeel, herring and cod for an estimated seal population of 29,242 individuals in 1985 and 42,252 in 2002 (Hammond et al., 2006; Harris, 2007). The per capita consumption rates in the West of Scotland for cod, haddock and whiting are given in Table 2.2 and taken from Harris (2007).

The increase in consumption can be related to the increase in grey seal population. However, looking at the consumption rates per seal, it is obvious that the per capita consumption of cod decreases slightly while the stock has decreased substantially (SSB of 24,827 t in 1985, 7,174 t in 2002 and 2,220 t in 2010-2011 (ICES, 2013b)). The big increase in haddock consumption in 2002 is also surprising but may be due to high SSB and recruitment observed during this period (ICES, 2013b).

In the North Sea, fish consumption by grey seals shows also an increase. Indeed, 39,000 t and 116,000 t of fish were consumed in 1985 and 2002 respectively. Cod consumption changes substantially from 4,100 t in 1985 to 8,300 t in 2002 (Hammond et al., 2006). For comparison purposes with the West of Scotland estimates, the consumption rates in the North Sea are given in Table 2.3 (Hammond and Grellier, 2006).

Table 2.2: Average per capita consumption rates in West of Scotland given in kg of fish consumed per grey seal per year, taken from (Harris, 2007).

	1985	2002
Cod	184	179
Haddock	52	188
Whiting	47	51

It can be seen that the trend in consumption is similar to the West of Scotland. However the decrease in cod consumption is greater in the North Sea.

Table 2.3: Average per capita consumption rates in the North Sea given in kg of fish consumed per grey seal per year, taken from Hammond and Grellier (2006).

	1985	2002
Cod	175	125
Haddock	26	98
Whiting	33	37

According to Boyd and Hammond (2010), the recent total annual consumption of fish by grey seals in the Scottish waters (West of Scotland, north of the North Sea) is 190,000 t. Even if seal predation does not seem significant with less than 5% of the total stock biomass consumed in the West of Scotland (Hammond et al., 2006), it seems that grey seal predation may be substantial on the depleted cod stock.

2.2.2.2. In the Baltic Sea

Papers assessing the annual fish consumption by Baltic grey seals are rare. On average, one adult grey seal is considered to eat 5 to 8 kg of fish a day (Ministry of Agriculture and Forestry, 2007; ICES, 2014a). More recently, Lundström (2012) argues that grey seal predation is not significant at the Baltic Sea scale but can be greater than fishing catches regionally.

2.2.2.3. Along the Canadian coast

In Canada, most of the studies concentrate in seal predation on cod because of the collapse of the stocks in 1990s. Benoît et al. (2011a) estimate cod consumption by grey seals in the southern part of the Gulf of St Lawrence to be between 15,800 t and 18,700 t. O'Boyle and Sinclair (2012) have estimated cod consumption by grey seals at 346,000 t per year in Sable Island and the eastern Scotian Shelf and 17,000 t per year in the Gulf of St Lawrence. They also concluded that after 1993 (year of the moratorium for fisheries closure), most of cod mortality may be due to seal predation. Trzcinski et al. (2006) have assessed that a male grey seal has to eat 1.61 t of cod per year and a female has to consume 1.35 t of cod per year to fulfil their energetics requirements for seal growth and maintenance, in the eastern Scotian Shelf. Furthermore, they estimated the mortality due to seal predation to be 0.21 out of a total natural mortality of 0.62. So seal predation represents a significant fraction of cod natural mortality (Benoît et al., 2011b).

2.3. Some initial findings on the impacts of seals on fish stocks

Opinions are mixed as regards to the impacts of seal predation on fish stocks. Since the situations differ regionally it has been chosen to present the conclusions for the UK and the Baltic Sea first and then for Canada.

2.3.1. In the Northeast Atlantic

Different hypotheses have been proposed to explain the decrease in fish stocks around the UK and the Baltic Sea. Among these, high levels of fishing (Myers et al., 1996; Christensen et al., 2003; Boyd and Hammond, 2010; Alexander et al., 2014) and climate change (Brander, 2005; Drinkwater, 2005; Heath et al., 2012a) are commonly accepted

and seal predation is not believed to be responsible for the stock decline in the Northeast Atlantic (MacKenzie et al., 2011; Alexander et al., 2014).

In the Baltic Sea, despite the fact that grey seal predation may be significant at a regional scale because seal consumption can be larger than fishing catches (Lundström, 2012), most studies agree that grey seals do not affect the fish stocks given that the stocks are currently recovering (Cardinale and Svedäng, 2011; Eero et al., 2012). Also, since the cod decline (Hutniczak, 2012; Isomaa et al., 2013), cod is not significant in the grey seal diet (Ministry of Agriculture and Forestry, 2007) and grey seal predation does not affect the herring assessment in the Bothnian Sea (Gårdmark et al., 2012; ICES, 2014a).

Around the UK, however, the demersal stocks have not yet recovered and grey seals may play a role in their non-recovery in certain regions. Cook et al. (2015) demonstrates that seal predation mortality on cod in the West of Scotland represents half the natural mortality on the stock and that this may be responsible for its non-recovery. A more recent study has however shown that the probability of cod recovery may be high at the current (2014) level of fishing but is still sensitive to an increase in seal predation or fishing mortality (Cook and Trijoulet, 2016). Nevertheless, grey seal predation was determined as being too low or uncertain to be considered in cod assessment in the West of Scotland (Holmes, 2008; Holmes and Fryer, 2011). In the North Sea, while seal predation on haddock and whiting is insignificant, grey seals are one of the most important predators of cod (Harwood and Walton, 2002). In Ireland, grey seals seem to have little or no impact on fish stocks (Houle et al., 2015).

These diverse opinions highlight the difficulty to conclude about the impact of grey seals on fish stocks in the Northeast Atlantic. It seems evident that not enough information is available yet to support any possible return to seal culls in the area (Harwood and Walton, 2002).

2.3.2. In the Northwest Atlantic

In the Northwest Atlantic, many groundfish stocks collapsed in the early 1990s and a fishing moratorium was established in 1993 to help the stocks to recover. The collapse has been marked by a change between a large cod-dominated ecosystem to a forage fish-dominated ecosystem (Frank et al., 2005; Bundy et al., 2009; Frank et al., 2011). This shift has induced a change in fishing regime where crabs and shrimps become the target species (Bundy, 2005), highlighting the process called by Pauly et al. (1998) “fishing down the food web”. Most studies agree that the collapse of the groundfish stocks is mainly due to a high fishing mortality rather than seal predation (Mohn and Bowen, 1996; Myers et al., 1997; Chouinard et al., 2005; Trzcinski et al., 2006; Morissette et al., 2012; O’Boyle and Sinclair, 2012; Buren et al., 2014). However some suggest grey seals are responsible for the non-recovery of the cod stock since the moratorium was established (Chouinard et al., 2005; DFO, 2011; O’Boyle and Sinclair, 2012; Sinclair et al., 2015; Ouellet et al., 2016). The non-recovery of the cod stock seems to be due to an increase in natural mortality and grey seal predation may be the main source of mortality in the area. Moreover, a recent study shows that cod and white hake are still an important portion of the grey seal diet since the collapse (Hammill et al., 2014). Grey seals may also be responsible for a change in fish distributions (Swain et al., 2015).

The role that grey seals may play in the non-recovery is contradicted by other studies which suggest no significant impact of grey seals on the fish stocks (Swain and Chouinard, 2008; Benoît et al., 2011b; Swain and Mohn, 2012). Some researchers highlight the importance of fish predation rather than seal predation on the stocks (Overholtz and Link, 2007) and affirm that the non-recovery is mainly due to the poor condition of the stocks which are unable to compete with other fish species (Bundy and Fanning, 2005). Others concluded the non-recovery is due to bottom-up controls and is driven by forage fish dynamics such as capelin (Buren et al., 2014). However, any removal on a poor stock will have a negative impact. So any predation on cod, white hake or herring, whether by seals or other predators, will have a negative impact on the stocks (Trzcinski et al., 2006).

As in the Northeast Atlantic, along the Canadian coast, it is also difficult to conclude on the impact of grey seals on the fish stocks (Benoît et al., 2011b) but most papers agree on the role grey seals currently play in the non-recovery of the demersal stocks. Despite the uncertainty of the studies, some stakeholders still ask for large seal culls (of more than 30,000 individuals) in the Gulf of St Lawrence to improve the groundfish recovery (Fisheries Resource Conservation Council, 2011; Standing Senate Committee on Fisheries and Oceans, 2012). This highlights the need of further studies quantifying the impact of grey seals on fish stocks but also on fisheries.

2.4. Grey seal impacts on fisheries

2.4.1. The different types of impacts

It has been established that grey seals are responsible for two kinds of impacts on fisheries, direct impacts and indirect impacts. The indirect impact corresponds to the fishing catch loss due to seal presence in the fishing area, by predation or by scaring fish away from nets and catch loss due to seal-induced fish infections. The direct impact relates to fishery income loss due to seal induced damage, such as damage to gear, damage to fish inside the net or also predation of fish inside the nets (Harwood, 1984; Lavigne, 2003; Moore, 2003; Cronin et al., 2014). This is called depredation. This latter aspect, being the most visible, is often the most commonly claimed by fishers. It is also the simplest to assess so often the most frequently considered in scientific papers.

2.4.2. Methods used to assess grey seal impacts on fisheries

Assessing the impacts of seals on the North Atlantic fisheries is not trivial. Many papers study the impact of seals on a specific fish stock in a specific region (see part 2.3). However, most do not link this impact with the possible impacts on fisheries in the

area. Nevertheless, some studies have tried to evaluate this effect, but the methods used are often incomplete.

Some studies consider the impact of grey seal predation on fisheries by comparing seal catch with fishing catch (Bjørge et al., 2002; Lundström, 2012). It is clear that this method is not adequate to assess the impact of grey seals on fisheries since no economic aspect is considered. Also, it is not possible to prove that seals are taking fish that would be available to fishers otherwise. To consider this aspect some researchers studied the possible overlap of seal distribution and fishing grounds (Cronin et al., 2012; Oksanen et al., 2014). While this represents a good attempt to determine competition zones, an overlap does not necessarily mean competition and grey seals may not be foraging in these areas. Even if the improvement of telemetry data enables scientists to determine when seals show feeding behaviour, it is still unclear what fish species they are targeting and if this coincides with what fishers are fishing.

A few publications estimate economic costs to fishers due to grey seal damage using questionnaires (Bjørge et al., 1981; Moore, 2003; Butler et al., 2011). Fishers are asked to give an estimate of the costs, usually of seal depredation impacts, on their business. These studies present limitations. Indeed some can argue that the number of respondents can be limited and only fishers who are concerned by grey seal impacts will respond. Also, these papers only look at one side of the problem since they don't compare economic loss due to seals with fishing profits. Others used observers on-board to estimate the depredation impacts of grey seals on fisheries (Kauppinen et al., 2005; Königson et al., 2005), but the economic impact is usually not quantified.

When considering grey seal impacts on fisheries it is also reasonable to compare the economic loss due to seals with the economic gain from their presence through tourism or conservation (Bosetti and Pearce, 2003).

2.4.3. The economic impacts of grey seals on fisheries in the North Atlantic

Following fishers perception of grey seals as a significant threat to their livelihood, much research looks at the impact of grey seals on fisheries (Lambert, 2001; Read, 2008). Such as before with the impact of grey seals on fish stocks (part 2.3), the opinions among scientists are divided.

Most of the studies looking at seal impacts on fisheries only describe the impact without relating it to any economic value. As previously mentioned, grey seals are mostly studied for their depredation impacts on fisheries by damaging the fish or gear or stealing fish from nets (Holma et al., 2014). These problems are something commonly recorded in the literature. Moore (2003) investigated the impact of seals on the Clyde Sea trawl and creel fisheries. It was reported that 95% of trawlers and 88% of creelers have or have had personal experience with seals interfering with fishing activities by damaging gear (60% of trawlers, 76% of creelers), damaging fish (91% of trawlers, 89% of creelers) or stealing fish inside the nets (82% of trawlers). Depredation impacts of grey seals on fisheries is also present along the Irish coast (Cronin et al., 2014). In the Baltic Sea, Kauppinen et al. (2005) also observed seal damage to catch and gear in the Finnish coastal trap-net fishery and Jounela et al. (2006) determined that seal-induced catch losses represented 3 to 29% of the total catch of the salmon fisheries. Also, much of the effects of seals go unnoticed because seals not only damage fish but also scare the fish away from the nets or consume the whole fish within them (Königson et al., 2005; Königson et al., 2007). So this hidden damage is a process that can have a large impact on fishing catch. In terms of fishery losses due to seal predation, in the North Sea grey seals may have a negative impact on gillnet and seine fisheries but may have a positive effect on the shrimp fishery by foraging on its predators (Bjørge et al., 2002). Oksanen et al. (2014) concluded on a possible impact of grey seals on fisheries due to the overlap between grey seal foraging grounds and trap-net fisheries in the Baltic Sea. However these studies do not consider the economic loss due to seal damage or predation so it is not possible to conclude on a significant grey seal impact on fisheries.

Some papers tried to estimate the loss due to seal damage on fisheries (Houle et al., 2015). Bjørge et al. (1981) estimated that grey seal damage to gear was between £13 and £3,337 per vessel and per year in the Norwegian fisheries. However this corresponds to estimates from only 18% of fishers. Also, Butler et al. (2011) have estimated the economic costs due to seal-damage on Atlantic salmon fisheries in the Moray Firth. Total seal-induced losses were estimated to be £14,960 per year for all rod fisheries and £16,500 per year for all netting stations, the fisheries the most impacted being the ones close to the river mouth. Finally, Cornish fleets have estimated the annual costs due to fish damage by seals to be of around £100,000 per year (Bosetti and Pearce, 2003). It is clear that those numbers are not particularly informative unless compared with the total value of the fishery.

Some researchers considered grey seal impacts on fisheries are insignificant. Bosetti and Pearce (2003) compared the estimated costs of seal induced damage with the gain obtained from their presence (tourism and conservation). They concluded that the benefits from seals are higher than the costs. However, their study is based on surveys of fishers and tourists. The respondents may then be mostly fishers impacted by seals and tourists already willing to pay to see seals or help for their conservation. In Ireland, there seems to be little evidence of competition for the resource between trawl fisheries and grey seals (Cronin et al., 2014) and of overlap between grey seal and fishing effort distributions (Cronin et al., 2012).

In summary, only few studies dealing with the economic aspect of the impacts are available, most of them acquiring their results by interviewing fishers. Even if some studies have tried to estimate the economic impacts of seals on fisheries, it remains difficult to draw reliable conclusions without comparing the economic loss with the total incomes of fisheries. Indeed the real impacts of grey seals will depend of the value of the fishery. A few thousand pounds of income loss due to seal depredation could be significant for a small scale fishery but not that important for a fishery with million pounds of benefits (Perring, 2001). Also, it almost only concerns depredation impacts and it seems that there are few studies considering the indirect economic impacts of grey seal predation on fisheries in the North Atlantic. This lack of data currently does not help to mitigate the seal-fishery controversy and fishers persist in asking for large

seal culls (Butler et al., 2011; Gruber, 2014). Some papers propose nevertheless some options to reduce these conflicts and these are discussed in the next part.

2.4.4. Proposals to mitigate the seal-fishery controversy

Most studies agree that improvements have to be made to determine the impacts of seals on fisheries. There is a consensus that the effort should concentrate on gathering long-term seal diet data, spatial data on seal, fish and fishing movements and use them to model the impacts of grey seals on fisheries (Yodzis, 2001). Meanwhile, local fisheries, seal management (Harwood, 1984; Bruckmeier et al., 2013) and seal-induced damage compensation can be considered (Bosetti and Pearce, 2003; Varjopuro, 2011; Werner et al., 2015).

There is an increase of studies looking at the development and effectiveness of seal safe equipment and deterrent devices to mitigate the direct impacts of seals on fisheries. These studies are mostly completed in the Baltic Sea where the seal-fishery conflict is severe notably for the salmon fisheries (Lunneryd et al., 2003; Lehtonen and Suuronen, 2004; Fjälling et al., 2006; Suuronen et al., 2006; Lehtonen and Suuronen, 2010; Varjopuro, 2011; Oksanen et al., 2014) while in the UK, salmonids do not represent a large part of grey seal diet even in estuaries (Matejusova et al., 2008). These devices seem to be relatively effective even if some improvements are still needed. A significant amount of work has been done in the Baltic Sea to propose modified nets and traps which reduce grey seal access to enter the net and/or steal fish from it (Lunneryd et al., 2003; Suuronen et al., 2006). This seems to be more effective for the salmon than the common whitefish fisheries (Lehtonen and Suuronen, 2004). Depredation impacts at netting stations are often believed to be due to few “problem” or “rogue” seals (Lehtonen and Suuronen, 2010; Graham et al., 2011), often big males (Konigson et al., 2013). Consequently Lehtonen and Suuronen (2010) proposed a modified salmon trap which captures the seal alive to improve selective removal, help researchers who need live individuals or help reduced lethal bycatch. Papers also look at the effectiveness of Acoustic Deterrent or Harassment Devices (ADDs or AHDs) to scare seals away from the netting areas. In the Baltic Sea this method has been proven effective (Fjälling et al., 2006). In the North Sea, the opinions are more divided. The use of ADDs at the salmon

trap nets has been ineffective in deterring grey seals at the vicinity of the nets but reduced seal upstream movements to river by around 50% (Graham et al., 2009). More recently, Harris et al. (2014) demonstrated the efficiency of ADDs to increase salmon landings and reduce seal damage to the bagnet fishery. However it is still not clear what the impact is of these devices on other marine mammals such as cetaceans which are more sensitive to noise and on seabirds which may also induce important impacts notably for fisheries using buoying or nets close to the surface (Gotz and Janik, 2013). This equipment can also scare the fish away from the nets and do not take into account the ability of seals to learn with time and to adapt their behaviour to new situations (Fjälling et al., 2006).

2.5. Summary and discussion

The controversy between fishers and conservationists regarding the role grey seals have played in the decline of the groundfish stocks in the North Atlantic has been amplified by the increase of seal depredation impacts at the netting stations. This highlights the necessity to study grey seal impacts on fisheries to help mitigate the conflicts.

Despite the fact that grey seal diet is mainly composed of fish species of low commercial value (Hammond et al., 2006; Harris, 2007; Lundström, 2012; Hammill et al., 2014), the proportion of commercial fish in the diet is sufficient for fishers to see grey seals as a threat to their livelihood.

The opinions regarding the relative impact of grey seals on fish stocks or on fisheries are still mixed and the studies are rare or incomplete. First, the studies mainly quantify grey seal consumption but do not convert it into economic terms. Also, when the economic impact is considered, the studies mainly focused on quantifying grey seal depredation impacts, principally via interviews to fishers, and the impact of grey seal predation is hardly evaluated. There is to our knowledge no study looking at the economic impact of grey seal predation in the North Atlantic.

Furthermore, grey seal predation is primarily studied on cod. However, seal diet data indicates that other commercial species are present in grey seal diet, and sometimes in the same proportion than cod (Harris, 2007). This highlights the necessity of studying grey seal predation on the other fish species to fully determine grey seal impacts on fisheries.

Despite divided opinions regarding grey seal impacts, fishers still seek a return to seal culls (Moore, 2003; Butler et al., 2011). However, there currently exists little evidence that grey seal culls are really effective (Yodzis, 2001; Morissette et al., 2012; Bowen and Lidgard, 2013). Also, even if the reduction of grey seal predation induces an increase in commercial fish stocks, this does not mean it increases the stocks available to fishers (Harwood, 1984).

Nowadays, the lack and uncertainty on grey seal diet and their foraging behaviour, on the ecosystem interactions and the fish stock dynamics, or on fishing income losses due to seals, do not enable scientists to draw sound management conclusions about the seal and fishery controversy (Harwood and Walton, 2002; Heymans et al., 2011). However, bioeconomic modelling is likely to be the best way to assess objectively the direct or the indirect impacts of grey seals on fisheries and to provide managers with information to deal with the problem.

The next chapter concentrates on the status of seals and fisheries in the West of Scotland.

Chapter 3

Fishing and grey seals in the West of Scotland

This chapter describes the West of Scotland ICES Division VIa, its topography and physical characteristics. The fishing activities in VIa are described and the choice of considering the demersal fishery for cod, haddock and whiting as case study is explained. The fleets and species caught in the mixed fishery are then detailed. Finally, grey seal population is considered in the area.

3.1. The West of Scotland area, ICES Division VIa

3.1.1. Physical characteristics

The West of Scotland area corresponds to the ICES Division VIa which is delimited in blue on the Figure 3.1. Half of the area comprised the continental shelf (less than 200 m depth). The continental slope is steep and descends quickly to 3,000 m which is the maximum depth. The slope acts as a barrier between continental shelf and deep regions (Baxter et al., 2008).

The seabed is mainly composed of gravelly sand and mud but there is a large untrawlable rocky area on the west coast of the Outer Hebrides (Marine Environmental Mapping Programme, 2015).

The Division VIa is marked by numerous protected areas (Marine Protected Areas and Special Areas of Conservation) associated with lochs and isles (Baxter et al., 2008) which highlight the importance of the natural ecosystems.

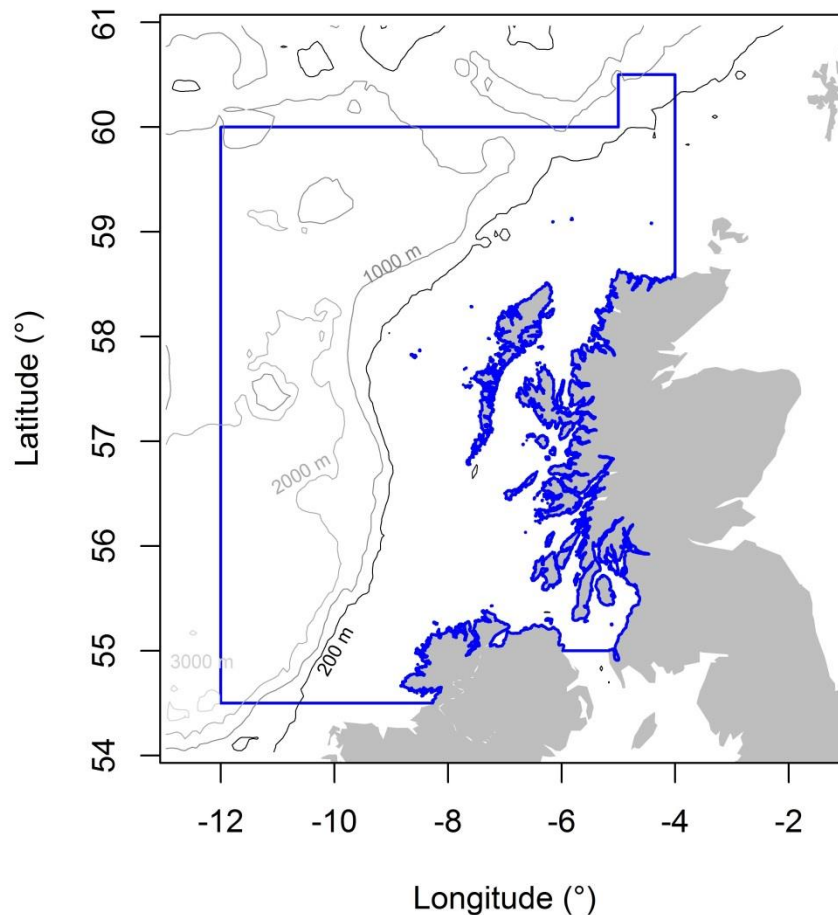


Figure 3.1: Map of the ICES Division VIa (blue box) indicating the bathymetry.

The West of Scotland received along the continental slope surface warm and saline waters coming from the North Atlantic current (Baxter et al., 2008). This current brings important nutrients and food to the area. The Scottish Coastal Current going north flows along the coast. Tidal currents can be strong with a tidal range between 0 and 6 meters. A deep cold current coming from the Arctic also exists.

The particular characteristics of the bathymetry and the oceanographic currents in VIa permit the development of complex natural ecosystems, notably on the continental shelf.

3.1.2. Connectivity to the other areas

The ICES Division VIa is a management zone. This means the boundaries of the area are not closed and the fish stocks can move between management zones. Connectivity with neighbouring fish stocks in the Irish Sea and the North Sea notably occurs. The VIa cod stock is believed to be connected to the North Sea stock (Wright et al., 2006; Holmes et al., 2008) and the haddock stock is considered as a single stock distributed between the West of Scotland, the North Sea (Division IV) and Skagerrak (Division IIIa) since 2014 (ICES, 2015c). However, the ICES areas represent fisheries management units and the large consumption of cod by grey seals in 2002 in VIa (Harris, 2007) motivates the study of grey seal predation in this area.

3.2. Fishing in VIa

3.2.1. The different fisheries in operation in VIa

In the West of Scotland, there are both inshore and deep-water fisheries (Scottish Government, 2015a).

The deep-water fishery occurs at 400 m depth or more (continental slope) and fishes around 12 fish species such as blue ling (*Molva dypterygia*) (ICES, 2013c). The continental slope is less productive than the continental shelf where the inshore fisheries take place.

There exist three main types of shelf fisheries in VIa: the pelagic fishery, the demersal fishery for whitefish and the demersal fishery for shellfish (Scottish Government,

2015a). The pelagic fishery targets herring, mackerel (*Scomber scombrus*) and blue whiting (*Micromesistius poutassou*). This fishery uses mainly pelagic trawlers. The demersal whitefish fishery is the fishery for cod, haddock and whiting and it uses mainly trawl gears (ICES, 2014c). The shellfish fishery catches molluscs and crustaceans of which the most important is *Nephrops* due to its high commercial value (ICES, 2014c). The shellfish are caught mainly by demersal trawlers, creelers and dredges. The demersal trawlers targeting *Nephrops* also land small amounts of whitefish as bycatch. The two demersal fisheries are often connected because the vessels have the possibility of switching gears to change the targeted species. This will be explained in part 3.3.2.

3.2.2. Current regulations in VIa

There exist currently different fisheries regulations in place in VIa (Scottish Government, 2015b). The West of Scotland fisheries are managed since the 1970s under the Common Fisheries Policy (CFP) giving registered European fleets equal access to European waters (European Commission, 2015). The CFP gives a framework to the fishing fleets with the aim to conserve the commercial stocks.

There exist total allowable catches (TACs) on fish species in the Scottish waters (Scottish Government, 2015b). This limits the catch to the level of harvest defined by managers (Anderson and Seijo, 2011). For TAC allocation, fleets are divided into three groups: 10 m and under, over 10 m under Producer Organizations (PO) and over 10 m non-PO. For vessels over 10 m the quotas are given to the vessels, and for vessels under 10 m, the quotas are a pool handed by the Fisheries Administration.

TAC values have changed over the years in relation to changes in fisheries management (Figure 3.2). While in the late 1980s the fishing mortality on whitefish was towards the fishing mortality at maximum yield per recruit (F_{max}), managers decided on reducing substantially the TACs in early 1990s in response to the decline in the demersal stocks in the Northeast Atlantic (ICES, 2013a). While the TACs for haddock stay reasonably high over the years, for cod and whiting the non-recovery of the stocks induced a constant decrease in the TACs. Under the CFP, between 2015 and 2020, the fisheries in

Europe must be fishing at maximum sustainable yield (MSY). For whiting the advice is currently to fish at the lowest possible level and the TACs are reduced to less than 300 tonnes per year. The cod stock showing a constant decline and being outside biological limits, the TACs are set to 0 since 2012 and bycatch and discards should be minimised (ICES, 2016b). The TACs of haddock follow the MSY framework since 2012 and are around 5,000 t per year.

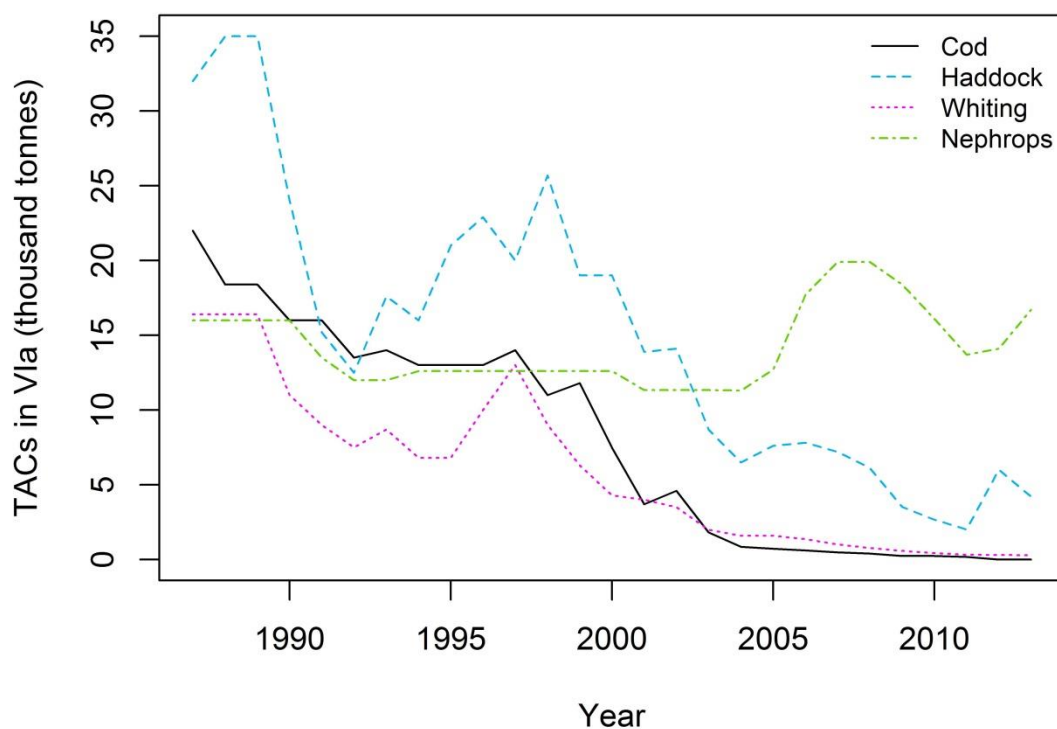


Figure 3.2: Total allowable catches (TACs) in VIa from 1987 to 2013 for the main stocks in the demersal fishery (ICES, 1990; 2013a).

TACs of cod, haddock and whiting have declined since the late 1980s because of the decrease in the fish stocks (ICES, 2013b). This shows how management evolves with changes in the resource abundance. In comparison, for non-depleted stocks such as *Nephrops*, the TACs are relatively constant, if not increased since the late 1980s (ICES, 1990; 2013a).

There is also a limitation in the fishing effort by limiting the number of days-at-sea (Scottish Government, 2015b). This attempts to reduce overfishing by reducing fishing activity directly (Anderson and Seijo, 2011). The Conservation Credits Scheme deals

with this limitation. There is a limited fishing time for vessels and some can be rewarded with additional time in return for the adoption of conservation minded fishing practices. These numbers of days are transferable and vessels can also receive a penalty if this limitation is not followed.

Under the CFP, from 2015 for the pelagic and 2016 for the demersal fisheries, discarding is controlled in Europe and all vessels need to land all their catches. The motivation around this is to improve fishing selectivity to reduce unwanted fish in the long-term. However, this regulation has created considerable controversy about its efficiency and many studies have shown that its consequences may be detrimental to the fish stocks and predators scavenging on discard (Votier et al., 2013; Heath et al., 2014a; Borges, 2015; Sardà et al., 2015).

Since 2005, UK fisheries are subject to the Registration of Buyers and Sellers Scheme which obliges all active vessels to be registered and to land their catch in registered ports to prevent illegal landings (Scottish Government, 2015b). Small quotas on the cod stock in VIa and the difficulty of landing the stocks illegally has notably been responsible for an unusual increase in discard of old cod from 2005 (ICES, 2014c).

Gear restrictions exist in Scotland. This concerns mesh size, shape and length of the gear. For instance, the mesh size restriction for the *Nephrops* trawlers is between 70 and 99 mm while the mesh size should be larger than 120 mm for the whitefish trawlers. This is to control fish selectivity and escapement from the net if the fish is under the minimum landing size (Table 3.1).

Furthermore, every vessel has to get a licence to fish, renewable every two years (Scottish Government, 2015b). There are no new licences. The only way to get a new entitlement is to have a vessel exiting the fishery, which means that the West of Scotland fishery is now closed to new vessels. This regulation is implemented to prevent overfishing in the long-run (Anderson and Seijo, 2011). The entitlement is transferable but only between vessels of the same fleet. In the case of aggregated licence, there is a penalty of 5% on tonnage and power (kW). There exist also parked licences which allow a vessel to possess several licences or to access additional effort by buying out those who want to exit the fishery.

Table 3.1: Current minimum landing size in VIa for the species considered in this study.

Species	Minimum landing size (cm)	Reference
Cod	35	ICES (2016b)
Haddock	30	ICES (2015c)
Whiting	27	ICES (2016b)
Saithe	35	ICES (2015c)
Anglerfish	None	ICES (2016b)
Hake	27	ICES (2014d)
Megrim	20	ICES (2016b)
Nephrops	2 (carapace length)	ICES (2016b)
Ling	63	ICES (2013c)

3.3. The VIa mixed demersal fishery for cod, haddock and whiting

The VIa pelagic fishery is the most productive but concerns fish which are widely distributed through the North Atlantic (ICES, 2014b). Herring is one of the prey of grey seals in VIa (Figure 2.1) but cod, haddock and whiting represent a larger proportion of grey seal diet (Harris, 2007) and the large spatial distribution of herring makes the study of grey seal predation on herring in VIa difficult. Also, cod, haddock and whiting are species that declined substantially in VIa (ICES, 2013b) and for which grey seal predation was proposed as one of the causes of the decline and non-recovery (Lavigne, 1996; Lavigne, 2003; Read, 2008; Cook et al., 2015; Cook and Trijoulet, 2016). Landings of herring in VIa have significantly declined in 1980 after the stock collapsed due to overfishing (ICES, 2015b) but grey seal predation has not been mentioned as a possible reason for its decline. For all these reasons, this study concentrates on grey seal predation on cod, haddock and whiting in VIa. Consequently, only the shelf demersal fisheries that land the three species are considered.

3.3.1. The gears used

There exist different types of gears that catch cod, haddock and whiting in VIa (Table 3.2). These are mainly trawlers, seines, lines and gillnets (STECF, 2015a).

Table 3.2: List of gear types catching cod, haddock and whiting in VIa (STECF, 2015a).

Gear code	Gear
DRB	Boat dredges
FPO	Pots and traps
GNS	Set gillnets (anchored)
HMD	Mechanised dredges including suction dredges
LHP	Handlines and pole-lines (hand operated)
LLS	Set longlines
NK	Unknown gear
OTB	Bottom otter trawls
OTM	Midwater otter trawls
OTT	Otter twin trawls
PTB	Bottom pair trawls
PTM	Midwater pair trawls
SDN	Danish seines
SSC	Scottish seines
TBB	Beam trawls

Recently, 88% of the catch for these species were made by demersal trawlers (Figure 3.3). Consequently, it seems reasonable to concentrate on these vessels when studying the demersal fishery in VIa. However, this means that the study does not take into account the impact of grey seals on local fisheries that may be disproportionately affected (Perring, 2001).

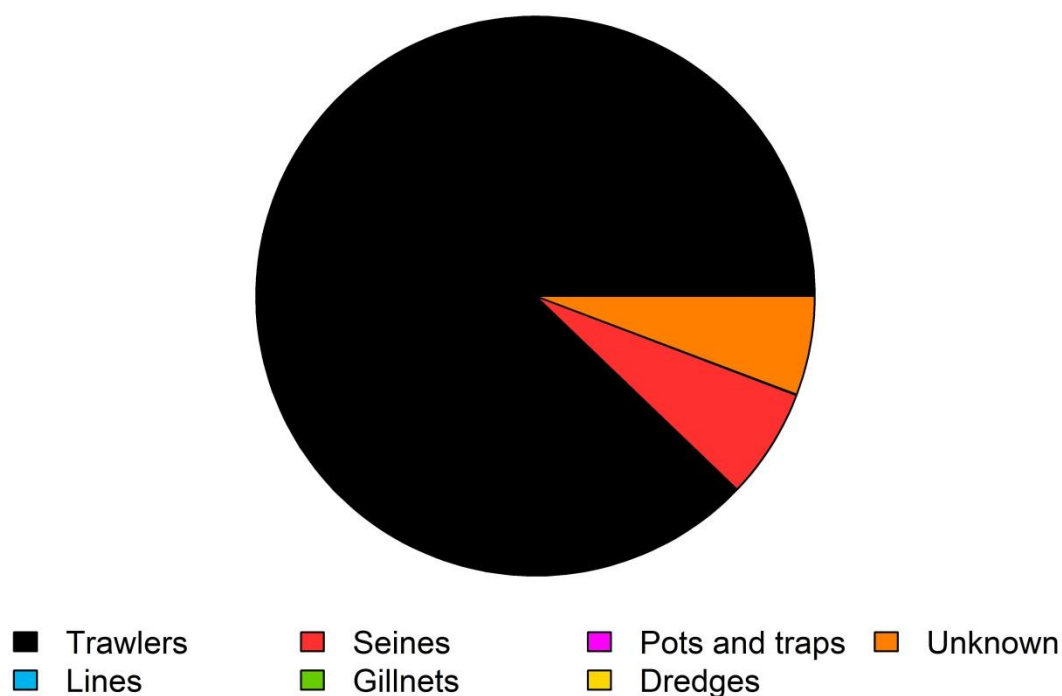


Figure 3.3: Gear usage in landings of cod, haddock and whiting between 2012 and 2014 in VIa (STECF, 2015a).

3.3.2. The trawlers that operate in the fishery

As mentioned earlier, the mixed demersal fishery in the West of Scotland is composed of UK and foreign vessels presenting two types of demersal trawlers: the whitefish trawlers targeting demersal fish and the *Nephrops* trawlers targeting Norway lobster and landing whitefish as bycatch. The difference between these trawlers is the mesh size of the net used. Following ICES conventions, the whitefish trawlers use a mesh size of more than 120 mm (ICES, 2014c). These trawlers are called TR1. The *Nephrops* trawlers use a mesh size between 70 and 99 mm and are called TR2. The trawlers can consequently change the fish species they target by switching their gears.

Ninety nine percent of the landings from *Nephrops* trawlers come from the UK vessels so the TR2 vessels are mainly British (ICES, 2013b). However, whitefish are caught by UK and foreign vessels in the area (Figure 3.4). Most of the catch of cod, haddock and whiting is made by the UK vessels of which 98-99% are Scottish (ICES, 2015a). Irish

and French landings contribute to most of the catches by foreign vessels. Grey seal predation being only considered on the three demersal species, the UK trawlers are therefore the ones of interest for this study. In the UK trawler groups (TR1 and TR2) a distinction is possible by vessel length. These lengths are partitioned in ICES as follows: <10 m, 10-24 m, 24-40 m, \geq 40 m.

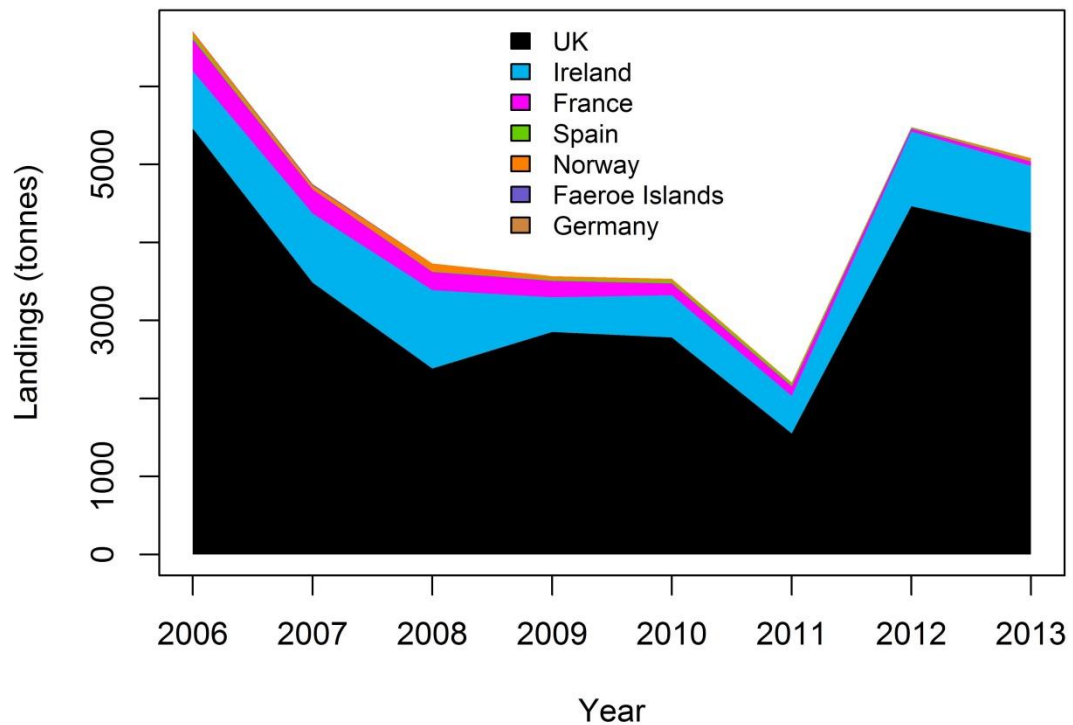


Figure 3.4: Sum of landings for cod, haddock and whiting in VIa by country for the period 2006-2013 (ICES, 2015a).

In the West of Scotland, the landings for the TR1 fleet is really low for small vessel (<10 m) and most of the landings are made by the *Nephrops* trawlers (Table 3.3). For the TR2 fleet, Marine Scotland data (available at the DOI [10.15129/ba3baf8c-17f6-471a-a84b-b15346642388](https://doi.org/10.15129/ba3baf8c-17f6-471a-a84b-b15346642388)) shows landings for the vessels larger than 24 m. However, economics data given by Seafish (available at the DOI [10.15129/ba3baf8c-17f6-471a-a84b-b15346642388](https://doi.org/10.15129/ba3baf8c-17f6-471a-a84b-b15346642388)) do not record TR2 vessels in VIa larger than 24 m between 2007 and 2012. There is consequently an inconsistency between biological and economic data in the area. Nevertheless, landings by large TR2 trawlers (>24 m) correspond to only 3% of the landings and most of these landings are *Nephrops* and not the demersal fish of interest for which grey seal predation is considered.

Table 3.3: Sum of UK landings in tonnes (all species including *Nephrops*) in VIa by demersal trawlers from 2007 to 2011 per mesh size and vessel length (Marine Scotland).

	<10 m	10-24 m	24-40 m	≥40 m
TR1	56	11,127	30,166	4,776
TR2	4,550	64,286	448	1,873

The costs recorded by Seafish of the UK vessels fishing in VIa are given in Figure 3.5. The vessels over 24 m are aggregated under the same fleet. All economic data is given in pounds and corrected for inflation using the GDP deflator with 2012 as the reference year. The variable costs correspond to costs associated with fishing that vary with fishing effort and landings: costs induced by the fuel, crew share and the other fishing costs (Anderson et al., 2013). Total vessel costs, depreciation, interest and other finance costs are mainly fixed costs.

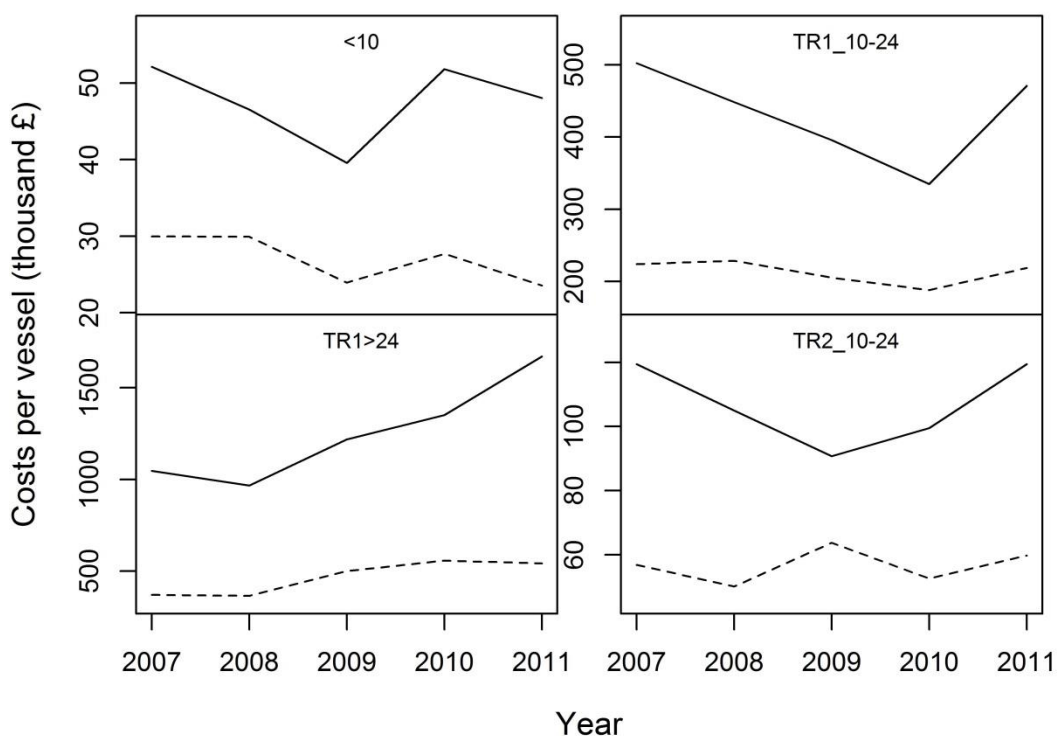


Figure 3.5: Variable (solid line) and fixed (dashed line) costs per vessel and per fleet recorded by Seafish.

For all the fleets the fixed costs are smaller than the variable costs. The large whitefish trawlers (TR1>24) presents the largest costs. The *Nephrops* trawlers and the small vessels have the smallest costs per vessel.

Data provided by Seafish also records the number of vessels in each fleet (Table 3.4). The largest fleet is the large *Nephrops* trawlers with more than 100 vessels. This fleet has expanded since the decrease in whitefish stocks due to whitefish trawlers switching to a *Nephrops* orientated fishery. The whitefish trawlers only represent between 14 and 22 vessels along the time series and are the smallest fleets. The number of foreign vessels is an approximation since the economic data is not recorded for these vessels in the UK.

Table 3.4: Number of vessels per fleet in VIa (Seafish). The “Others” fleet represents the foreign trawlers. For this fleet vessel number in 2012 is not available.

Year	<10	TR1_10-24	TR1>24	TR2_10_24	Others
2007	38	5	9	174	19
2008	36	10	10	174	19
2009	31	9	11	152	17
2010	24	11	11	133	24
2011	28	9	9	124	15
2012	29	6	9	132	NA
Average 2007-2011	31	9	10	151	19

For the UK trawlers, fishing and non-fishing incomes (of which 50% corresponds to oil industry incomes (Anderson et al., 2013)) are also recorded. Comparing revenues and costs per vessel for the four UK fleets highlight the small net profits that currently exist in the fishery (Figure 3.6). The net profits are positive but sometimes the benefit is due to non-fishing incomes. Nevertheless, it is obvious that the UK fleets in VIa are close to the break-even point where revenues equal costs, notably when other sources of revenue are ignored. This corresponds to the bioeconomic equilibrium that is usually observed in open-access fisheries (Bjørndal and Conrad, 1987; Kronbak, 2005) despite the fact that the VIa fishery is currently closed to new entrants.

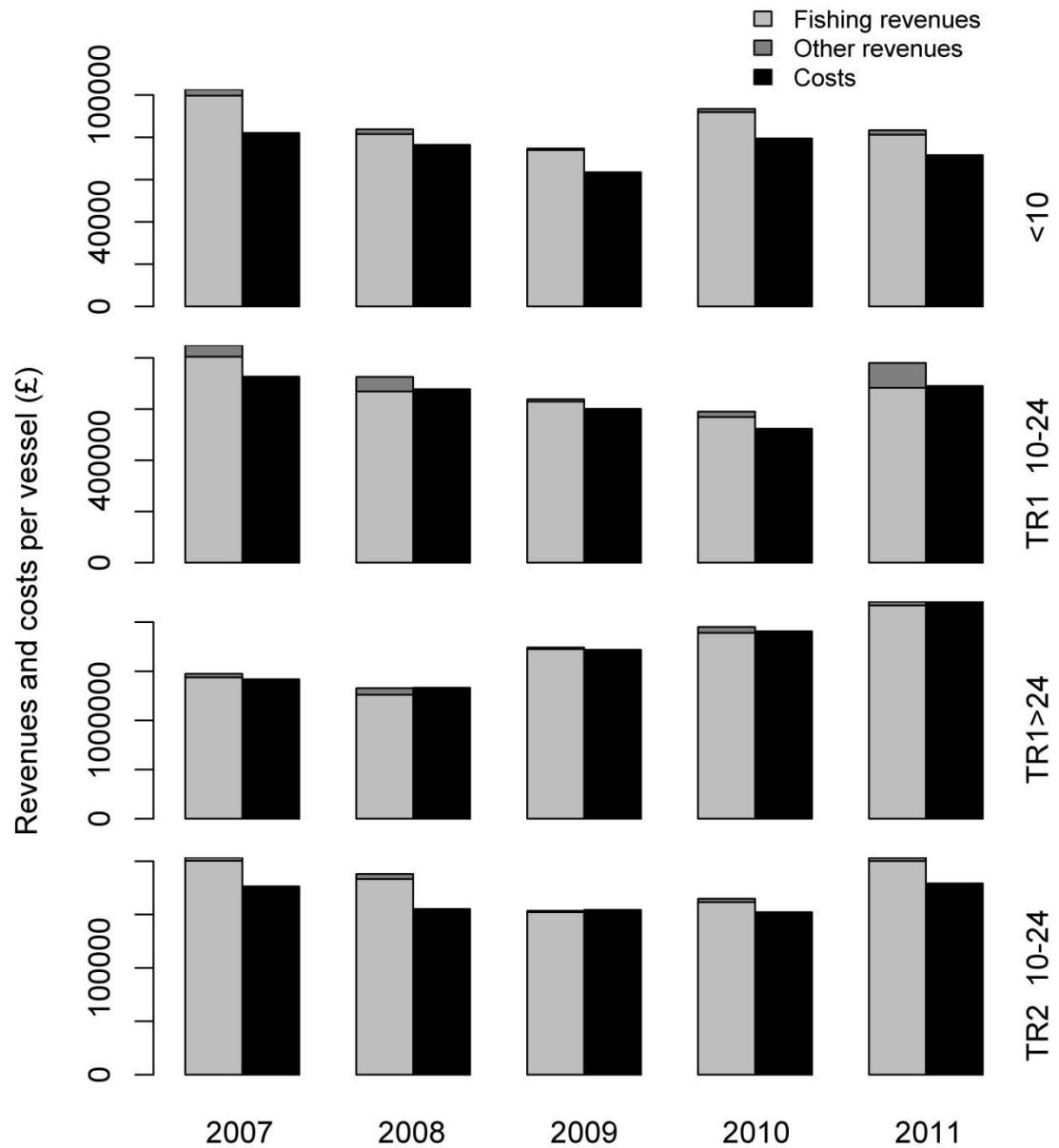


Figure 3.6: Revenues and total costs per vessel for the UK trawlers (Seafish).

The large whitefish trawlers fleet presents the largest revenues and costs per vessel with values larger than 1 million pounds. The TR1 fleets are the ones presenting the largest non-fishing incomes which help providing positive net profits.

3.3.3. The species caught

The mixed demersal fishery targets demersal fish such as cod, haddock, whiting (TR1 fleets) and *Nephrops* (TR2). In the 1980s, these species represented most of the landings (UK and foreign vessels) in VIa (Figure 3.7). However, the decline of cod and whiting has been responsible for a change in main landed species where the European hake, saithe and haddock are the most abundant. Catches of *Nephrops* have stayed more or less constant if not increased over time in relation with the switch of gears from TR1 to TR2 to counter the decrease in demersal whitefish.

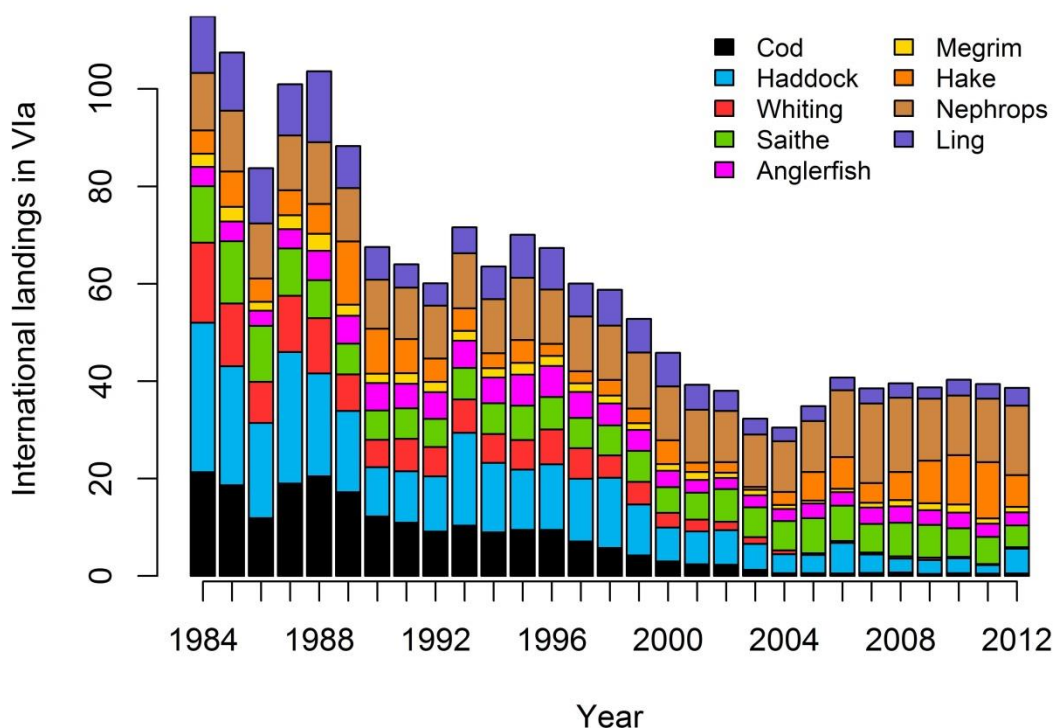


Figure 3.7: International landings (thousand tonnes) by demersal trawlers (and creelers for *Nephrops*) in VIa (ICES, 2011; 2015a).

Concerning the fishing catches by the British vessels, which are the vessels of interest, the recent distribution of the landings and revenues in VIa is given in Figure 3.8. *Nephrops* is the most important species landed in weight followed by haddock and saithe. The group “Others” represents species for which landings are not large enough to be recorded at individual levels or species of low commercial value. This is

confirmed by the distribution of the incomes which shows the small revenues obtained from these species.

Nephrops is the species bringing the biggest incomes to the UK vessels (80%). This is explained by the large weight of *Nephrops* landed in VIa (Figure 3.8) but also the large value of the species (Figure 3.9).

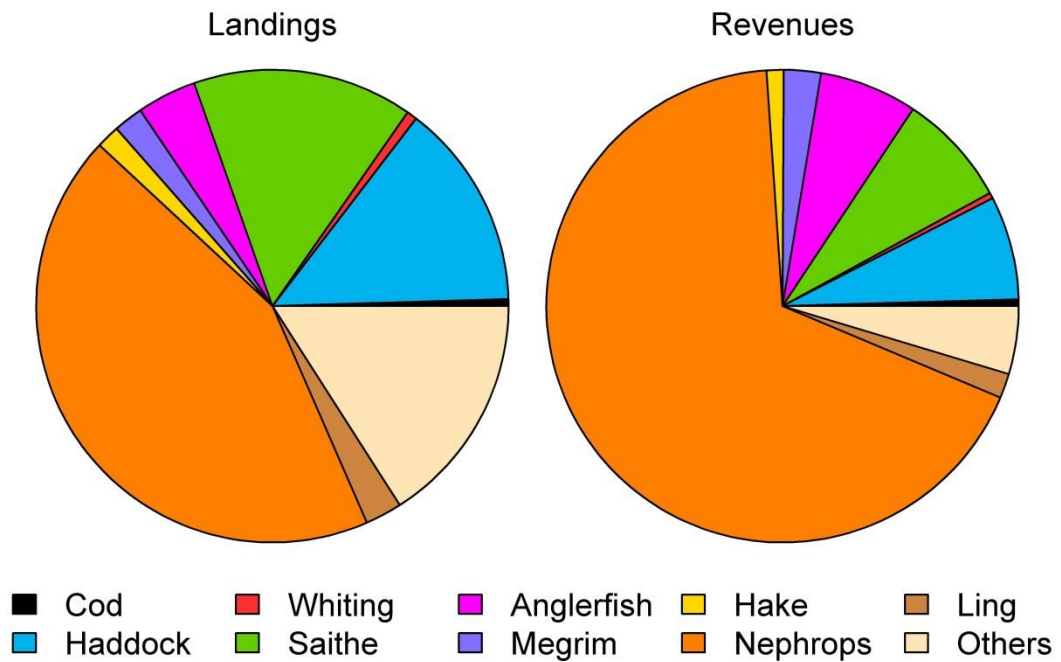


Figure 3.8: Distribution of 2012 landings and revenues by species for demersal UK trawlers in VIa (STECF, 2013).

Megrin and anglerfish are also fish of large current commercial value. Saithe is the fish with the lowest price per tonne. Haddock and whiting are not of high commercial value compared to the other species despite the decline in their landings in the West of Scotland.

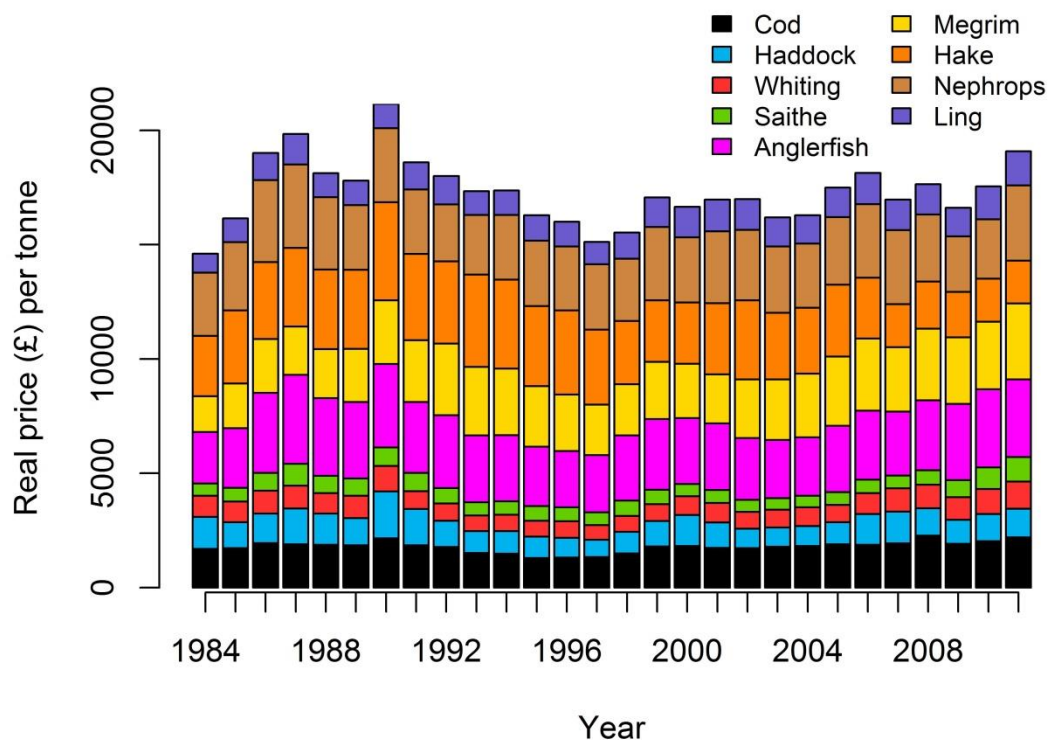


Figure 3.9: Real price (i.e. price corrected for inflation) for the main species landed by trawlers in VIa (Marine Management Organisation, 2012).

3.4. Grey seals in VIa

The West of Scotland possesses a breeding zone for grey seal colonies in the Outer Hebrides. Pup counts in the area enables the estimation of the total grey seal population in VIa (Thomas, 2014). The estimation is done using a Bayesian state-space model. The population estimates are updated every year using the new year counts and investigating new priors. These are available in the Special Committee on Seals (SCOS) yearly reports (Thomas, 2012; 2013; 2014). These represent estimates from 1984 to 2013. The estimates obtained since the beginning of this study (2012) are presented in Figure 3.10.

The estimates from the three reports (2012, 2013 and 2014) change in scale but the trends in seal population are relatively similar. Since the 1980s grey seal population in VIa has increased but has stabilized in the recent years if not decreased.

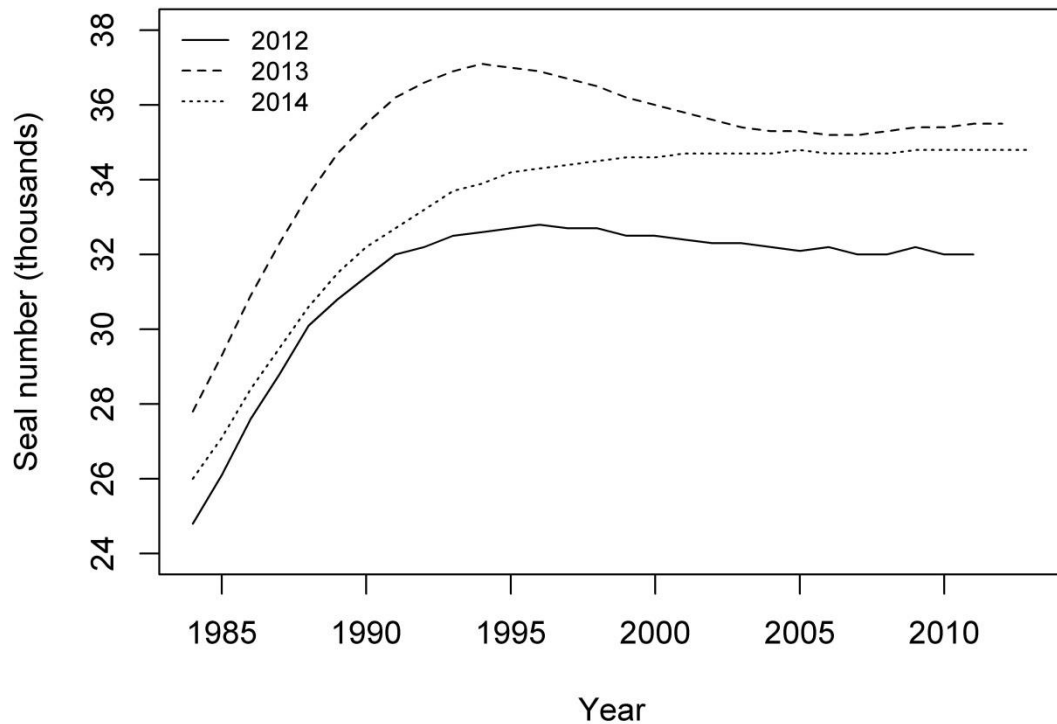


Figure 3.10: Estimated seal number in VIa (Inner and Outer Hebrides) from three consecutive SCOS reports (Thomas, 2012; 2013; 2014).

These estimates are uncertain since the pup counts are scaled up to account for the entire grey seal population using Bayesian estimation. It is therefore difficult to know with certainty the size of the grey seal population in VIa. The estimates present consequently large confidence intervals. Currently, the West of Scotland grey seal population represents 33% of the total UK grey seal population (Thomas, 2014).

3.5. Comparison of grey seal distribution and fishing effort in VIa

The Sea Mammal Research Unit provides at-sea and on-land usage maps of grey seal population around the UK (Jones et al., 2013). These maps are obtained by studying telemetry (2001-2012) and count data (1988-2012). They give an idea of seal distribution around the UK but do not account for seasonal variation in grey seal spread. They represent an average picture of grey seal distribution over the years 1988

and 2012 but may not be representative of recent dispersal and are limited by grey seal temporal movements.

Maps of fishing effort for the VIa trawlers are also available from STECF (2015b). They represent an average picture of yearly fishing effort. Figure 3.11 compares at-sea usage map for grey seals with 2012 effort maps for whitefish (TR1) and *Nephrops* (TR2) trawlers in VIa. The grey seal usage map being an average distribution over 20 years and the fishing effort maps giving the 2012 distribution of trawling effort, the maps are not directly comparable. However, this can give a certain idea the possible competition between fishers and seals if we assumed that the grey seal usage map is representative of the current distribution of grey seals in VIa.

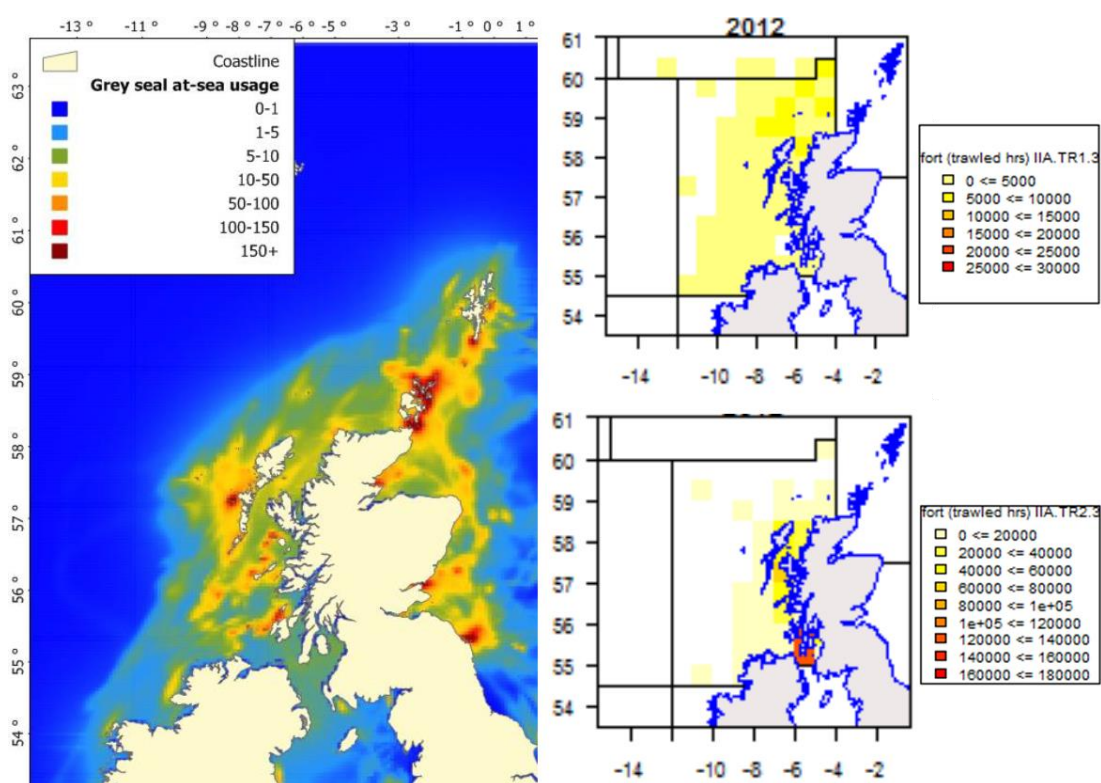


Figure 3.11: Grey seal at-sea usage map over the 20 last years (number of seals per 5x5 km cell, left map) taken from Jones et al. (2013) and whitefish (TR1, top right map) and *Nephrops* (TR2, bottom right map) trawlers' effort (trawled hours) in 2012 taken from STECF (2015b).

The maps show an overlap between fishing effort and grey seal distribution for both trawler types. It is interesting to see that both distribution of seals and fishers stay on the continental shelf (cf. Figure 3.1). The TR2 trawlers will not be highly impacted by

grey seal predation since they target *Nephrops* but may be subject to depredation impacts. However, the *Nephrops* trawlers fish mainly in the Clyde area where seal density is low and this should reduce competition. If these maps are close the real distribution of trawlers and seals in VIa, it seems that the whitefish trawlers are the ones having the most chance to be impacted by grey seal predation and depredation.

However, it has to be kept in mind that overlap does not mean seal foraging behaviour or competition. Also, usage areas are average pictures of the distribution while the entire ecosystem is dynamic: fish, seals and fishers move. Seals are notably large scale travellers that can do foraging trips of hundreds of kilometres (Cronin et al., 2013; Klimova et al., 2014) and follow seasonal fish migrations (Harvey et al., 2012; Hammill et al., 2014). Concluding on competition between grey seals and trawlers in VIa is consequently more complicated than comparing spatial distributions.

3.6. Summary and link with the study

The West of Scotland is an interesting management zone for its physical characteristics but also for its resource diversity. Different fisheries exist in the area but given the interest of this study in grey seal predation, the demersal fishery for cod, haddock and whiting is the one considered in this study and more importantly, the demersal trawlers which bring most of the catch in the area. These are the whitefish and *Nephrops* trawlers.

There exist complex fisheries regulations in the West of Scotland. Some of them are difficult to consider within a bioeconomic model such as the quota restrictions. Indeed, fishers may change gears or change of fishing areas or stop fishing while the quotas are reached. These fishing behaviours may be difficult to implement mathematically. Also, the flexibility in season length in the area makes its consideration in bioeconomic modelling difficult. This is why bioeconomic models often are a simplification of the current state of the fisheries.

All data on fishing catches, abundance indices from research survey vessels and estimates of mortalities for the different fish species considered in this study are available in the ICES reports. The last VIa assessment for haddock comes from ICES (2013b) since the species is integrated to the North Sea assessment from 2014 onwards.

Spatial modelling is a difficult task which demands the availability of consistent spatial data and the choice of numerous assumptions. Therefore this study does not consider spatial distribution of fishing effort, fish and grey seal populations and assumes a homogenous distribution of fish, seals and fishers in the entire Division VIa.

The next chapter presents the simulation model created to study grey seal predation impacts on the West of Scotland fishery. The chapter also presents its parameterisation using the Bayesian state-space stock assessment model and data from the literature. The chapter also checks the consistency of the outputs of the simulation model.

Chapter 4

Presentation, parameterisation and validation of the simulation model

It has been seen in Chapter 2 that among the species studied here, only cod, haddock, whiting, saithe, megrim and ling are present in the diet of the West of Scotland grey seals. Recent grey seal consumption on megrim is very small (25 tonnes in 2002) (Harris, 2007) so grey seal predation on this species is ignored. Saithe is assessed as a northern stock (ICES Divisions III, IV and VI) of which only 6% occurs in VIa (ICES, 2013d). So it is assumed that seal predation in the West of Scotland will have an insignificant impact on the overall saithe stock. The limitation in empirical data for ling prevents the consideration of seal predation on this species. For these reasons, the study only considers grey seal predation on cod, haddock and whiting.

This chapter describes the modelling used in the study. It comprises two main components: the parameter estimation necessary to estimate grey seal predation mortality on cod, haddock and whiting and the simulation study which uses these estimates and some from the literature to assess the bioeconomic impacts of grey seal predation projection the fish stocks to equilibria (Figure 4.1).

The parameter estimation is done using the state-space model previously used for cod in Cook et al. (2015) and Cook and Trijoulet (2016). This model is a stock assessment model which differs from ICES model by explicitly considering grey seal predation as one component of the total mortality on fish. To prevent confusion between the different models used or mentioned in the study, the stock assessment model will be called the state-space model and the bioeconomic model the simulation model. In the

current study, the state-space model is developed for haddock and whiting so provides updated estimates for cod and new estimates for haddock and whiting. It will be seen in part 4.2.1.1 that this model estimates large grey seal mortality on cod but minor seal predation mortality on the two other species.

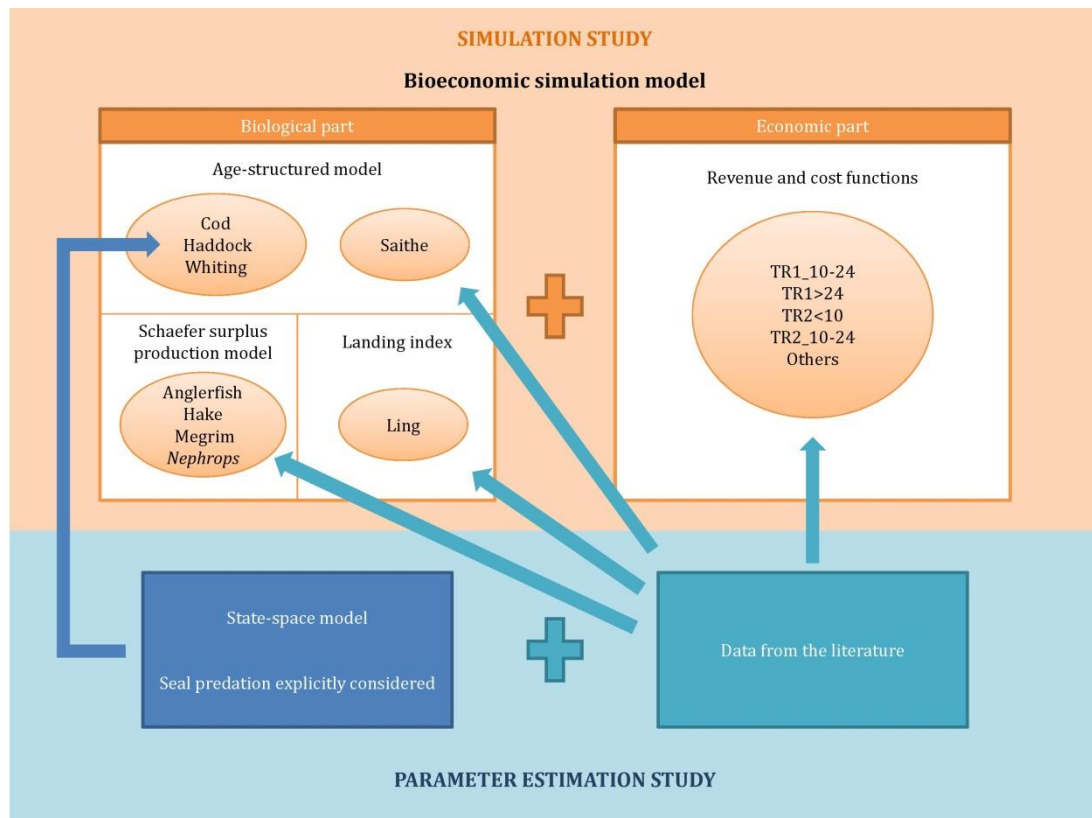


Figure 4.1: Schematic diagram highlighting the two main studies and how they are linked to each other in this chapter.

The main component of this study is the simulation study. This consists on the development of a simulation model which is a forecast model accounting for nine species and five fishing fleets. The model is age-structured for species age-structured data is available for. For the other species a Schaefer surplus production function is assumed. The simulation model explicitly considers grey seal predation but also the economic component of the fishery by estimating fleet revenues and costs. The stocks are projected forward using the estimates of the state-space model for the three species of interest but also biological and economic data from the literature.

The chapter is partitioned into three main parts. The part 4.1 presents the simulation model. A summary of this model is given in Appendix A and of all the symbols used in the study in Appendix B. The values of all the parameters used in the model are also available at the DOI [10.15129/ba3baf8c-17f6-471a-a84b-b15346642388](https://doi.org/10.15129/ba3baf8c-17f6-471a-a84b-b15346642388). The parameterisation of the simulation model is discussed in part 4.2. This part therefore comprises the description of the state-space model and its outputs but also the parameterisation done with the data from the literature. Finally, investigating runs of the simulation model are done in part 4.3 to check the consistency of its outputs before the scenario results are analysed in Chapter 5.

4.1. The simulation model

In this study, to assess the bioeconomic impacts of grey seal predation on fisheries, a stock assessment model is considered where grey seals are one of the predators with fishers and where an economic component is added to evaluate seal impacts on fisheries revenues and profitability.

In the literature most of the fisheries bioeconomic models are single species models and do not consider predatory interactions between fish stocks. Likewise, the current fish stock assessments are often done on a single species basis. This is currently the case in the West of Scotland for cod and whiting and it was the case for haddock until 2013 (ICES, 2013b), while a multispecies stock assessment model is currently used in the North Sea including these three species of interest (ICES, 2015c). A single species model has the advantage of being simple and less data demanding than a multispecies model and is considered reliable for short-term predictions because the modelling assumptions are less critical in making forward projections. For instance, the differences in modelling assumptions about natural mortality tend to accumulate over time and they are going to be bigger over a long period of time. However, single species models are not realistic for mixed fisheries which land several species which all contribute to an important part of the fishing revenues. This is the case for the current case study fishery, the VIa mixed demersal fishery for whitefish. All landed species

contribute to fishing benefits so it is important to consider a mixed species model in this study.

It may seem important to consider biological interactions, when they occur, to construct a fisheries bioeconomic model (Anderson and Seijo, 2011). Indeed, interdependency can impact the fish stock or the fishery profits (Flaaten, 1998; Boncoeur et al., 2002; Chakraborty and Kar, 2012). It can therefore be unrealistic to consider a mixed species fishery model with no interaction between fish species. In fisheries bioeconomics, studies often considered two interacting species models (Chaudhuri, 1986; Flaaten, 1991; Boncoeur et al., 2002; Kar and Chakraborty, 2010; Chakraborty and Kar, 2012; Pal et al., 2012) or a greater numbers of species (Flaaten, 1998; Kar and Chaudhuri, 2004). Large scale multispecies models or even programming software able to include all these types of biological interactions have been developed. Some use Ecopath with Ecosim (Beattie et al., 2002; Harvey et al., 2003; Christensen et al., 2005; Alexander et al., 2014), the FISHRENT model (Salz et al., 2011) which includes management options, or others use multispecies models which may account for more than 50 stocks (Ulrich et al., 2002a; Speirs et al., 2010). The software TEMAS (technical management measures), for instance, is also able to account for fishers behaviour and management solutions in a framework permitting multispecies studies (Marchal, 2005; Vermard et al., 2005; Ulrich et al., 2007; Kronbak et al., 2009; Andersen et al., 2010). The software package FLR also enables complete multispecies analysis including risk analysis (Kell et al., 2007; Hoff and Frost, 2008). However, it would be demanding to include interdependency since the interactions need to be defined and modelled. Entire ecosystems cannot be completely and exactly described within a bioeconomic model. Adding complexity also makes models less stable and the results may often be more uncertain. Large numbers of parameters to estimate can also lead to greater imprecision and result in overfitting (Babyak, 2004; Hawkins, 2004). This can be the case when the model possesses too many parameters or equations that are actually needed to fit the model or describe the biological processes. In this case using the model for prediction would results in unreliable outputs. It is therefore necessary to check the statistical fit of the model and validate the results.

In this study, a mixed species model is considered to describe fish dynamics in the West of Scotland in accordance with the different fish species landed by the fishery (cf. Chapter 3). However, no interaction is considered between the fish species as there is little or no data available to parameterise such models. Nevertheless the simulation model accounts for the economic part each landed fish species represents in the total fishing revenues. Not considering the trophic interactions between the fish species means that the model gives information about the likely direction the results would take given the initial parameters but the model outputs are not predictive of a true biological equilibrium.

4.1.1. The biological model

The biological model considers nine fish species which have been chosen because they represent 95.4% of the revenues of the UK vessels fishing in VIa (STECF, 2013). The model calculates fish populations and catch by fishers for cod, haddock, whiting and saithe, the only species for which age-structured data was available. The model also estimates the landings for the other species of interest (anglerfish, megrims, hake and *Nephrops*) following a Schaefer surplus production function and a landing index for ling. Seal predation is only considered for cod, haddock and whiting because they are the species most represented in the grey seal diet of the species in the fishery.

4.1.1.1. Dynamics of cod, haddock, whiting and saithe

For cod, haddock, whiting and saithe, fishing and seal selectivity varies with fish size (or age). The 2013 ICES stock assessments provide age-structured empirical data for the four species (ICES, 2013b; d) which motivates the use of an age-structured biological model in this study.

The model follows therefore conventional fish stock assessment models. The fish population is assumed to follow a cohort (Hilborn and Walters, 1992) where the number of fish $N_{a,y,j}$ at age a and year y for species j is given by the following equation where Z is the total mortality at age:

$$N_{a,y,j} = N_{a-1,y-1,j} e^{-Z_{a-1,y-1,j}} \quad (4.1)$$

In order to model the entry of new fish to the population it is necessary to describe how young fish are produced. It is commonly assumed in fisheries modelling that the number of new recruits produced each year (N_1) is a function of spawning stock biomass (SSB) which is calculated as follows:

$$SSB_{y,j} = \sum_a (N_{a,y,j} m_{a,j} w_{a,j}) \quad (4.2)$$

The spawning stock corresponds to the proportion of sexually mature fish (m) present within the total population of fish (N). Since it is expressed in biomass, this is multiplied by the stock weight at age (w). The values of m and w are considered constant within the simulation model.

Different stock-recruitment models exist to describe the relationship between recruitment and SSB and it seems that choosing the right model to use in population modelling is a difficult task, mostly because the chosen assumption can have significant consequences on the stock dynamics.

Three different types of stock-recruitment relationships are often used in the literature: Ricker (1954), Beverton and Holt (1957) and the hockey-stick. One version of the latter is the smooth hockey-stick (Froese, 2008). These relationships are all used in VIa cod assessments to estimate management reference points (ICES, 2014c). The equations for these relationships are given in Table 4.1.

The Ricker curve presents a maximal recruitment at $\frac{\alpha}{\beta} e^{-1}$ and a slope at the origin α . This curve presents an overcompensation effect where the number of recruits decreases at high level of SSB (Myers, 2001). The assumption behind this shape is that the population of new recruits is affected by mature fish (as through cannibalism) so the mortality on fish is driven by SSB (Quinn II and Deriso, 1999; El-Shaarawi and Piegorsch, 2001).

The Beverton-Holt curve presents a density-dependent asymptote when recruitment equals $\frac{1}{\alpha}$ and a slope at the origin $\frac{1}{\beta}$. The assumption here is that the recruits compete also with immature fish for reasons such as food or space and therefore the mortality on fish is dependent on the total number of fish in the population (Quinn II and Deriso, 1999; El-Shaarawi and Piegorsch, 2001). Bjørndal et al. (2004) suggest that this function can be used for long-lived species with variable year class strength. Also, Anderson and Seijo (2011) added that this function is applicable to fish stock where recruitment is limited by food availability or habitat or where a predator continually modifies its own attack rate to changes in prey abundance.

Table 4.1: Equations for the three most commonly used stock-recruitment relationships. α , β and K are constants.

Stock-recruitment function	Equation
Ricker	$N_{1,y,j} = \alpha_j SSB_{y-1,j} e^{-\beta_j SSB_{y-1,j}} \quad (4.3)$
Beverton-Holt	$N_{1,y,j} = \frac{1}{\alpha_j + \frac{1}{\beta_j SSB_{y-1,j}}} \quad (4.4)$
Smooth hockey-stick	$N_{1,y,j} = K_j (1 - e^{-\frac{\alpha_j}{K_j} SSB_{y-1,j}}) \quad (4.5)$

The shape of the smooth hockey-stick curve is close to the Beverton-Holt function. The slope at the origin (α) and the carrying capacity (K) are direct parameters of the equation. According to some studies, by fitting a straight line through the origin for density-dependent recruitment and a second line parallel to the x-axis for density-independent recruitment, the hockey-stick may provide more robust parameter estimates than Ricker or Beverton-Holt (Froese, 2008; Mesnil and Rochet, 2010). The continuous smooth hockey-stick presents the same advantages than the original piecewise relationship but is as easy to fit as Ricker and Beverton-Holt with only two parameters to estimate (Froese, 2008).

According to Myers and Barrowman (1996), if the fish population is aggregated to the North Atlantic level, it seems that cod and haddock describe a stock-recruitment relationship following Beverton and Holt (1957) and whiting and saithe present some

evidence of overcompensation (Ricker, 1954) which could be explained by a high cannibalism at early life stages. However results taken on the West of Scotland level show different trends with cod and saithe showing some evidence of overcompensation (Myers and Barrowman, 1996).

The choice between the three relationships is important, notably for population with high SSB. Indeed, according to the Beverton-Holt and smooth hockey-stick curves when SSB tends to infinity the recruitment is maximal. However taking the assumption of a Ricker stock-recruitment relationship will lead to a completely different result where the recruitment tends to 0 when SSB is very large. Consequently, the choice of stock-recruitment relationship has to be considered with great care. Unfortunately, recruitment is inherently highly variable and data points are often not observed at high SSB values which makes the form of the stock-recruitment relationship difficult to identify.

In the VIa ICES stock assessments, a Ricker curve is considered for cod and haddock and a hockey-stick curve is considered for whiting (ICES, 2013b) and saithe (ICES, 2013d). As a result in this study, for consistency reasons, a Ricker relationship is assumed for all species (Equation (4.3)) and the sensitivity of the model to the other types of relationships is discussed in Chapter 6.

Recruitment and SSB are subject to different type of errors which increase the difficulties to fit the stock-recruitment curves and makes the choice of a specific relationship more challenging (Hilborn and Walters, 1992; El-Shaarawi and Piegorsch, 2001). Indeed, recruitment and SSB are limited by measurement errors following their estimation in stock assessments and this could bias the parameter estimates that give the shape of the stock-recruitment curve (Walters and Ludwig, 1981; Fulton et al., 2011). Recruitment and SSB estimation is also subject to process errors due to the variability in environmental factors such as temperature, currents or weather which affect fish growth and larvae survival and in biological processes such as mortality and growth (Myers and Pepin, 1994; Myers, 2001). Therefore, the stock-recruitment curves represent average relationships and the observed stock-recruitment data do not lie exactly on the average curve due to the process errors. To account for this variability, log normal noise (ε) is added around the curve.

$$N_{1,y,j} = (\alpha_j SSB_{y-1,j} e^{-\beta_j SSB_{y-1,j}}) e^{\varepsilon_j} \quad (4.6)$$

Where: $\varepsilon_j \sim Normal(0, \sigma^2)$ (4.7)

The parameter σ^2 is the variance of the distribution.

In order to account for seal predation and fishing, the total mortality on fish (Z) is given by sum of natural mortality (M), fishing mortality (F) and seal predation mortality (P):

$$Z_{a,y,j} = M_{a,y,j} + F_{a,y,j} + P_{a,y,j} \quad (4.8)$$

Natural mortality comprises all sources of mortality other than fishing and seal predation such as disease, aging and other predators. Natural mortality is difficult to quantify and different methods exist to estimate it. In this study the relationship due to Lorenzen (1996) is used for the four species to estimate natural mortality at age from mean weight at age where γ and δ are constants.

$$M_{a,y,j} = \gamma_j W_{a,y,j}^{-\delta_j} \quad (4.9)$$

This method has been chosen because it is widely used and enables simple estimation of mortality at age using fish weight at age recorded in ICES reports. In the ICES VIa haddock and saithe assessments, the natural mortality is considered as a known constant (0.2) and implicitly takes into consideration the mortality by seal predation (ICES, 2013b; d). The Lorenzen (1996) method is used for cod and whiting in VIa assessments (ICES, 2014c). The Lorenzen method is used for all species in this study since the conventional fixed value of 0.2 is not consistent with size related mortality.

The main difference between the current model and conventional ICES assessments is that the seal predation mortality has been extracted and considered as an independent component of the total mortality that can be estimated using grey seal diet data. Seal predation is only considered explicitly for cod, haddock and whiting as they are the main demersal species that appear in the grey seal diet. The mortality due to seals is assumed to be the product of three components as follows:

$$P_{a,y,j} = sel_{a,j}q_jG_y \quad (4.10)$$

The term G is the number of seals, sel represents seal selectivity for a fish species of a certain age (or size) class and q is the seal predation rate. The latter describes the ability of seals to catch fish and, with sel , is kept constant in the simulation model.

Estimating seal selectivity can be a challenge. Grey seals present evidence of a size selectivity for the different fish species (Harris, 2007) that may be due to a size preference or to an ability to eat and process certain fish size. This selectivity may also reflect the sizes of fish present in the foraging areas. It is therefore fair to assume that similarly to fishing, grey seals select their prey according to their size. Consequently, the selectivity is modelled as a gamma curve assuming the selectivity changes with mean fish length at age (l_a) (Millar and Fryer, 1999).

$$sel_{a,j} = \left(\frac{l_{a,j}}{(\zeta_j - 1) \left(\frac{\eta_j}{\zeta_j - 1} \right)} \right)^{(\zeta_j - 1)} e^{(\zeta_j - 1) - \frac{l_{a,j}(\zeta_j - 1)}{\eta_j}} \quad (4.11)$$

The parameter ζ is the shape parameter and η is the mode of the distribution.

Fisheries bioeconomic studies, often consider only single fleet models. The fishery is considered as a whole and no distinction is made between vessels within the fishery. This reduces the uncertainty around the fleet partition that is often present when considering multifleet models.

Single fleet models may be suitable in certain cases. For instance, single fleet models can be satisfactory when the interest is in the variation in revenues or profit for one single fleet, in the change in stock size for a certain fishing mortality or when estimating the optimal level of fishing mortality or stock biomass to obtain a sustainable stock population. However, a fishery is rarely comprised of only one type of vessel and these models do not consider the impact of other fleets on the fish stocks. They represent therefore a high degree of simplification compared to the reality.

Multifleet models have the advantage of being closer to reality than single fleet models. They are increasingly used in fisheries bioeconomics because a fishery is often, if not always, a mixture of different vessel types using different gears and having different fishing selectivity.

Multifleet models are not necessary if the interest is only given to the fish stocks since an overall fishing mortality is sufficient in this case. However, if the change in revenues and profitability at a fleet basis and the impact of change in fish stock on fleet revenues and costs rather than on the whole fishery are of interest, a multifleet model is necessary. The profit of a fishery depends on the interactions between fleets and the fleets may react differently to a change in stocks or fisheries management. When looking at fisheries management, it is important to consider the different fleets inside the fishery, notably in the case of imperfect competition with a competitive fringe. In this case, some fleets are “price makers” and the quantity they land determines the price of fish, and others are “price takers” and their landings do not impact fish prices (Ulrich et al., 2002a). Fleets will therefore be differently impacted by fisheries management and have different profitability (Hilborn, 1985). It is important to consider the difference in impacts to avoid reducing the overall fishery profitability and propose the best management strategies (Laukkanen, 2001; Beattie et al., 2002; Ulrich et al., 2002b; Lleonart et al., 2003; Simons et al., 2014). Multifleet models are also certainly important to study the interactions between fleets and fishing behaviour within a specific fishery (Ulrich et al., 2007; Hoff and Frost, 2008; Andersen et al., 2010; Nøstbakken et al., 2011; van Putten et al., 2012).

In this study, the West of Scotland demersal fishery is marked by different trawlers targeting different species and using different nets which are responsible for different fish selectivity (cf. Chapter 3). The study is notably interested in the investigation of the impacts of grey seal predation on the different fleets. Biological (Marine Scotland) and economic (Seafish) data for most of the fleets are available. For these reasons, it has been chosen to consider a multifleet component for the simulation model.

Therefore, the fishing mortality (F) is assumed to be the product of two components, an age component which describes the selectivity of the fleet for a certain fish age class (s) and a year component, fishing effort index (E), which describes the annual change

in fishing mortality (Pope and Shepherd, 1982). If there are k fleets, the fleet fishing mortality can be described as:

$$F_{a,y,j,k} = s_{a,j,k} E_{y,k} \quad (4.12)$$

The total fishing mortality is therefore given by:

$$F_{a,y,j} = \sum_k F_{a,y,j,k} \quad (4.13)$$

Since the fishery is a mixed fishery, the effort index for a fleet is the same on all species caught by this fleet and this explains why there is no species subscript for E .

The estimates of the fishing mortality enable the estimation of the number of fish caught at age each year ($C_{a,y,j}$) following the commonly used Baranov equation (Baranov, 1945):

$$C_{a,y,j} = \frac{F_{a,y,j}}{Z_{a,y,j}} N_{a,y,j} (1 - e^{-Z_{a,y,j}}) \quad (4.14)$$

The catch per fleet is estimated following the proportion of each fleet in the total fishing mortality:

$$C_{a,y,j,k} = \frac{F_{a,y,j,k}}{F_{a,y,j}} C_{a,y,j} \quad (4.15)$$

Landings (L) are also estimated each year using the proportion of the catch at age landed (λ) by each fleet.

$$L_{a,y,j,k} = \lambda_{a,j,k} C_{a,y,j,k} \quad (4.16)$$

Discards are then calculating using the difference between catches and landings (Stratoudakis et al., 1999; Millar and Fryer, 2005; Fernandes et al., 2011). These values can be converted into weight by multiplying by the average fish weight at age in landings and discards.

4.1.1.2. Dynamics of the other species

As noted earlier, only cod, haddock, whiting and saithe dynamics are considered in the age-structured part of the model for data availability reasons. However, five other species have been considered since they make an important contribution to the fishing revenues: anglerfish, megrims, hake, *Nephrops* and ling.

The Schaefer surplus production function (Schaefer, 1954; Quinn II and Deriso, 1999) is one way to estimate fish population dynamics when few empirical data are available (Yoshimoto and Clarke, 1993; Thorson et al., 2013). It assumes a fish logistic growth but the fish stocks are subject to catches. The model is not age-structured. It means that all fish inside a population have the same growth and natural mortality rate. Here the fish biomass (B) is projected annually as follows (Fletcher, 1978):

$$B_{y+1,j} = B_{y,j} + \frac{4msy_j}{K_j} B_{y,j} \left(1 - \frac{B_{y,j}}{K_j}\right) - L_{y,j} \quad (4.17)$$

The second term represents natural growth and death due to natural mortality and density dependence as a function of maximum sustainable yield (msy) and carrying capacity (K). The final term expresses the deaths due to fishing assuming zero (or negligible) discards. This assumption is broadly consistent since these stocks present small proportions of fish discarded (Heath and Cook, 2015). The landings can be approximated given an estimate of fishing mortality as follows:

$$L_{y,j} = (1 - e^{-F_{y,j}})B_{y,j} \quad (4.18)$$

This equation corresponds to the Baranov catch Equation (4.14) for biomass assuming $F = Z$. This is biased since the natural mortality M is considered small enough to be ignored for these species but it gives a good approximation of the total mortality for small value of M and F . All species present relatively small values of M and F so this assumption is valid. For instance *Nephrops* have a natural mortality between 0.2 and 0.3 (ICES, 2016b) so the landings approximation is good even for large values of F . The landings are thereafter partitioned into fleets.

For ling, only landing data is available and the landings were almost constant in the past 10 years (ICES, 2013c). Consequently, for this species a Schaefer model is not considered and the landings are directly estimated using an index of landings. When a simulation starts, this index equals the current observed landings per fleet. The landings for ling vary thereafter linearly with the fleet effort index.

4.1.2. The economic model

The economic part of the simulation model estimates fishing revenues and costs. Fishing revenues are obtained by multiplying price with landings and the fleet costs are estimated following a cost function.

There are two principal ways of modelling fish price in bioeconomic models. Either the fish price is exogenous and therefore considered constant, it is the most common assumption used in fisheries bioeconomics, or the price is endogenous and varies with supply (landings) and consumer's demand (Barten and Bettendorf, 1989; Delgado et al., 2003).

When the price is exogenous, the fishers face perfect competition and the implicit assumption is "price taking". It means the price is independent of the other variables in the model and its value is usually given by the market price. If the fishery is a small scale fishery, it is unlikely that the landings are responsible for a change in the market price. Similarly, if the fishery is a large scale fishery but the fish price depends on the international demand or supply, the price should be considered as exogenous despite the size of the fishery.

When the price is endogenous, the fishers are "price makers" and the price is a function of the supply and demand on fish (Ulrich et al., 2002a). This case is rarely considered in the literature often because it may be difficult to find a clear relationship between price and supply or demand (Herrmann, 1996).

In this study, it will be seen in a latter chapter, the simulation model is examined at the equilibrium so supply equals demand (Barten and Bettendorf, 1989; Herrmann, 1996;

Delgado et al., 2003). It makes sense then to express the price as a function of landings. However, the whitefish price in VIa is dictated by larger producers such as Norway and Iceland and Norwegian imports notably make the price of cod in the European market (Scottish Fishermen's Organisation, 2013). Regarding *Nephrops*, its real price (i.e. corrected for inflation) in the past 30 years is relatively constant (Figure 3.9) in relation with the relatively constant landings in VIa (Figure 3.7). Keeping its price constant may be a good representation of the current situation in the West of Scotland. Consequently, the input price in the simulation model is assumed to be exogenous, so constant.

The annual revenues for each fleet ($R_{y,k}$) are simply estimated by taking the sum over all species of the average price of a fish species per tonne (p) multiplied by the fleet landings as below:

$$R_{y,k} = \sum_j (p_j L_{y,j,k}) \quad (4.19)$$

Since this study considers equilibrium states, the revenues do not need to be discounted. Indeed the number of years to get to the equilibrium is not directly representative of the actual years needed for the current stock to reach the equilibrium. This reduces the problem of having exact current stock values needed for short-term projections.

Each fleet is assumed to incur two types of costs: variable and fixed costs. The variable costs per vessel (cv) are the fishing costs. In this study, these are proportional to the fishing effort index assuming the proportional constant ρ such as:

$$cv_k = \rho_k E_k \quad (4.20)$$

This presents limitation since the costs induced by the crew shares depends on the volume of catch landed. However, the lack of long data series on fleet costs do not permit the consideration of a robust second variable costs function varying with landings. Therefore, the crew shares are assumed to vary only with effort in this model and are comprised in variable costs with other fishing costs such as fuel costs. Assuming Equation (4.20) means that the marginal cost of effort is assumed constant.

In other words, the cost produced by one unit of effort is constant no matter the quantity landed and the amount of fish in the sea.

The total fishing costs (ct) are estimated within the simulation model using the Equation (4.21), where cf are the fixed costs per vessel and v is the number of vessels.

$$ct_k = v(cv_k + cf_k) \quad (4.21)$$

The fixed costs and the number of vessels are constant. Any change to the fleet fishing mortality is done through modifying activity.

4.2. Parameterisation

This part estimates and presents the parameters used in the simulation model. This comprises the Bayesian estimation of the biological parameters for cod, haddock and whiting using the state-space model (Cook et al., 2015; Cook and Trijoulet, 2016) but also the estimation of the other parameters necessary to the simulation model using data from the literature (Figure 4.2). The data used to parameterise the state-space and simulation models is given in Appendix C.

First the estimation of the fish stock parameters is described in part 4.2.1. The state-space model is used to estimate the parameters for cod, haddock and whiting via a Bayesian analysis (part 4.2.1.1). This model explicitly estimates grey seal predation and its outputs are the ones which mainly inform the simulation model for the three species. The parameters of the Schaefer production function and landing index are estimated using data from the literature for the other species and the estimation is explained in part 4.2.1.2.

Finally, part 4.2.2 presents all the final inputs used in the simulation model. Some come from the estimation studies in part 4.2.1 and others are directly taken from the literature.

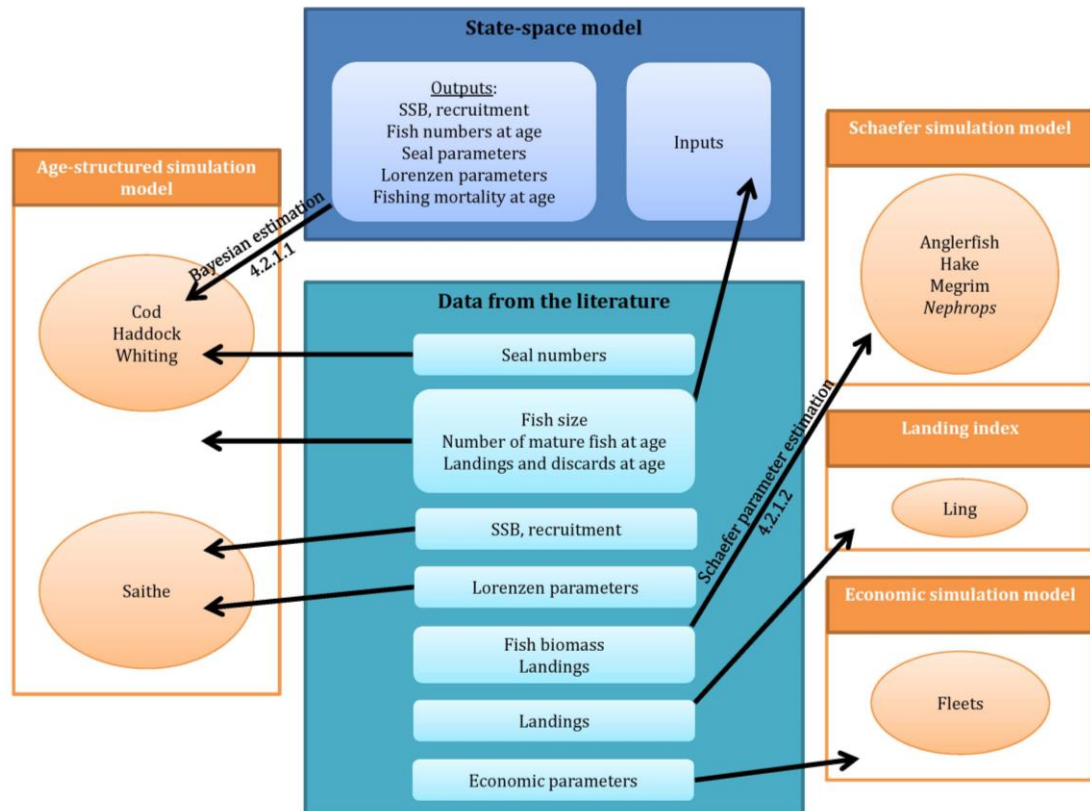


Figure 4.2: Schematic diagram of the parameterisation of the simulation model.

4.2.1. Estimation of the fish stock parameters

This corresponds to the estimation of the data necessary to parameterise the biological part of the simulation model. The age-structured parameters are estimated through a Bayesian analysis for cod, haddock and whiting. This enables the estimation of grey seal predation mortality for the first time in Vla on haddock and whiting and to provide updated estimates for cod. Data from the literature is used to estimate the parameters for the other species.

4.2.1.1. Estimation for cod, haddock and whiting

4.2.1.1.1. The state-space model

The state-space model used comes from Cook et al. (2015). It consists of an age-structured fish stock assessment model, similar to the biological part of the simulation model, which includes fish removals by seals as well as fishers. It notably enables the explicit estimation of grey seal predation in contrast to the conventional ICES assessments that assume grey seal predation is subsumed into the estimates of natural mortality. A full description of the model is available in Appendix D.

The model differs from the simulation model for several reasons. First, no stock-recruitment relationship is explicitly estimated. Recruitment and SSB are derived from the fish number estimates. Also, the Lorenzen estimates are directly estimated within the model and natural mortality varies with time following the change in fish weights. Fishing and grey seal predation mortalities are modelled as a time series with Normally distributed random effects.

Except for this, the state-space model shares similar assumptions to the simulation model where the fish stock is modelled as a series of cohorts subject to the sum of natural, fishing and grey seal predation mortalities.

The state-space model for cod has been extended from the version available in Cook et al. (2015) who run the model to 2005. The current model is run to 2012. However there is an change in the pattern of cod discards data since 2006 which is due to the implementation of the Registration of Fish Sellers and Buyers in the UK in 2005 which specifies that fish can be sold or bought only by registered sellers and buyers. This means that before 2006, fish were often sold illegally rather than discarded when tight quota restrictions existed. As a result most fish discarded were due to size restrictions rather than quota limits. Since 2006, with tighter regulation, very low catch quotas on cod induced high numbers of larger fish to be discarded (ICES, 2013b) as it was difficult to sell them illegally. To accommodate this change in fish retention after 2006 only total catch of cod is considered in the model from 2006 onwards so no partition is made

between landings and discards after this year. This circumvents the model assumption prior to 2006 of a fixed discard ogive dependent on size.

4.2.1.1.2. Empirical data used for the state-space model

The state-space model uses biological data on fish stocks, fishing mortality and grey seals (Table C.1). All fish and fishing data are taken from ICES (2013b). This consists on fish biological data: proportion of mature fish at age, fish weight at age (the weight at age in the total catch is used here) but also on fishing data (discards and landings at age in numbers).

Every year, bottom trawl survey vessels sample the VIa zone as part of the North-eastern Atlantic International Bottom Trawl Survey (IBTS) (ICES, 2016a). These surveys have the goal to provide indices of abundance for the demersal stocks present at different quarter of the year. Four different research vessel surveys provide abundance indices in the West of Scotland for the three species of interest over the time series 1985-2012 (Table 4.2). The abundance indices were used in this study as input parameters for the state-space model.

Table 4.2: North-eastern Atlantic IBTS surveys used to parameterise the state-space model (ICES, 2013b).

Survey	Survey code	Running years
Quarter 1 Scottish West coast groundfish survey	ScoGFSWIBTS-Q1	1985-2010
Quarter 4 Scottish West coast groundfish survey	ScoGFSWIBTS-Q4	1996-2009
Quarter 4 Irish West coast groundfish survey	IRGFSWIBTS-Q4	2003-2012
Irish groundfish survey	IreGFS	1993-2002

In 1999, the Scottish survey vessel has been replaced as well as the length of the tow being reduced from 60 to 30 minutes (ICES, 2013b). Preliminary simulations have shown this change is responsible for a variation in vessel's catchability. Since vessel's catchability is constant within the model, this could cause a problem for the estimation. To counter this problem the Scottish quarter 1 survey (ScoGFSWIBTS-Q1) has been split into two different surveys (1985-1999 and 2000-2010). This has not been applied

for the ScoGFSWIBTS-Q4 survey since it would result in a survey of only four years from 1996 to 1999. When the abundance index was 0, it was treated as missing value to avoid calculation error when taking logs. This only accounts for a small number of observations.

Fish length at age is also used as input into the state-space model to estimate seal selectivity. The lengths are estimated, similarly to Cook et al. (2015) and Cook and Trijoulet (2016), using the inverse weight to length relationship given in Coull et al. (1989). The gutted weight at age ($GW_{a,y,j}$) is estimated each year using the total weight at age $w_{a,y,j}$ from ICES (2013b) as follows:

$$GW_{a,y,j} = \frac{w_{a,y,j}}{RF_j} \quad (4.22)$$

The term RF_j corresponds to a raising factor responsible for the conversion from total weight to gutted weight and is given for each species in Coull et al. (1989). The gutted weight obtained, it is possible to estimate the length at age of the fish following the equation (4.23) below:

$$l_{a,y,j} = \left(\frac{GW_{a,y,j}}{\theta_{1,j}} \right)^{\frac{1}{\theta_{2,j}}} \quad (4.23)$$

The parameters θ_1 and θ_2 are taken from Coull et al. (1989) for the three species. In Coull et al. (1989), it is the length of fish which gives the gutted weight. In this study, a back transformation is done and this is biased and may not give the exact length of the fish. However, this estimation gives size indices which are assumed satisfactory to estimate seal selectivity as a function of fish length.

Seal diet data in terms of numbers at length and average per capita consumption rates (in kg per seal per year) are taken from Harris (2007). Length-structured data has been kindly converted into age-structured data to be directly used within the model by the Marine Laboratory (Marine Scotland) using a combined age-length key obtained from the Scottish quarter 1 and 4 research surveys.

Seal numbers over time comes from Thomas (2012). Grey seal population varies from 26,100 individuals in 1985 to 32,000 in 2011. The per capita consumption rates are multiplied by the numbers of seals in 1985 and 2002 to obtain the total annual consumption (in tonnes) scaled to the seal population used in the model. The seal number estimates from 2012 were used since using more recent estimates (Thomas, 2013; 2014) does not impact the parameters estimated by the state-space model. Indeed, the different estimates having similar trends (Figure 3.10) investigating runs updating the estimates to more recent ones gave similar outputs and validated the use of the 2012 estimates.

4.2.1.1.3. The choice of priors

In Bayesian analyses, it is necessary to define prior distributions on all the estimated parameters which correspond to the belief we have on the value the parameters can take.

The priors are mainly taken from Cook et al. (2015). Non-informative priors are used on precision parameters for the abundance indices and the catch and seal consumption estimates. Some of the priors have been modified to be also applicable to the three species of interest. The initial population size and minimum landing size are different for the three species. The priors on seal selectivity have been modified to be less informative. Trial runs showed that the original priors had undue influence on the estimates and tended to force similar selectivity across species. An updated table of prior distributions is given in Appendix E.

Most of the priors are non-informative notably for process and measurements errors and the priors on seal parameters were informed by real data. Also, the robustness of the state-space model to the choice of priors has been already demonstrated by Cook et al. (2015). For this study a lot of different model configurations were run and confirmed the insensitivity of the model to the priors used. The seal estimates can therefore be seen as reliable, at least for the two years where seal diet data is available.

4.2.1.1.4. Model fitting

The simulation model aims to be a good approximation of the current state of the West of Scotland demersal fisheries, particularly for cod, haddock and whiting, the three species of interest for which grey seal predation is considered. There exist currently two years of data (1985, 2002) on grey seal diet which have been published by the SMRU (University of St Andrews). This limited data makes it challenging to estimate the value of mortality due to seals on fish stocks for a specific fish or seal population over the time series (1985-2012). A Bayesian approach is one way to estimate parameters when only limited empirical data is available. This approach uses prior belief about the parameters of interest to constrain parameter estimates. It facilitates the inclusion of random effects into the models compared to other fitting techniques such as maximum likelihood estimation. This approach has been employed to estimate biological parameters that have been used as inputs into the simulation model such as fishing mortality, stock numbers and seal predation parameters.

Similarly to Cook et al. (2015), three different scenarios were tested for the state-space model:

1. Seal predation is considered as subsumed within the natural mortality M and is not explicitly estimated in the model (i.e. $Z = F + M$). This most closely resembles the standard VIa ICES assessments and was used to compare estimated stock trends and fishing mortality with the current ICES stock assessments.
2. Seal predation rate is allowed to vary annually according to a simple time series model following a random walk with a multiplicative random effect $\varepsilon \sim \text{Normal}(0, \sigma^2)$ as in Equation (4.24). This parameter determines the efficiency of seals to find and consume fish. Therefore it incorporates rate of search (or attack rate) and handling time from the Holling functional response equations (Holling, 1959) and is expected to vary over time.

$$q_{y+1} = q_y e^{\varepsilon_y} \tag{4.24}$$

3. The seal predation rate (q) is fixed over time (i.e. the process error standard deviation (σ) equals 0 in the Equation (4.24)). Given the paucity of seal diet data, estimating annual values of q may over-fit the data.

The fact that the haddock per capita rate increases a lot between the 1985 and 2002 (Harris, 2007) while the haddock population has not changed much (ICES, 2013b) or the fact that cod SSB has significantly declined between 1985 and 2002 (ICES, 2013b) while the per capita rates are of the same order of magnitude (Harris, 2007) seems to give evidence for variable seal predation rate (Cook and Trijoulet, 2016). Comparing these two models should help investigating this uncertainty.

In Cook et al. (2015), the state-space model is run from 1985 to 2005. In this study, the model is run from 1985 to 2012 because some investigating runs with the new unpublished seal diet data (2010-2011) made available by the SMRU shown that the model gives estimates very close to the ones with the new seal diet data even if the only seal diet data considered are 1985 and 2002. Consequently the model appears robust in the recent years even when seal diet data is not present.

The simulations were run in the WinBUGS 1.4.3 (2007) software (Lunn et al., 2000) directly from the software R using the R2WinBUGS package (Sturtz et al., 2005). A three chains simulation was preliminary run for 10,000 iterations for each species. The chains converged after 5,000 to 8,000 iterations so the analysis was run with one chain, 40,000 iterations and a burn-in period of 10,000 iterations for all species. It has to be noted that the convergence is slow for the seal parameters in the years for which no observations are available. This is expected since only two years of empirical data are available for seal diet data. However the convergence was quick for these two years and, as these are the years used to derive inputs to the simulation model, this supported the choice of number of iterations.

Standard statistics were run after each simulation to record mean, median, and 95% credible interval for all variables recorded. These outputs were compared to empirical data to determine the goodness of the fit. The Deviance Information Criterion (DIC) was also recorded to determine to best fit between the variable and fixed predation rate models, the two simulations using the same empirical data.

4.2.1.1.5. Model fit to empirical data

The outputs were compared to observed and estimated data on fish stocks and catches from ICES (2013b) and to grey seal diet data from Harris (2007). The respectable fit between the estimated and the observed variables confirmed the consistency of the data and validated their use as inputs in the biological part of the simulation model.

The simulations when seal predation is subsumed within natural mortality most closely resemble the method currently used in VIa stock assessments. The obtained results should therefore be close to what is predicted in ICES reports.

Figure 4.3 compares the values for SSB, recruitment and average fishing mortality estimated by the state-space model with the values reported in ICES (2013b) for the three species. For whiting the results presented here come from simulations where some of the survey data (2001-2005) have been omitted due to an inconsistency which will be discussed in part 4.2.1.1.6. For cod the estimates are really close to those estimated in routine ICES assessments. For haddock and whiting, the stock-recruitment estimates of the model are slightly larger than the ones estimated by ICES (2013b) but follow the same trends. This can be explained by the estimates of natural mortality. For cod, the estimates are similar to what is used in ICES but for haddock and whiting, the assessments estimate a larger natural mortality than the one in ICES and this is responsible for larger values of SSB and recruitment.

Overall, the state-space model estimates smaller values of fishing mortality than ICES but the trends are similar except for cod in the last ten years. This is also due to the difference in estimated natural mortality between the state-space model and ICES assessments. The state-space model gives similar stock trends than ICES assessments so forms the basis of further analysis where seal predation is explicitly accounted for.

Bayesian statistics have the advantage of being able to use priors on the parameters to aid estimation. In common stock assessments, the natural mortality already implicitly incorporates grey seal predation. In this model, grey seal predation is extracted from the natural mortality and the use of priors enables the model to shift the Lorenzen's estimates of natural mortality (Lorenzen, 1996) to give a part of the mortality to grey

seal predation. This and the priors on the other parameters should improve the fit of the seal predation simulations.

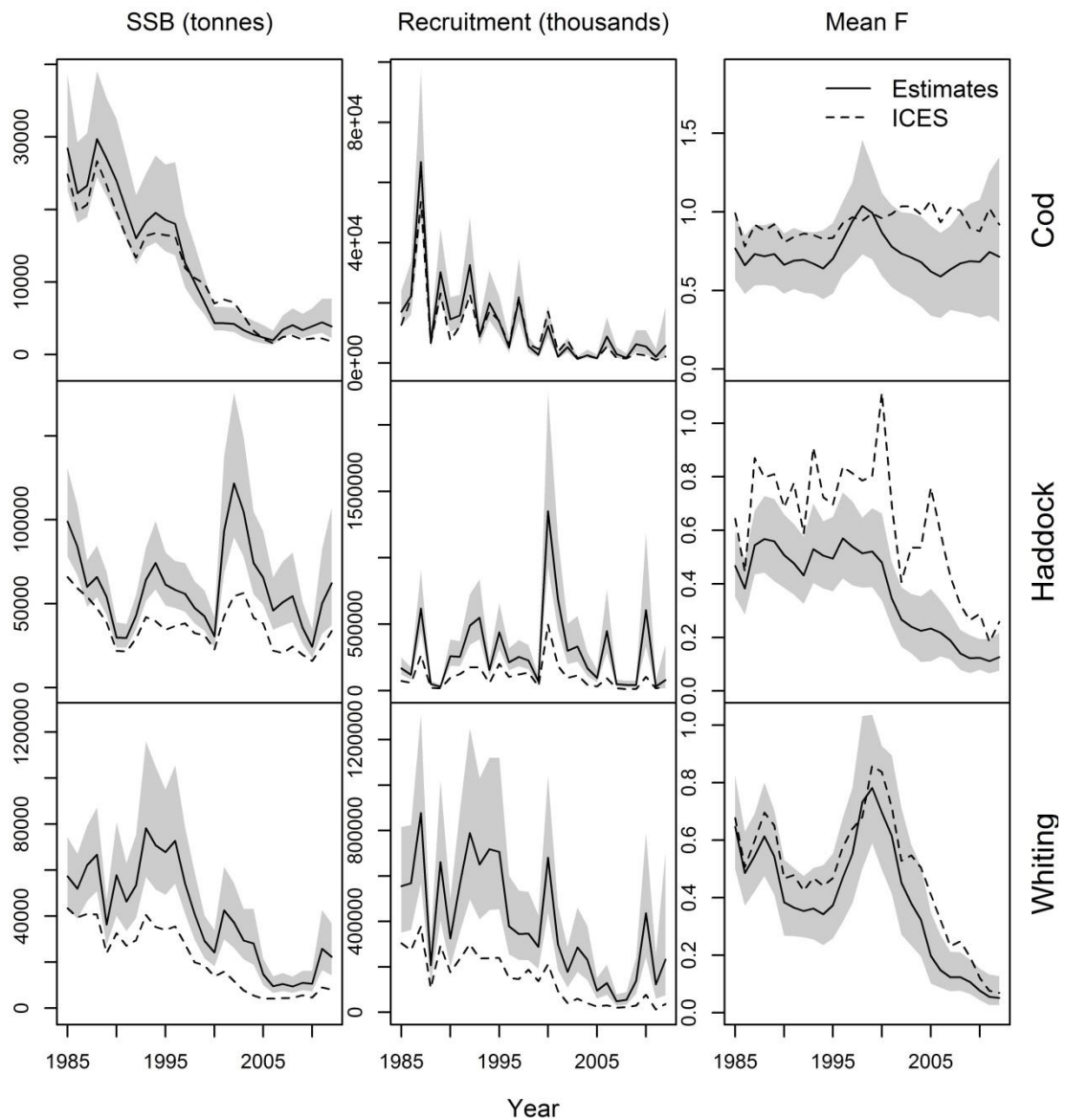


Figure 4.3: Comparison of model estimated values when seal predation is subsumed within natural mortality with values reported by ICES (2013b) for SSB, recruitment and average fishing mortality over the age ranges used in ICES (2013b). The black line is the median and the grey area is the 95% credible interval. The estimates for whiting come from simulations where survey data from 2001 to 2005 were omitted.

The fit to empirical and ICES data for both state-space models considering seal predation and the three species is given in Appendix F. Both assessments give similar fits. For the three species, the fit for the estimated log landings is very good (Figures

E.1-E.2, E.23-E.24, E.43-E.44) but the discards are less well fitted (Figures E.3-E.4, E.25-E.26, E.45-E.46). The catches from 2006 to 2012 are well fitted for cod (Figures E.5-E.6). The survey abundance indices for the three species are reasonably fitted but some points lie outside the credible intervals (Figures E.7-E.16, E.27-E.36, E.47-E.56). Similarly to what was visible for the model that does not explicitly consider seal predation, the trends in recruitment and SSB are respected for the three fish species (Figures E.17-E.20, E.37-E.40, E.57-E.60) but the estimated values are slightly larger than what is estimated by ICES due to larger estimated non-fishing mortality ($M + P$).

The observed proportion of fish caught by seals in a specific age class is well fitted for the two years of data and for both state-space models although for haddock some points of the data lie outside the 95% credible intervals (Figures E.21-E.22, E.41-E.42, E.61-E.62).

Overall, the model fits the data well and seems to give reliable outputs when considering seal predation as part of the total mortality on fish stocks. It provides an adequate basis to use these outputs as input parameters for the simulation model. However, a choice has to be made as regards to the use of the fixed or variable predation rate simulation outputs.

4.2.1.1.6. Outputs of the state-space model

This part compares the model outputs for the fixed and variable predation rate simulations. The latter simulation assumes grey seal predation rate can change annually, while the other sets the rate as a constant.

Figure 4.4 gives the estimates of grey seal predation mortality for the three species of interest and both state-space models. The mortality is averaged over ages 2-5 for cod, 2-6 for haddock and 2-4 for whiting. These age intervals are used in ICES (2013b) and enable a direct comparison with the average fishing mortality in the report.

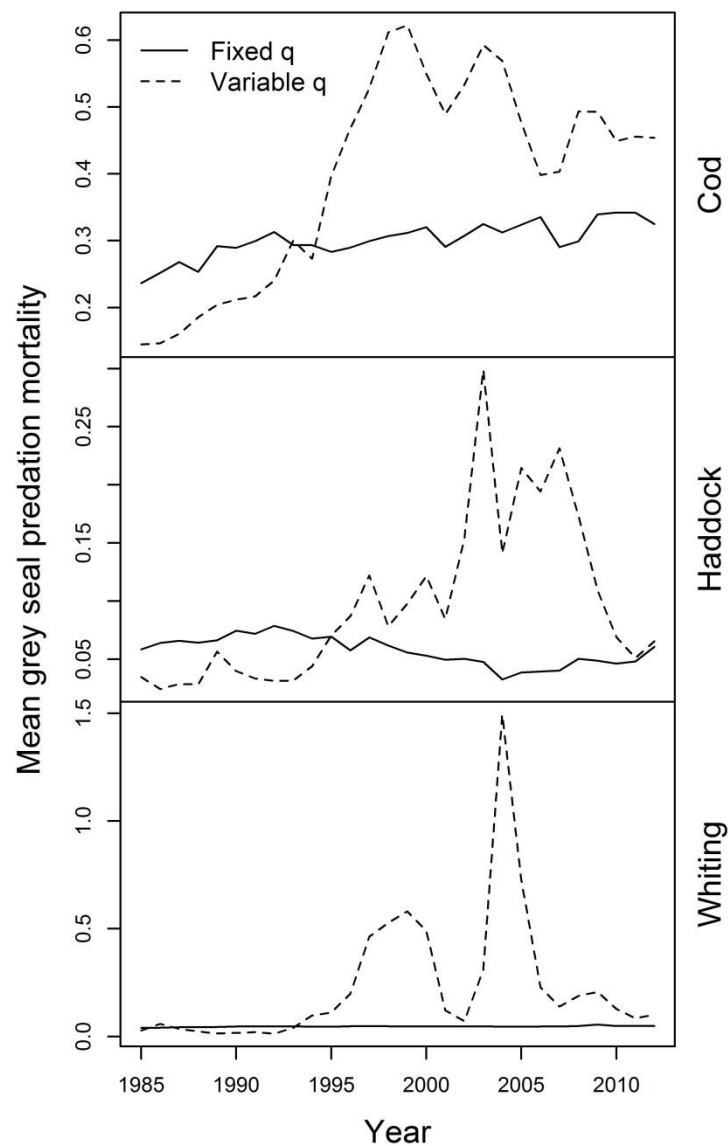


Figure 4.4: Comparison of average grey seal predation estimates along the time series for the three species in the case of fixed and variable seal predation rate. The averages are taken over ages 2-5 for cod, 2-6 for haddock and 2-4 for whiting following ICES (2013b).

The plots highlight the fact that the estimated grey seal predation is greater from 1995 when a variable seal predation rate is considered. In the case of a fixed seal predation rate, the mortality due to seals on the three species is almost constant over the 28 years of simulation. This is explained by only small changes in seal population and fish weight at age (which influences seal selectivity). When the rate is allowed to vary, the variations are important. For cod, the predation rate seems to increase and stays practically constant and high in the last 10 years. For haddock and whiting, the seal

predation rate is more or less constant in the first 10 years, then increases and decreases in the last years of the time series. A substantial increase in grey seal predation rate is observed for whiting in the variable predation rate simulation for the years 2004 and 2005, with a seal predation of 1.5. This increase seems improbable and is investigated later on in this chapter.

No grey seal predation estimates currently exist so it is difficult to set one of the mortality estimates as more realistic than the others. To help choosing the best values, the fit of the different state-space simulations were compared.

Figure 4.5 shows the difference in seal consumption fit for the two seal predation simulations. Since only two years of data exist on seal consumption it is difficult to predict how the consumption varies between these years.

Not surprisingly, it is clear that for cod and haddock, the variable predation rate simulations seem to give a better fit than the fixed rate simulations because there is more flexibility for this model. It is particularly evident for the haddock estimates in 2002. The lack in fit for the haddock fixed rate simulation is due to the fact that the predation rate is constant over time and this reduces the range of values the estimated consumption can take. However, for the variable rate simulations, the consumption varies a lot over time and, because of the lack of empirical data on grey seal predation diet, it is difficult to know about the reliability of these estimated changes.

The spike previously observed in grey seal predation for whiting appears in the seal consumption when the seal predation rate is variable where the model estimates a consumption of more than 45,000 t in 2004. With an observed whiting consumption of 1,647 t in 2002, it seems implausible to have a figure so high for this year.

Differences in fit exist also for the estimated fishing mortality (Figure 4.6). Overall, the fishing mortality is lower than the one estimated in ICES (2013b) partly because seal predation is considered but also because, as mentioned earlier, contrary to the common stock assessments, Lorenzen's estimates are estimated within the state-space model and the non-fishing mortality ($M + P$) is larger than the natural mortality estimated by ICES. In ICES assessments, the natural mortality on haddock is constant for all ages and

is set to 0.2 (ICES, 2013b). This means the partition of the total fish mortality into fishing and natural mortality may differ with the partition obtained with the state-space model. The estimates of non-fishing mortality for haddock in this study are substantially larger than the ones observed in ICES (2013b).

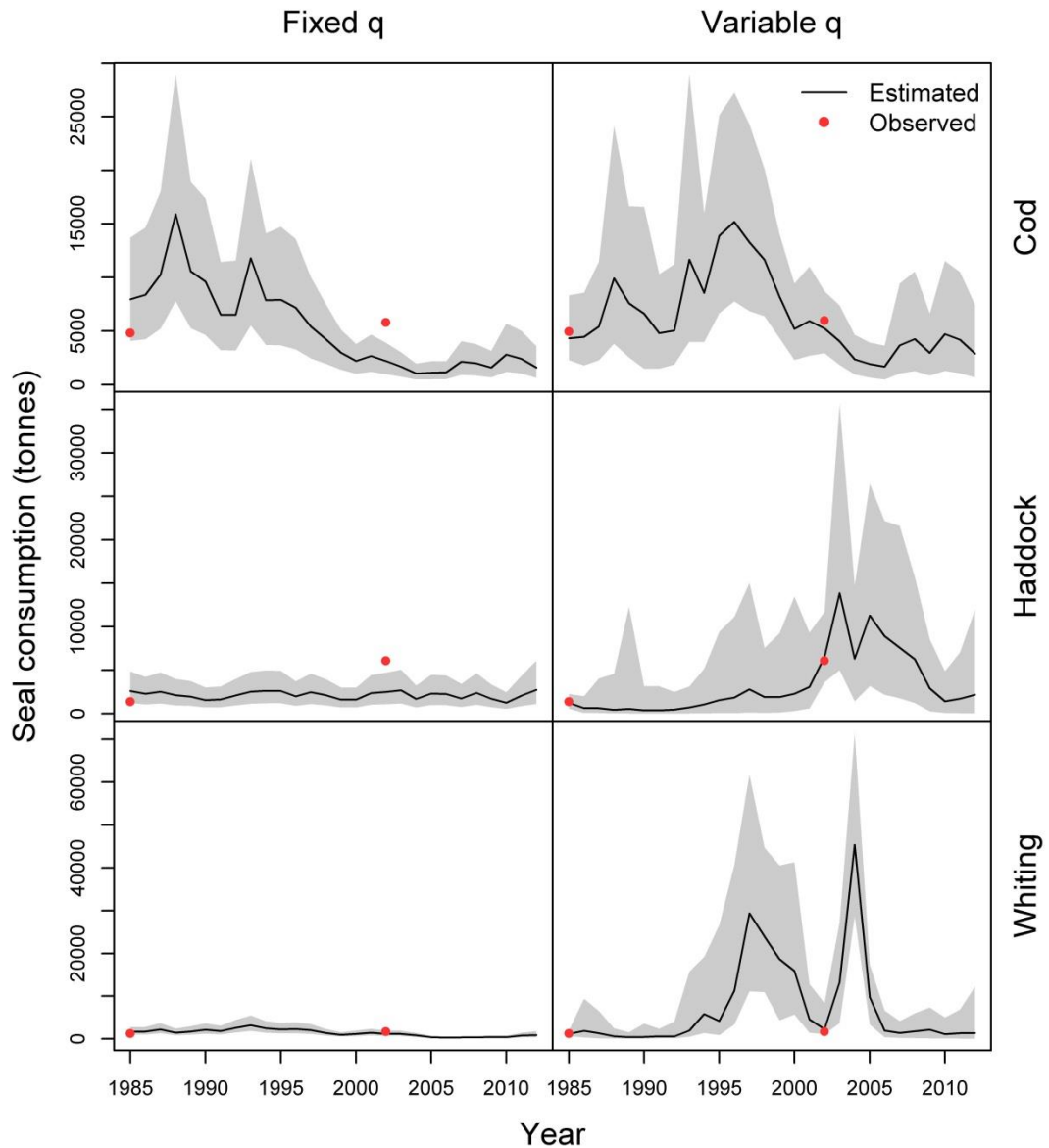


Figure 4.5: Estimated fish weight consumed (in tonnes) by grey seals along the time series for the fixed (left-hand panel) and variable (right-hand panel) seal predation rate simulations. The black line is the median consumption and the grey area is the 95% credible intervals.

The model predicts a fishing mortality which declines in the last 10 years for haddock and whiting. Fishing mortality on cod decreases from 2000 but increases from 2005

while ICES (2013b) predicts a fishing mortality fairly constant and high. This can be explained by the fact that in ICES assessment more of the total mortality is attributed to fishing because the non-fishing mortality is smaller. The Lorenzen estimates from the state-space model and the consideration of seal predation induce larger estimates of non-fishing mortality. This will be discussed in more detail in part 4.2.2.1.3.

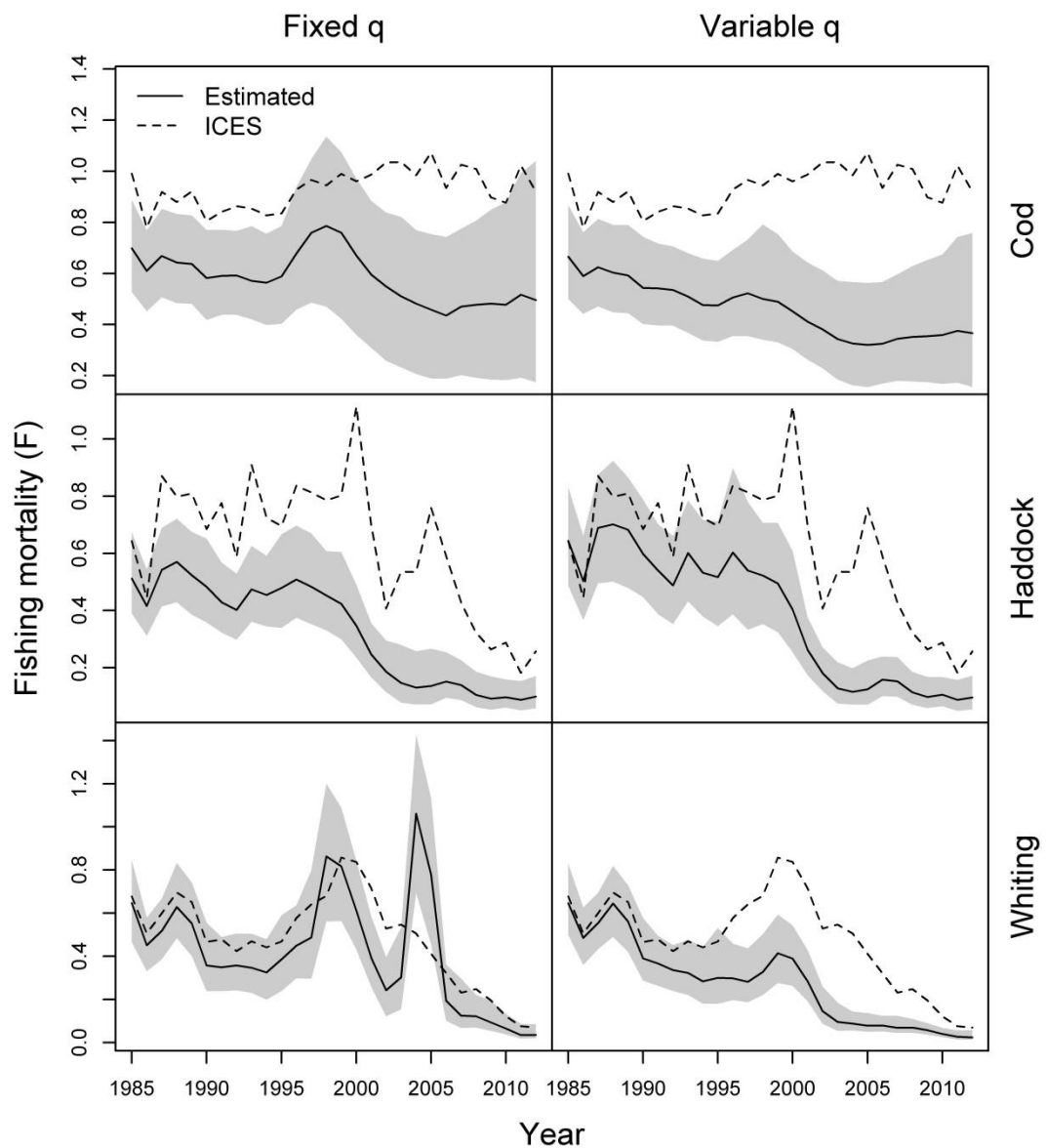


Figure 4.6: Comparison of estimated mean fishing mortality with the fishing mortality in ICES (2013b) for the fixed (left-hand panel) and variable (right-hand panel) simulations. The averages are taken over ages 2-5 for cod, 2-6 for haddock and 2-4 for whiting. The black line is the median fishing mortality and the grey area is the 95% credible intervals.

The main difference in fit between the two state-space models is for whiting. Indeed in the fixed seal predation rate simulation, the fishing mortality shows the spike for the years 2004 and 2005 which is not present in ICES estimates. Also, this spike is allocated to misreported catch (Figure 4.7 top left panel). The spike does not appear for the variable predation rate simulation but it appears in the mortality due to seal for the same years (Figure 4.7 bottom left panel). A similar spike is observed in average fishing mortality for some runs in ICES (2013b; 2014c) but these runs are not kept as final outputs in the reports. As the ICES assessment uses a different model but also shows this effect, it suggests the anomaly is related to the input data rather than the modelling assumptions alone. This means there is something in the empirical data which induces a high total mortality on whiting for these two years and this explains the high seal predation mortality and consumption previously observed. Because the empirical data does not show high levels of landings for these years, when the predation rate is fixed, the state-space model allocates the mortality to misreported catch and when it is variable, the model allocates the increase in mortality to an increase in grey seal predation.

Extensive work on different test simulations for whiting seems to show that large mortality in the survey data from 2001 to 2005 may be responsible for this spike. Indeed, the same simulation when treating the survey data as missing values from 2001 to 2005 gives results for which the spike is absent or considerably reduced (Figure 4.7 right-hand panels). Other investigating runs considering certain surveys only showed that the two Scottish surveys (ScoGFSWIBTS-Q1, ScoGFSWIBTS-Q4) and the Irish quarter 4 survey (IRGFSWIBTS-Q4) are responsible for this spike, with the quarter 4 surveys having the largest impact.

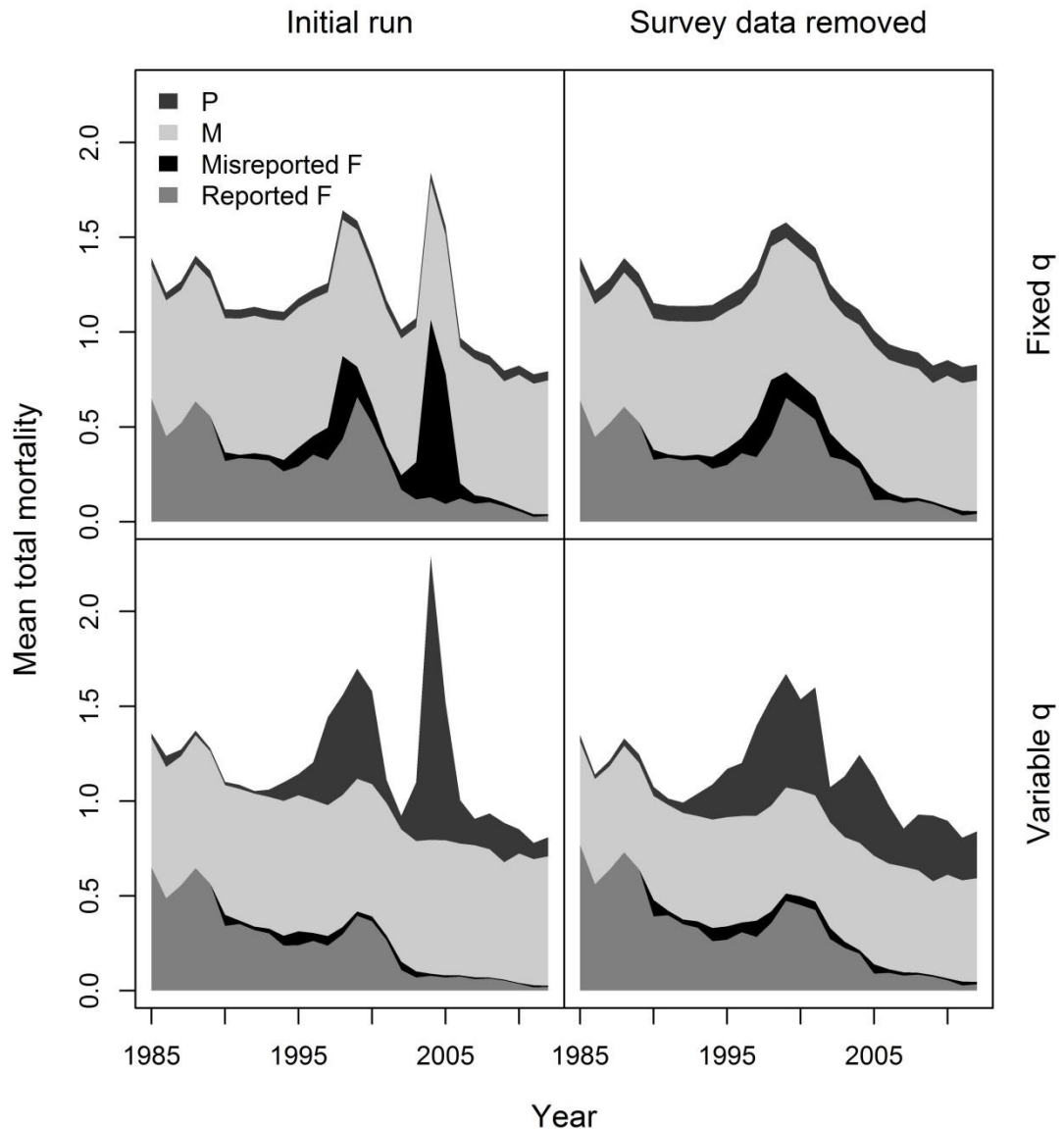


Figure 4.7: Whiting mean estimated total mortality partitioned into reported and misreported fishing mortality, natural mortality and grey seal predation mortality for the initial run and when survey data is treated as missing values from 2001 to 2005. The averages are taken for ages 2 to 4.

Runs without the catch data for these years still present a spike while it does not appear when ignoring surveys and catch data. This means that the surveys only are responsible for this spike. Clearly the spike is unrealistic because leading to seal catches or misreported fishing mortality with inconsistent high values. It is evident that the simulations for which the survey data is removed between 2001 and 2005 are more likely to provide the appropriate state-space outputs for whiting.

Concerning the rest of the variables, the visual fit for both seal predation simulations is similar with sometimes the fit being slightly better for the fixed rate simulations and other times the fit being better for the variable rate simulations (Appendix F). It is therefore difficult to choose the outputs to use looking at the visual fit. However, the DIC estimates for the variable predation rate simulations for the three species are slightly lower than the fixed rate simulation DIC estimates (Table 4.3). The DIC values and the better seal consumption fit (Figure 4.5) demonstrate that the overall fit is better for the variable rate simulations.

Table 4.3: DIC estimates for the different seal predation simulations. A lower DIC illustrates a better fit (Spiegelhalter et al., 2002). For whiting the DICs correspond to the simulations when the survey data 2001-2005 is removed.

	Fixed q simulations	Variable q simulations
Cod	3,496	3,480
Haddock	8,702	8,640
Whiting	7,031	6,917

However, when the fits are compared between the fixed and variable predation rate simulations for whiting when the survey data 2001-2005 are omitted, the most realistic fit is given by the fixed q simulation (Figure 4.8). Indeed, even if the spike in 2004-2005 is reduced in the variable q simulation, a large seal consumption is estimated in 1998-2000 (almost 30,000 t of whiting consumed). This increase seems to be due to a large mortality for these years. However, in the case of the variable q simulation, the model attributes the mortality to seal predation while it is attributed to the fishing mortality when the seal predation rate is fixed. The fit for F is better for the fixed q simulation than the variable q simulation. Also, the most recent estimates of seal consumption for the fixed q simulation are more consistent with the recent seal diet data. For all these reasons, for whiting, the outputs from the fixed q simulation removing the survey data from 2001 to 2005 seem the most satisfactory.

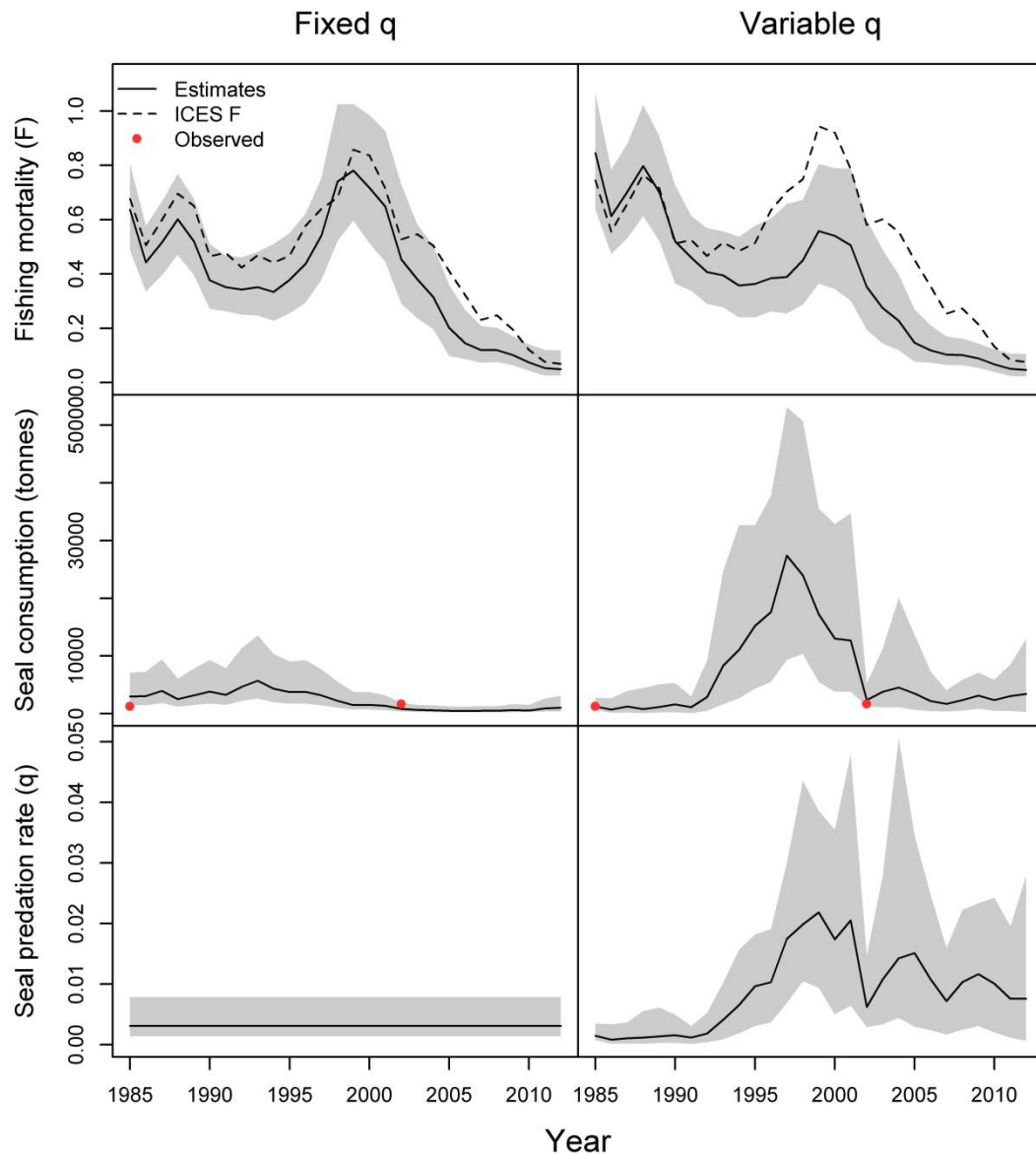


Figure 4.8: Mean fishing mortality, seal consumption and seal predation rate estimates obtained for whiting when the survey data 2001-2005 are omitted. The black line is the median fishing mortality and the grey area is the 95% credible intervals.

For the two other species, the fit being better for the variable seal predation rate simulations, these simulations provide the preferred outputs. It is important to note that for haddock, a large seal consumption is estimated in 2003 with around 15,000 t of haddock consumed (Figure 4.5). The observed consumption in 2002 being around 6,000 t, this estimate seems also surprisingly large. However, for the simulation model, it has been chosen to take an average seal predation mortality of the two years of observed data (1985 and 2002). The variable q simulation fits the seal consumption in

2002 better than the fixed q simulation. The estimates for these years being informed by real data this reduces some of the uncertainty around grey seal predation mortality estimates. Consequently, for cod and haddock the variable q estimates and for whiting the fixed q outputs when the survey data is omitted provide the preferred estimates for the simulation model.

4.2.1.2. The Schaefer surplus production model for the other species

As previously mentioned, besides cod, haddock, whiting and saithe, five other species are considered within the simulation model for which no age-structured data is available (anglerfish, megrims, hake, *Nephrops* and ling). A Schaefer surplus production function is used to estimate fish biomass and determine fleet landings for the first four species. It is therefore necessary to estimate the initial fleet fishing mortality and biomass on the different species and the constants in the Schaefer equation: msy and K . A summary of the empirical data used to estimate these parameters is given in Table C.2. The landings in VIa, when not available in the reports, were found in the ICES online databases (ICES, 2011; 2015a).

The initial biomass was estimated taking the average biomass in VIa for the years 2007-2011 from ICES reports. When not available (for megrim and hake), the biomass for the entire stock was scaled to the biomass in VIa by applying the proportion of the landings in VIa to the total landings for the stock.

The mean fishing mortality is not available in the ICES reports. Consequently the fishing mortality has been estimated using the average biomass and landings between 2007 and 2011 in VIa assuming the Equation (4.18). This gives an average fishing mortality on the stock in VIa. This fishing mortality is then partitioned by fleet according to the proportion of each fleet in the total landings for this species (Appendix G).

To estimate the constants msy and K of the Schaefer surplus production function (Equation (4.17)), a least square regression was done in the software R. The landings were considered as known values and the biomass was estimated by fitting to the

observed biomass. The fits are given in Figure 4.9 and the fitted values are discussed in part 4.2.2.1.6.

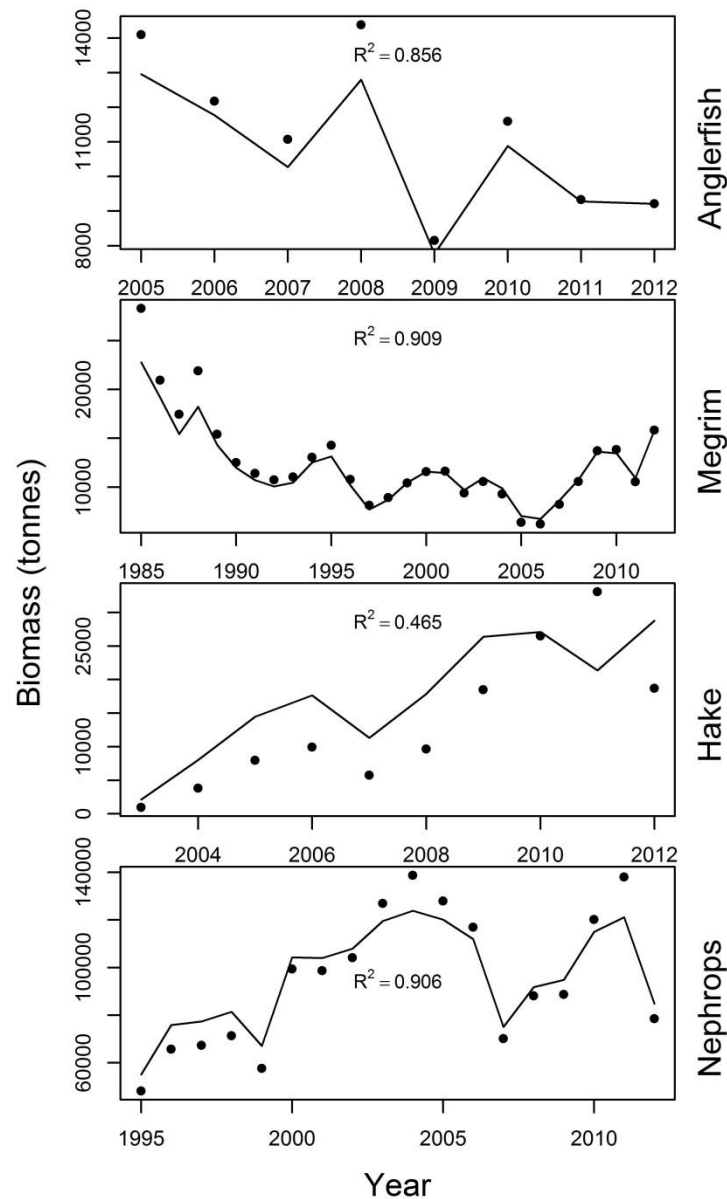


Figure 4.9: Fit of the Schaefer surplus production function (line) to the biomass data (dots) estimated by ICES and given coefficient of determination.

The fit is good but less so for the European hake for which the coefficient of determination is lower but still acceptable. The trend in fitted hake biomass is similar to the data but the biomass is overestimated over much of the time series. More data points were available for hake but the trends in biomass vary a lot along the time series

and increase the difficulty to fit the model. Selecting a recent period gives parameter values closer to the current environment so explains the choice of considering the last years of data to estimate Schaefer parameters. Consequently for hake, the lack of fit is not due to a lack of data but to a difficulty of fitting the Schaefer function. This may come from the fact that the biomass for the entire Northern stock is scaled to the proportion of landings in VIa. In ICES, the Northern hake stock is assessed in the length-based Stock Synthesis 3 (SS3) assessment model (ICES, 2014d). Because grey seal predation is not studied on hake, a simpler Schaefer surplus model was preferable in this study. This overestimation in hake biomass needs to be kept in mind when analysing the results of the simulation model. However, this fish is one of the least valuable among the other species and preliminary runs show that hake biomass does not substantially vary over time compared to the initial biomass. Consequently, we can think that the lack of fit for hake will not substantially impact the whitefish fleets revenues.

4.2.1.3. The landing index for ling

It has been seen in part 4.1.1.2, that the landings for ling are directly estimated using an initial landing index. To create this index, average landings in VIa were taken between 2007 and 2011 and then partitioned by fleet (Table C.2). This partition is assumed to be the one at the current level of effort and landings change linearly with the change in the effort index. The details about the partition of the landings into fleets can be found in Appendix G.

4.2.2. Inputs for the simulation model

4.2.2.1. Biological parameters

Biological parameters were taken from the results of the preferred state-space model for the three species of interest (Table C.3) and from the literature for the other species. For cod and haddock it corresponds to the variable seal predation rate model and for whiting to the fixed rate model removing the survey data from 2001 to 2005.

Since the goal of the simulation model is to be a good approximation of the current state of the West of Scotland fishery, and because economic data is only available for the years 2007-2011 (cf. part 3.3.2), the preferred model outputs from the Bayesian analysis averaged from 2007 to 2011 were used to parameterise the biological part of the simulation model. This period differs from the period used for seal predation parameters (two years average 1985 and 2002) but this is unavoidable since these years are the only ones informed by grey seal diet. Runs with the recent year (2011) of unpublished seal diet data give estimates really close to the ones with only two years of seal diet and show the robustness of the state-space model even with limited empirical data available.

For saithe, the data used to parameterise the simulation model were averages over 2007-2011 taken from ICES (2013d).

A summary of the data used from the literature is also given in Table C.4.

4.2.2.1.1. Initial number of fish at age

The simulations were started with an average population estimated following the Equation (4.25) where \bar{N}_1 and \bar{Z} represent respectively the average recruitment and total mortality at age from the state-space outputs between 2007 and 2011.

$$\begin{aligned}
 N_{1,j} &= \bar{N}_{1,j} \\
 N_{a+1,j} &= N_{a,j} e^{-\bar{Z}_{a,j}}
 \end{aligned}
 \tag{4.25}$$

To be consistent with the literature (ICES, 2013b), age plus groups of “7+” for cod and whiting and “8+” for haddock were assumed.

For saithe, the data is taken from ICES (2013d) and the maximum age already represents an age plus group. The first age class for saithe corresponds to age 3 so the last age class is the “10+” age group. The average fish number at age between 2007 and 2011 is simply used for this species.

4.2.2.1.2. Stock-recruitment parameters

The 28 years recruitment and SSB estimates from the state-space model were used to estimate the stock-recruitment parameters (Table 4.1). For saithe, ICES data over 1967-2012 is used (ICES, 2013d).

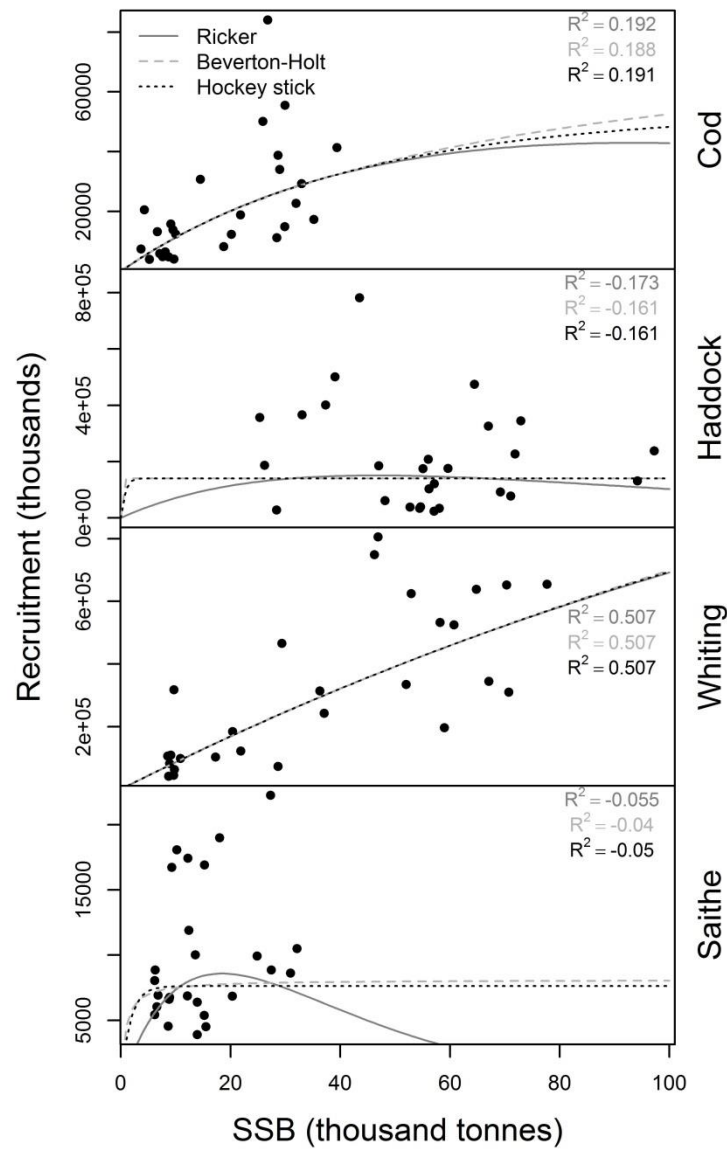


Figure 4.10: Fit of the stock-recruitment data for the three assumptions on stock-recruitment relationship and corresponding coefficient of determination.

The parameters were estimated using a least squares fitting method in R assuming a lognormal distribution for recruitment after testing the normality with a Shapiro-Wilk test.

While Ricker is used by default in the bioeconomic simulations, the sensitivity of the model to a change in the stock-recruitment relationship is considered in Chapter 6. As a result, the Beverton-Holt and hockey-stick stock-recruitment parameters were also estimated. The fits of the three stock-recruitment curves are given in Figure 4.10 and the corresponding parameter values in Table 4.4. Overall, the coefficient of determination is low. Only whiting shows a coefficient of at least 50%. For haddock and saithe the coefficient is negative. This means that the mean recruitment provides a better fit than the modelled values. The mean recruitment is very close to the asymptote value for both stock-recruitment functions and species so this should not be a problem when simulating populations away from low values of SSB.

Table 4.4: Estimated stock-recruitment parameters used in the simulation model. The values in parenthesis indicate the standard errors. These are not given for haddock in the Beverton-Holt and hockey-stick cases because the estimates being not unique, given that a horizontal line is fitted in both cases, the standard errors cannot be estimated.

Species	Ricker		Beverton-Holt		Hockey-stick	
	α	β	α	β	K	α
Cod	1249.503 (±0.248)	0.011 (±1.064)	1.128E-05 (±1.016)	1290.561 (±0.283)	53227.786 (±0.917)	1262.617 (±0.259)
Haddock	8796.285 (±0.659)	0.021 (±0.527)	7.125E-06	2.682E+18	1.403E+05	1.916E+05
Whiting	8879.860 (±0.198)	0.002 (±1.824)	3.057E-07 (±1.856)	8897.394 (±0.208)	1.731E+06 (±1.730)	8884.988 (±0.202)
Saithe	1263.153 (±0.203)	0.054 (±0.240)	1.235E-04 (±0.216)	10258.365 (±3.065)	7626.679 (±0.092)	4556.625 (±2.869)

For cod and whiting the three curves give a similar fit over the range of observed data. For haddock, due to the lack of data at low SSB values, the Beverton-Holt and hockey-stick curves go almost directly to the maximum recruitment and a straight line is fitted to the data. This explains the coefficient of determination really close to 0. This could be

a problem at low SSB values because the recruitment could be greatly overestimated. This also motivated the use of the Ricker curve as default in this study.

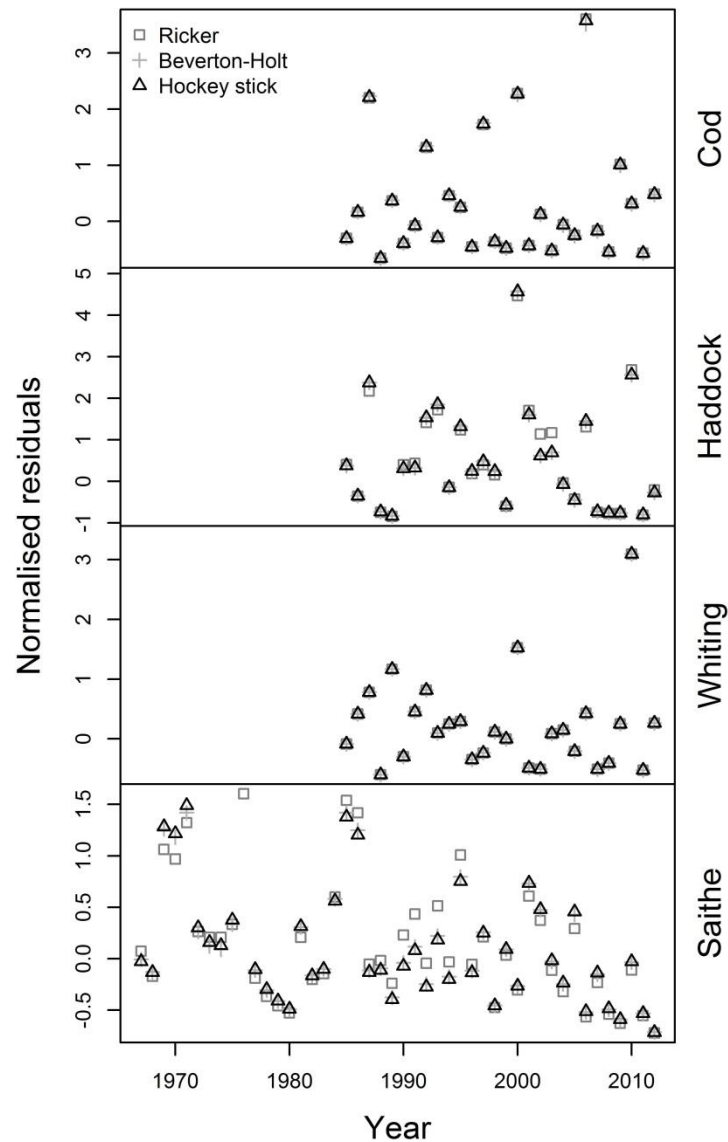


Figure 4.11: Normalised residuals from the stock-recruitment fits.

For whiting, no density-dependence is observed over the range of SSB values. This may be a problem in the simulation model because at low total mortality the stock may increase to high biomass at the equilibrium. However this is not a problem in this study because it will be seen in Chapter 5 that the average stock stays inside the range of observed SSB values.

This lack of fit highlights the uncertainty around the stock-recruitment curves which are fitted using estimated data points and subject to measurement and process errors. Adding stochasticity to the stock-recruitment curves can account for process errors. Measurement errors will be investigated in part 6.1.1 where the sensitivity around the parameters will be tested.

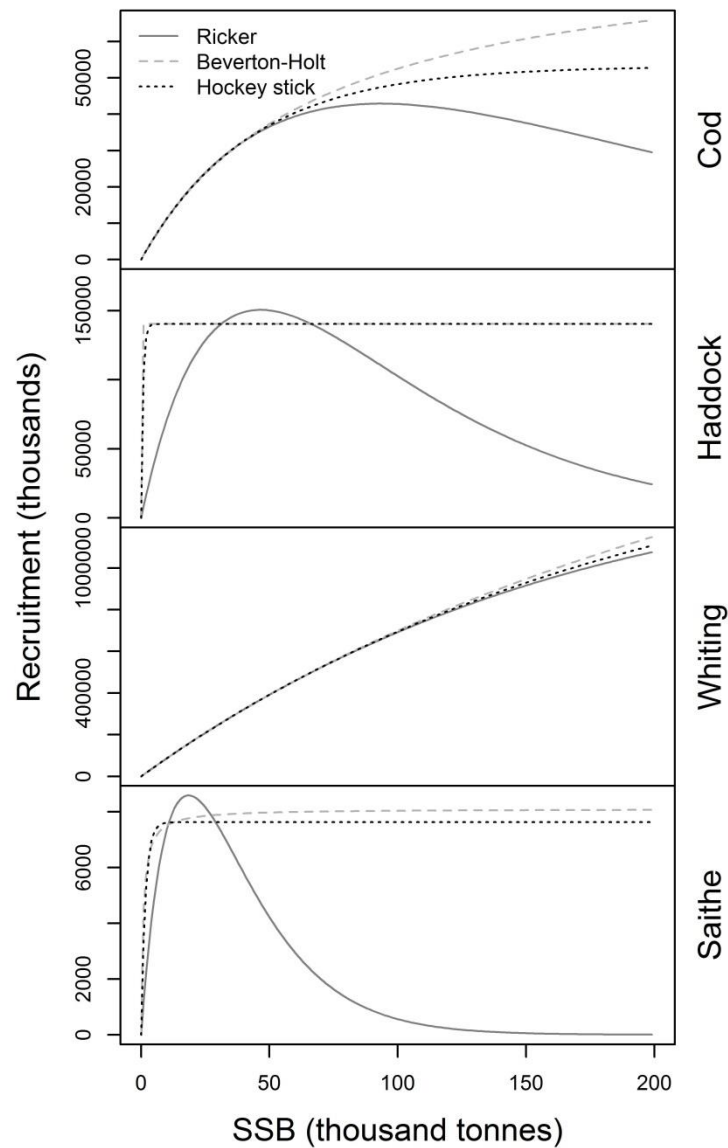


Figure 4.12: Estimated stock-recruitment relationship curves for the four species using parameter estimates from the Table 4.4.

Figure 4.11 shows the residuals from the stock-recruitment fits. The residuals are similar for the three assumptions and present no trends except a slightly decreasing one for saithe. This justified the assumption of independent random noise when adding stochasticity to the stock-recruitment within the simulation model.

The different stock-recruitment curves obtained with the estimated parameters for a large SSB range are given in Figure 4.12. It can be argued that the choice of the Ricker stock-recruitment relationship is mostly important at high SSB since it predicts overcompensation (mainly for cod, haddock and saithe). The three stock-recruitment curves give almost identical fits inside the data bounds (Figure 4.10) but the curves vary at high SSB (Figure 4.12). A problem may be encountered if the stocks go beyond the bounds of estimated SSB during the simulations. Sensitivity of the bioeconomic results to the assumption of stock-recruitment will be therefore investigated in part 6.1.

4.2.2.1.3. Mortality estimates

The average estimated mortalities at age from the state-space models are given in Figure 4.13. As regards to the natural mortality estimates, the general Lorenzen (1996) parameters (γ and δ) were used for saithe while the model estimates were used for cod, haddock and whiting (Table 4.5).

The average grey seal predation mortalities across ages are given in Table 4.6. Cod may be the fish the most impacted by seal predation because of the high seal predation mortality for this species. Grey seal predation mortality on haddock and whiting is comparable or slightly lower than the estimated fishing mortality making seal predation mortality the smallest component of the total mortality. Both mortalities are lower than the natural mortality for these species with an exceptionally high natural mortality at age 1 for whiting (above 1.2). For haddock, natural mortality from Lorenzen gives values larger than 0.3 for all age classes. Clearly the conventional V_{la} value of 0.2 assumed by ICES appears too low compared to our results and this may affect the perception of the stock. The recent amalgamation of the West of Scotland and the North Sea stock assessments by ICES should overcome this problem (ICES, 2015c).

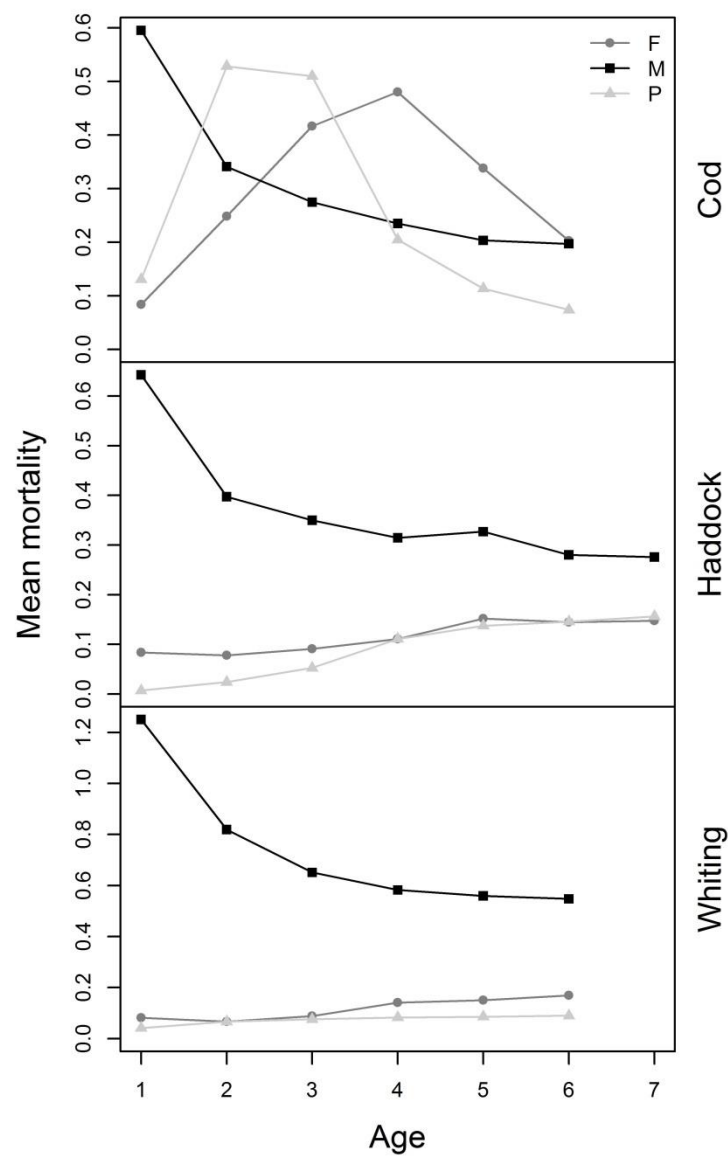


Figure 4.13: Average (1985, 2002) estimated fishing mortality, natural mortality and mortality at age due to seals for cod, haddock and whiting used to parameterise the simulation model.

The estimates of fishing mortality are the average fishing mortalities at age between 2007 and 2011, from the state-space model outputs for cod, haddock and whiting and from ICES (2013d) for saithe. Overall, for the three species, the estimated fishing mortality at age is much lower than the one estimated by ICES (2013b). This is especially noticeable for cod which shows a mean fishing mortality of 0.34 with this model compared to an estimated fishing mortality of 0.97 in ICES (2013b) for the same time period. If the estimates obtained with this Bayesian analysis are correct, this

means the estimated fishing mortality in current ICES assessments is overestimated due to an underestimation of the natural mortality and this could have a significant impact on the current and future fisheries management. This is investigated further in Appendix H.

Table 4.5: Parameter values used to estimate the natural mortality in the simulation model. For saithe the values are taken from Lorenzen (1996). The values in the parenthesis are the 95% confidence intervals estimated in the Bayesian analysis for cod, haddock and whiting and the 90% confidence interval given by Lorenzen (1996) for saithe.

Species	γ	δ
Cod	3.319 (2.449, 4.272)	-0.3214 (-0.3678, -0.2773)
Haddock	2.981 (2.315, 3.568)	-0.36 (-0.4008, -0.3202)
Whiting	3.852 (2.972, 4.606)	-0.305 (-0.3477, -0.2704)
Saithe	3 (2.70, 3.30)	-0.29 (-0.315, -0.261)

Table 4.6: Average seal predation mortality (for 1985 and 2002) used in the simulation model. The averages are taken over the age ranges for fishing mortality in ICES (2013b).

Species	Average seal predation mortality
Cod	0.37
Haddock	0.12
Whiting	0.10

4.2.2.1.4. Partition of the fishing mortality by fleet and estimation of fleet selectivity

The West of Scotland fishery is a mixed demersal fishery composed of vessels targeting whitefish and vessels targeting *Nephrops* and catching whitefish as bycatch (cf. Chapter 3). The main focus of this study is on the UK trawlers targeting cod, haddock and whiting since grey seal predation is only considered on these species. However, it is necessary to take into account the entire fishery configuration to be able to compare

revenues and costs for the whole fishery. Consequently, the simulation model considers all types of vessel catching the three species of interest in VIa.

Following the availability of fishing and economic data, the biological part of the model is disaggregated into five fleets which are believed to correspond to the entire demersal fishery in the West of Scotland. The fleets are partitioned first by mesh size and then by vessel length (Table 4.7). This partition has been chosen because it is the partition used by ICES (ICES, 2014c). Since most of the landings by vessels smaller than 10 m are caught by *Nephrops* trawlers, it is assumed that the small vessel fleet is only composed by TR2 vessels. Because no economic data is available for TR2 trawlers larger than 24 m and their proportion of landings in total TR2 landings is small, it is assumed that the maximum length for the *Nephrops* vessels is 24 m. Landings of TR1>40 m vessels are small so they are aggregated into the TR1>24 fleet. The “Others” fleet corresponds to the other gears used in VIa and the foreign vessels.

Table 4.7: Fleets considered in the simulation model and their particularities.

Fleet code	Definition	Vessel length	Net mesh size	Target species
TR1_10-24	UK whitefish trawlers	10-24 m	≥120 mm	Whitefish
TR1>24		≥24 m		
TR2<10	UK <i>Nephrops</i> trawlers	<10 m	70-99 mm	<i>Nephrops</i>
TR2_10-24		10-24 m		
Others	Other gear types and foreign vessels	Any	Any	Whitefish and <i>Nephrops</i>

To partition the fishing mortality by fleet, catch at age data from Marine Scotland for cod, haddock and whiting were used in conjunction with catch at age data from the ICES reports (ICES, 2013b). Marine Scotland data were available for the years 2012-2014 (Table C.4), however, from 2014 onward, ICES merged the haddock stock in VIa with the North Sea as a single northern stock and no VIa assessment is available after 2013 for this species. Consequently, for spatial consistency with seal diet data, earlier 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.

Because no catch at age data exist for the foreign vessels, it is necessary to estimate it. To do so, the number of fish caught at age (C_a) by the fleet called “Others” was estimated following Equation (4.26).

$$C_{a,j,others} = C_{a,j,ICES} - (C_{a,j,TR1} + C_{a,j,TR2}) \quad (4.26)$$

The “Others” fleet representing the foreign vessels and the other gears than the whitefish (TR1) and *Nephrops* (TR2) trawls, its catch at age can be estimated by deducting the catches at age from the UK fleets (TR1+TR2) from the total catch at age recorded by ICES ($C_{a,j,ICES}$). For saithe the catch at age by mesh size is obtained by scaling the total ICES catches at age in VIa 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 is possible to estimate the proportion ($\varphi_{a,j,gr}$) that each group represents in the total catch at age for the four species.

The average (2007-2011) total fishing mortality at age ($\bar{F}_{a,j}$) obtained from the state-space model for cod, haddock and whiting and the average 2007-2011 in ICES (2013d) for saithe were used to calculate the fishing mortality at age for the three fleet groups ($F_{a,j,gr}$) by multiplying \bar{F} by the proportion of each fleet in the total catch at age.

$$F_{a,j,gr} = \varphi_{a,j,gr} \bar{F}_{a,j} \quad (4.27)$$

Finally, it is 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 the respective fleets (ψ_k) into the TR1 and TR2 total landings (Table 4.8).

Table 4.8: Estimated proportion of each fleet in the total catch of the respective mesh size group.

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

$$F_{a,j,k} = \psi_k F_{a,j,gr} \quad (4.28)$$

This partial fishing mortality was used to determine the values of the selectivity at age ($s_{a,j,k}$) used in Equation (4.12) of the simulation model. Here, it is assumed that the initial effort index for each fleet ($E_{1,k}$) is 1. Consequently, the selectivity at age for each fleet is given by the partial average fishing mortality at age ($F_{a,j,k}$) and is kept constant within the model.

4.2.2.1.5. Partition between landings and discards

Within the age-structured biological model, the catches at age in numbers for cod, haddock, whiting and saithe estimated with the Baranov Equation (4.14) are then partitioned into landings and discards at age.

To partition the catches, the catch at age data (2012-2014) made available by Marine Scotland was used to estimate a proportion of fish retained in the total catch. The data give the partition only by mesh size not by vessel length, so it is assumed that the proportion of fish retained only depends on the mesh size. Also, no data exists for the foreign vessels but because most of the foreign vessels are whitefish trawlers (only 1% of total catch of *Nephrops* in VIa comes from foreign vessels (ICES, 2015a)), it is assumed that the proportion of fish retained at age for the “Others” fleet is the same than the TR1 fleets.

Some age classes are not represented in the data making it difficult to know if it is because these classes are not landed or discarded or if it is due to errors in the sample process. As a result, a regression model has been fitted to the three years data to estimate the missing data. Within the simulation model, the mean proportion of fish retained in 2012-2014 is used to partition catches into landings following Equation (4.15) and is assumed to correspond closely to the actual proportion observed in 2007-2011. Following ICES (2013d), the simulation model assumes there is no discard of saithe.

For the other species, only the landings are modelled because the discards rates are low (Heath and Cook, 2015). The landings are partitioned by fleet following landing data (ICES, 2011; 2015a). The partition is given in Appendix G.

4.2.2.1.6. The Schaefer estimates for the other species

The fit of the Schaefer surplus production function to the empirical data on biomass and landings (part 4.2.1.2) provided the estimates of msy and K given in Table 4.9.

Table 4.9: Estimated Schaefer surplus production function parameters. The values in the parenthesis are the standard errors.

	Anglerfish	Megrim	Hake	Nephrops
<i>msy</i>	2,677.918 (±0.287)	1,464.048 (±0.017)	16,909.580 (±0.208)	21,383.440 (±0.072)
<i>K</i>	18,250.775 (±2.114)	21,345.112 (±0.289)	32,997.690 (±0.446)	13,2275.990 (±0.307)

These parameters with the initial biomass and fishing mortality enable the estimation of fleet landings for these species within the simulation model following Equations (4.17) and (4.18).

4.2.2.1.7. The landing index for ling

It has been seen in part 4.1.1.2, that the landings for ling are directly estimated using an initial landing index. To create this index, average landings in VIa were taken between 2007 and 2011 and then partitioned by fleet. This partition is assumed to be the one at the current level of effort and landings change linearly with the change in effort index. The details about the partition of the landings into fleets can be found in Appendix G.

4.2.2.2. Economic parameters

Some preliminary estimation is also necessary to parameterise the economic part of the simulation model. Costs data from 2007 to 2012 for the four UK fleets was made available by Seafish. Table C.5 summarises the empirical data used.

4.2.2.2.1. Fish prices

As mentioned earlier, the whitefish price in the West of Scotland is dictated by the European market and most notably by the Norwegian and Icelandic imports (Scottish Fishermen's Organisation, 2013). It means that the change in landings in the West of Scotland has little effect on fish prices. While it may not be the case for *Nephrops*, its landings were relatively constant in the last 30 years as well as its price. As a result, the fish prices are assumed to be exogenous in the simulation model. They correspond to average real prices between 2007 and 2011 taken from Marine Management Organisation (2012) and corrected for inflation using the GDP deflator with 2012 as the reference year.

4.2.2.2.2. Costs parameters

The parameters used within the economic part of the simulation model which are necessary to estimate fleet costs are the number of vessels per fleet and the variable and fixed costs per vessel (Equation (4.21)). All economic data is corrected for inflation taking 2012 as the reference year. The estimation of the costs differs between the British fleets and the "Others" fleet because the latter corresponds mainly to foreign vessels for which economic data is not available.

For the four UK fleets, the economic data from 2007 to 2011 made available by Seafish (part 3.3.2) enabled the estimation of variable and fixed costs. Averages are taken between these years. The average costs per UK vessel (2007-2011) are given in Table 4.10. Since E_k is initially set to 1 (part 4.2.2.1.3) in the model, the proportionality constant ρ_k in Equation (4.20) equals cv_k .

Table 4.10: Average fixed and variable costs (£) per vessel between 2007 and 2011.

Type of costs	TR1_10-24	TR1>24	TR2<10	TR2_10-24
Variable costs	430,480	1,250,760	47,633	137,717
Fixed costs	212,965	467,311	27,007	73,016

The number of vessels (v) used within the simulation model is the average number of vessels between 2007 and 2011 for each fleet (Table 3.4) assuming that all the vessels less than 10 m are TR2 vessels (TR2<10).

Preliminary runs of the simulation model highlighted the fact that most of the fleets presented initial revenues and costs close to the break-even point. This was expected since the West of Scotland fishery was previously an open-access fishery and the Seafish data show relatively small net profits for the four fleets (cf. Figure 3.6). However, the simulation runs show that the fleet TR2_10-24 presents revenues much larger than the costs. The revenues calculated from Marine Scotland landings data for this fleet were compared with the fishing income recorded by Seafish. They appeared to be different with larger revenues for Marine Scotland than for Seafish. This could be due to different reasons such as a lack of update for one of the database or a different partition for this fleet (S. Lawrence, Seafish, pers. comm.). Since Marine Scotland data was used to partition species landings into fleets, the costs observed by Seafish for TR2_10-24 have been scaled up to correspond to what was recorded by Marine Scotland. This decreases the difference between revenues and costs at the current level of fishing mortality and seems more realistic.

For the “Others” fleet it is more challenging because no empirical data is available. Some assumptions are therefore needed to consider a cost function for this fleet. The mean number of foreign trawlers (2007-2011) catching cod, haddock and whiting is 19

(Seafish). Because no cost data is available, it seems that the safest assumption is to consider that the “Others” fleet starts the simulations at the break-even point where total revenues equal total costs preliminary estimated from simulation runs (Table 4.11).

Table 4.11: Estimated variable and fixed costs (£) per vessel for the “Others” fleet.

Variable costs	Fixed costs
1,236,293	618,146

It has been noticed that the UK fleets have fixed costs per vessel which present a value which is around the half of the variable costs. Consequently, a ratio of 2 is assumed between variable and fixed costs for this fleet and the total aggregated costs scaled to the number of vessels (19) are partitioned using this ratio. It will be seen in a later chapter that the cost function for this fleet matters only when dynamic scenarios are considered.

4.2.2.2.3. Precision on revenues

It has been previously seen that the nine species considered in the simulation model represent the largest part of the current demersal trawlers fishing revenues (95.4%) in the West of Scotland (part 3.3.3). The 4.6% left are ignored in the model because the contribution to revenues is very small and not enough data is available to partition the remaining revenues into the different fleets.

4.3. Consistency check of the simulation model

This part demonstrates the consistency of the simulation results with the literature and validates the number of stochastic iterations.

4.3.1. Comparison of the outputs with the literature

An easy way to check the consistency of the results of the simulation model is to compare the results obtained with observed data. This data was used to parameterise the model so if the model is correct the results should be closed to the observed data.

Simulations were run with the initial stock numbers at age taken from ICES (2013b; 2013d), the current number of seals in the West of Scotland and the current fishing mortality taken from the Bayesian parameter estimation for the years 2007-2011. This enables checking that the landings are correctly estimated in the simulation model. However the fishing mortality from the state-space model differs from ICES reports due to the partitioning of the total mortality into three types of mortality (natural, fishing and grey seal predation) so the results are expected to be slightly different. The important point is that the order of magnitude of the results is close to ICES (2013b; 2013d). Also the proportion between landings and discards should be respected as well as the partition of the landings per fleet. Finally for the other species the estimated UK and non-UK landings in VIa should be similar to the observed landings since observed data was used to partition fishing mortality into fleets for these species.

The outputs of the simulation model are compared in the first year of simulation, which should be the closest to the data observed in ICES reports, but also at the steady state or biological equilibrium to see how the catch varies in the long-run keeping everything constant.

For cod, haddock, whiting and saithe, the estimates of landings and discards can be compared to the observed data in recent ICES reports (ICES, 2013b; d). Overall, the results obtained with the simulation model are of the same order of magnitude than the observed data (Figure 4.14). The ICES figures correspond to averages over 2007-2011 for the four species. The estimated landings and discards in the first year of simulation are closer to the ICES results than at the equilibrium. This makes sense since the equilibrium is the long-run solution. Haddock is the species for which the estimated catch in the first year is the furthest to the ICES estimates. Even if not perfect, the proportion of landings in the total catch seems respected in the simulation model.

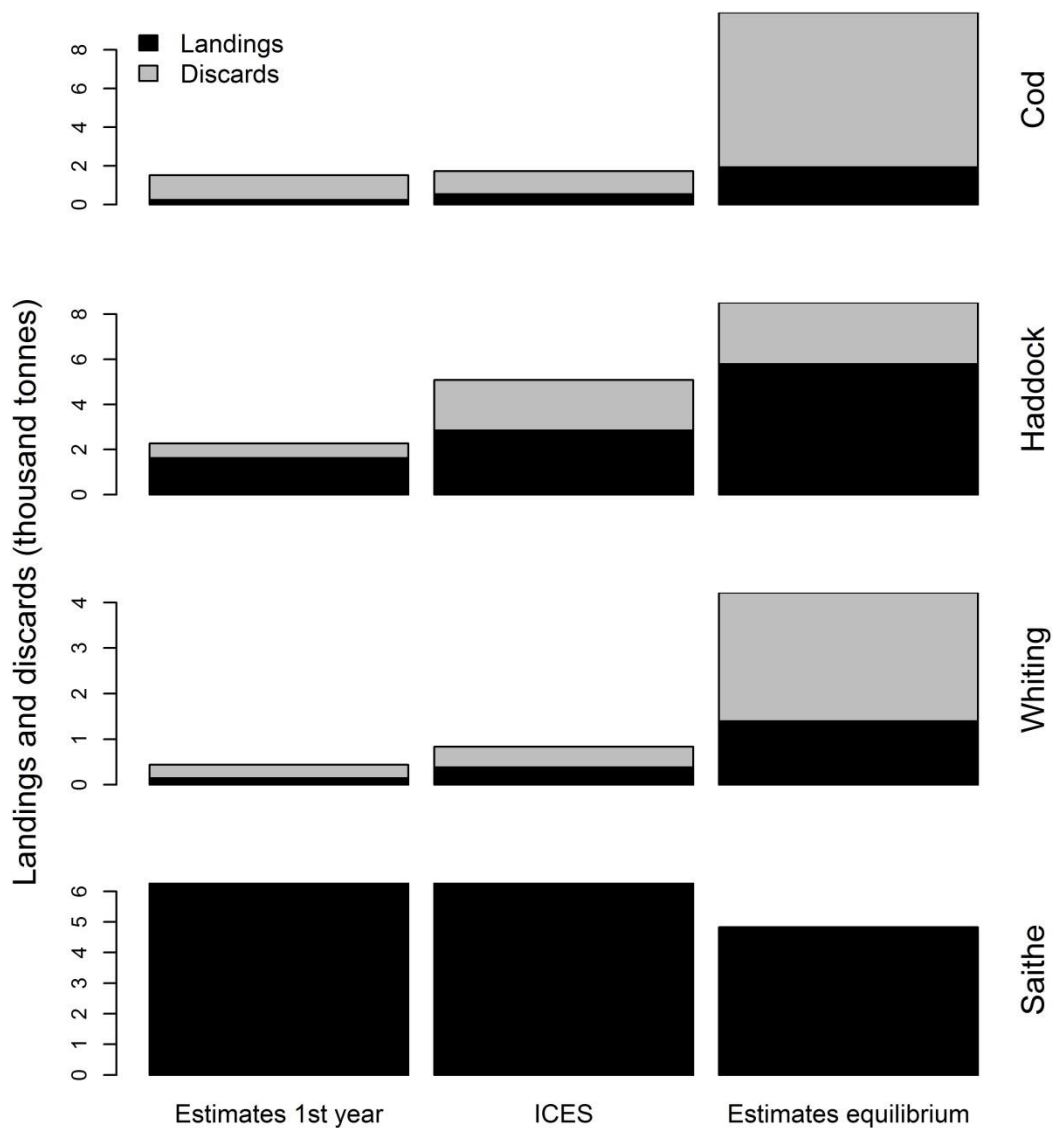


Figure 4.14: Comparison of the landings and discards (thousand tonnes) estimated with the model in the 1st year and at the steady state with the observed values from the literature (ICES, 2013b; d).

Figure 4.15 shows the comparison of the landings of other species obtained from the simulation model with the quantities observed in the literature (ICES, 2011; 2013b; 2014d; 2015a). For these species discards are not considered within the model. The results are very close to the observed landings with good estimation in the first year for the five species. The landings vary only slightly at the equilibrium. The proportion of the UK landings in the total landings in VIa is well estimated. It should be noted that the landings of *Nephrops* by the UK creelers have been attributed to the “Others” fleet since

they do not represent landings from trawlers. The observed landings from ICES have been allocated the same way for comparison purposes. The availability in observed data on landings per fleet (Marine Scotland) enables the analysis of the estimated landings by fleet. However, not all the species are recorded and therefore these are aggregated under the term “Others”. These correspond to hake, megrim, ling and anglerfish in the simulation model and to all other species in the observed data.

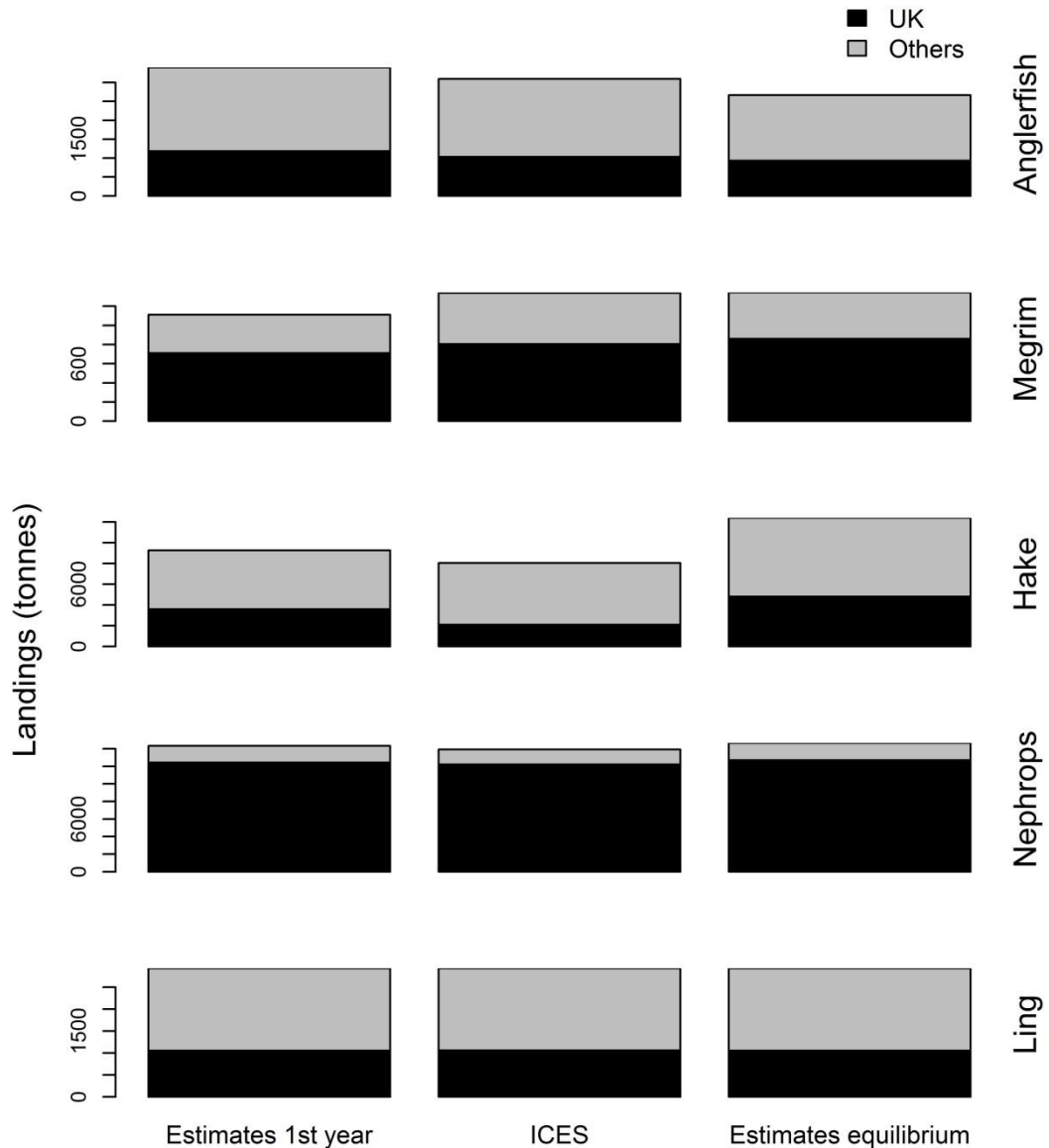


Figure 4.15: Comparison of the landings (tonnes) estimated with the simulation model in the first year and at the steady state with the observed values from the literature (ICES, 2011; 2013b; 2014d; 2015a).

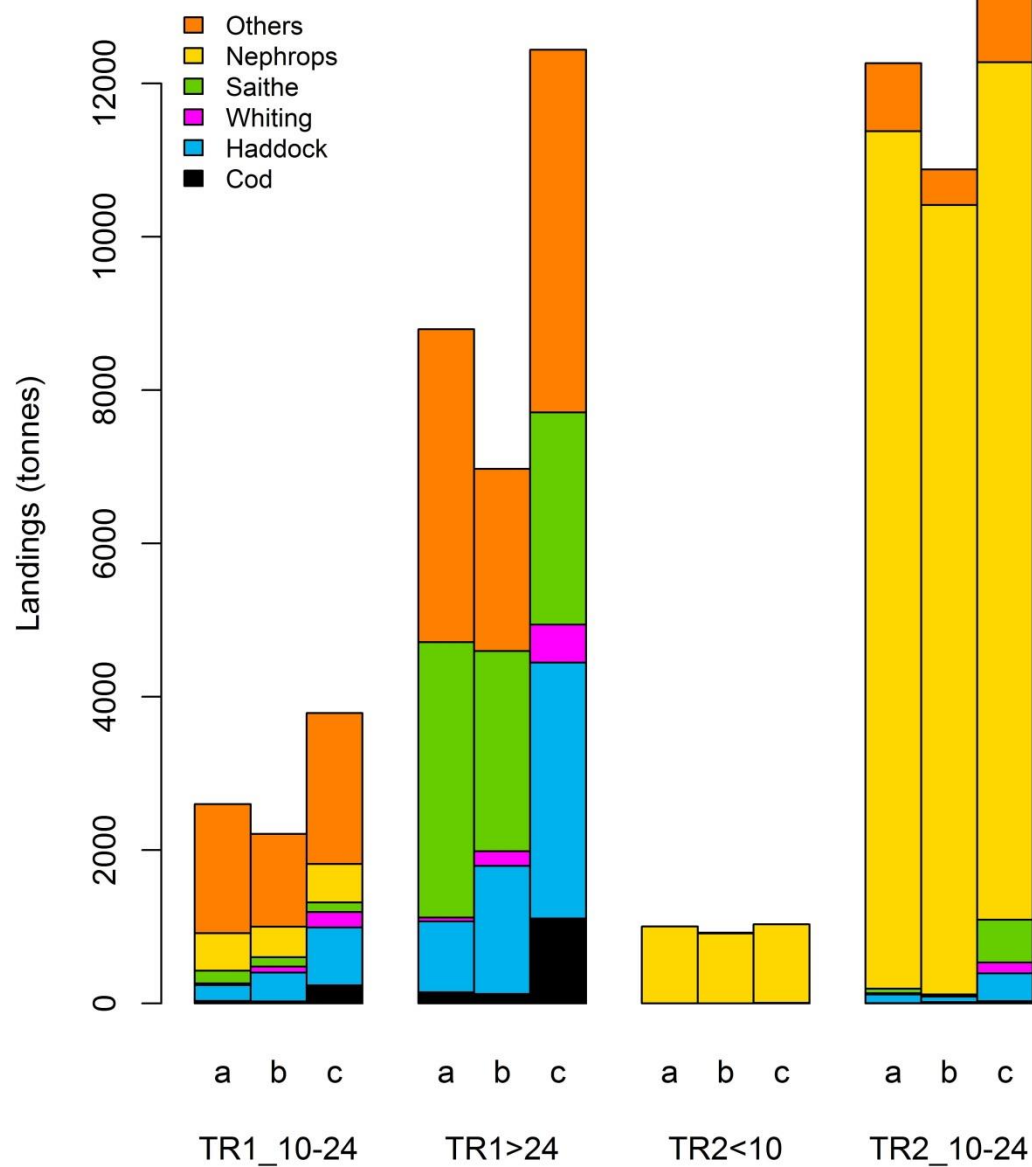


Figure 4.16: Landings (tonnes) per fleet and species in the first year of simulation (a), as observed by Marine Scotland (b) and at the steady state (c).

Figure 4.16 gives the landings for the UK fleets in the first year of simulation, at the steady state and as recorded by Marine Scotland. It can be seen that the estimates are not far from the observed ones, notably in the first year of simulation. The landings from other species seem to be slightly overestimated for the whitefish trawlers (TR1) and the TR2_10-24 fleet. An underestimation was expected since the term “Others” corresponds to more species in Marine Scotland data. The overestimation is however more surprising. Nevertheless, since the others species are not of large economic value,

this should not significantly impact the revenues. This is confirmed by the fleet revenues (Table 4.12) which differ from the observed revenues by a maximum factor of 1.16 in the first year of simulation.

Table 4.12: Revenues per fleet (£) estimated by the model in the first year and at the steady state, compared to the revenues recorded by Seafish or Marine Scotland (for TR2_10-24 only). The ratios highlight the difference between the estimated results and the observed revenues.

	TR1_10-24	TR1>24	TR2<10	TR2_10-24
a. First year	6,038,268	12,970,986	2,902,778	33,379,292
b. Seafish/Marine Scotland	5,396,528	15,967,732	2,503,728	31,333,552
c. At steady state	7,892,340	18,821,100	2,974,274	34,883,597
Ratio a/b	1.12	0.81	1.16	1.07
Ratio c/b	1.46	1.18	1.19	1.11

In conclusion, the figures obtained from the initial run appear sufficiently close to support the simulation model.

4.3.2. Validation of the stochastic outputs

In order to obtain reliable results for the variables of interest it is necessary to check if the number of iterations (stochasticity around the stock-recruitment curve) of the simulation model is sufficient. In this part, the interest is given to the fleet revenues since grey seal impacts on the fishery can be estimated as the change in fleet revenues for a change in grey seal predation.

Two simulations were run for 1,000 and 2,000 iterations. The distribution of the values that the equilibrium revenues per fleet can take over the number of iterations was examined (Figure 4.17). It is clear that the distributions of the revenues per fleet are similar no matter the number of iterations. Most importantly, a non-parametric Mann-Whitney U test was performed on both revenue distributions (1,000 and 2,000

iterations) and the average fleet revenues are significantly not different. This means that 1,000 iterations are enough to obtain consistent average revenues.

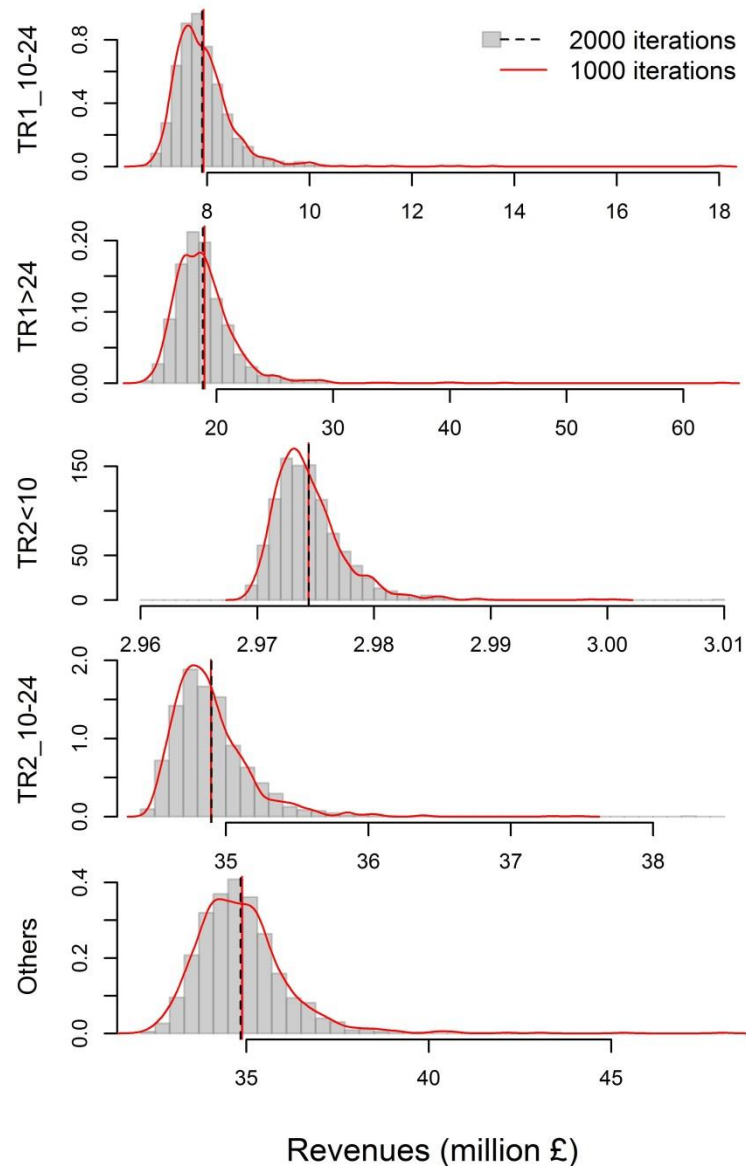


Figure 4.17: Histogram of the fleet revenues at the steady state for 2,000 iterations and density curve for 1,000 iterations. The y-axis represents probability densities so that the histogram has an area of 1. The vertical lines represent the average fleet revenues for simulation with 2,000 iterations (black dashed line) and 1,000 iterations (red solid line). It is clear that for both number of iterations, the distributions of revenues and the average fleet revenues are similar.

4.4. Summary

The simulation model was presented in part 4.1, parameterised in part 4.2 and its consistency was checked in part 4.3. It enables the estimation of fleet revenues and costs giving initial value of fish abundance, fishing mortality and seal predation and it can be run for a certain number of years or to equilibrium. Some examination can be done by varying initial parameters by small amounts, such as seal numbers, with the aim to investigate the impacts of grey seal predation on the VIa demersal fishery for cod, haddock and whiting. Since no trophic interaction exists between the fish species, the simulations indicate the direction seal impacts would take if the current conditions remain but are not quantitatively predictive. The following chapter presents the different bioeconomic scenarios considered in this study and their results.

Chapter 5

Scenario analyses

This chapter presents the three equilibrium scenarios considered for the simulation model and their assumptions in part 5.1. The scenarios of change in seal predation are also described (part 5.1.3). The part 5.2 presents the results of the simulation model. First, the results at status quo seal predation are presented to see how the simulation model progresses to the different equilibria (part 5.2.1). Then, the biological impacts of grey seal predation are studied, i.e. the impacts on the stock sizes (part 5.2.2). The impacts of grey seals on fishing revenues are presented in part 5.2.3. Because one equilibrium scenario assumes the maximisation of the fishery net profit, the sustainability of the current VIa demersal fishery is discussed compared to this scenario in part 5.2.4. Finally the final part (5.2.5) highlights the importance of cod in grey seal impacts.

5.1. Scenarios

The simulation model is run in three different scenarios which represent three different fisheries and equilibrium assumptions (Table 5.1). All the scenarios share the common characteristic to be at the biological equilibrium or steady state but two scenarios consider also an economic equilibrium. The steady state is reached for a constant fishing mortality when the change in SSB (in thousand tonnes) from a year to another does not exceed 0.01% (i.e. for 1 t of fish this corresponds to a change of 100 kg or less). The nine species should be at the equilibrium to consider the model at the steady state. The economic equilibria are reached dynamically by allowing the fishing

mortality to change according to the net profits after the steady state is reached, or maximising the steady state fishery net profit.

The “status quo F” model studies the impacts of grey seal predation on fishing revenues and profitability at the steady state keeping the initial average fishing mortality 2007-2011 constant. It represents therefore a biological equilibrium and the equilibrium ignores the economic aspect of the fleets. This model can serve as baseline for comparison with the other scenarios where the fishery economics is considered. This model indicates the direction grey seal impacts would take if fishing mortality and behaviour does not change in the West of Scotland.

Table 5.1: The different scenarios considered in the study.

Scenario	Fishery	Equilibrium	Details
Status quo F	Current 2007-2011 state	Biological equilibrium	Long-run equilibrium scenario where the current fishing mortality is kept constant
BE	Open-access	Bioeconomic equilibrium (BE)	Steady state + economic equilibrium assuming the net profits are dissipated in the long-run
MEY	Closed to vessel entry and exit	Maximum Economic Yield (MEY)	Steady state + economic equilibrium assuming the total fishery net profit is maximised in the long-run

The Bioeconomic Equilibrium (BE) model assesses the impacts of grey 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, when the fishery is open-access, fishers act independently and try to maximise their individual profit so that entry and exit will continue until the net profit is competed away. Consequently, in the long-term the fishery tends to the bioeconomic equilibrium where total revenues equal total costs (Knowler, 2002). Since the fishery is unregulated, it is assumed that, the fishery reaches the BE when each fleet sees its net profit dissipated.

Open-access fisheries can be therefore economically unsustainable since vessels exiting the fleet because they are non-profitable are balanced by those entering the fleet to

seek to make a profit. This is an example of “the tragedy of the commons” (Hardin, 1968; Ostrom, 2008) where people seek private profit without considering the consequences on others. This often leads to overcapacity and overfishing (Clark, 2006). This can be detrimental to the fish stocks and fishing revenues in the long-run (Mackinson et al., 1997; Puga et al., 2005; Armstrong and Skonhøft, 2006). Open-access fisheries generally result in lower stock size and catches at the equilibrium than managed fisheries such as private property or regulated open-access fisheries due to the high level of fishing mortality and negative impacts on the stock growth (Laukkanen, 2001; Armstrong, 2007).

The BE is often used as baseline for the comparison of the impacts of management policies (McConnell and Strand, 1989; Mackinson et al., 1997; Hannesson, 1998; Pezzey et al., 2000). It is also often used to determine the maximal level of effort the fishery should operate at since efforts larger than the bioeconomic equilibrium effort lead to negative net profits (Clark, 2006). The fact that the current fleets in the West of Scotland present small net profits (Seafish) motivates the choice of considering this scenario in this study despite the fact that the fishery is currently closed to new vessels.

The Maximum Economic Yield (MEY) scenario represents the economic equilibrium assuming the fishery is closed to vessel entry and exit and the total net profit is maximised in the long-run. Many management studies suggest MEY as a target equilibrium for a sustainable system. Only few of them consider multifleet models (Brasao et al., 2000; Hutniczak, 2012; Guillen et al., 2013). In this case, the fleets are assumed to collaborate to obtain a sustainable fishery where the aggregated fishery net profit is maximised at the equilibrium (Armstrong, 2007; Guillen et al., 2013). The goal is to determine the optimal level of effort per fleet which maximises the fishery net profit. Contrarily to biological equilibria such as the steady state and the maximum sustainable yield, the MEY considers the economic component of the fishery. It can sometimes induce overcapacity (Clark, 2006) but closing the fishery to new vessels prevents this problem. This scenario is less practical because it assumes that the fleets collaborate to maximise the total fishing net profit which may be difficult to implement in reality as it necessitates the managers to tell the fishers how to fish and the fishers to accept the propositions. It is however interesting to consider this scenario as opposed

to the extreme unregulated open-access equilibrium and to see how grey seal impacts may differ depending on the fisheries regulations.

These three scenarios can be compared and used to investigate the sensitivity around grey seal impacts on fishing revenues.

5.1.1. Modelling assumptions for the dynamic scenarios

The BE and MEY scenarios permit to account for fleet behaviour (change in fishing mortality with the net profit) and to see if considering fleet behaviour affects the impact of grey seal predation on the fishery.

Because the cost function for the “Others” fleet is uncertain due to the lack of economic data for this fleet, it has been chosen to consider this fleet as an externality when working with the two dynamic scenarios. This means the effort index for this fleet is kept constant in the BE and MEY models and this fleet does not modify its fishing behaviour with its net profit.

As with the “status quo F” scenario, the dynamic models are run to the steady state. At the steady state, the fleet net profits are estimated and it is assumed that the fleets will change their effort according to the value of their net profit until they reach the specific economic equilibrium. The net profit by fleet (π_k) is defined as follows:

$$\pi_k = R_k - ct_k \tag{5.1}$$

Where R_k are the fleet revenues and ct_k the fleet total costs.

In the BE scenario, each UK fleet can invest or disinvest in effort or vessel capacity following the value of its net profit. If the net profit is positive the fleets are assumed to increase their effort and the model is re-run for a larger effort index; inversely if the net profit is negative. Here, it is assumed that the fleet investment or disinvestment impacts the fleet total costs. The difference with the simulation model is that the costs by fleet are not partitioned into variable and fixed costs but are aggregated such as:

$$ct_k = E_k c_k \quad (5.2)$$

The term c_k is the initial costs per fleet when $E_k = 1$. The vessels within a fleet are assumed identical and the marginal cost constant so a change in fishing mortality induces a linear change in costs and can be interpreted as a change in effort and/or vessel capacity. For instance, a decrease in fishing mortality of 10% induces a reduction in total costs of 10% (both the variable and the fixed costs change). This assumption may seem simplistic but it seems difficult in the model to choose how the fishers will react to a change in net profit. Indeed they could change their effort and this will only affect the variable costs and/or they can change their number of boats and this will impact also the fixed costs. This assumption on costs in the BE scenario seems therefore reasonable in this study. Except for this difference in fleet costs, the BE model shares the same properties and assumptions than the simulation model.

The model is considered to be at the BE when the difference between revenues and costs is less than 1%. This limit was chosen because it seems small enough to represent a difference between revenues and costs. Some investigative work shows similar equilibrium results for smaller differences. The entire fishery is assumed to be at the BE when all the fleets are at the BE.

In the MEY scenario the fleet effort indices are estimated such as the total fishery net profit is maximised at the steady state. This scenario shares the same cost assumptions than the simulation model (Equations (4.20) and (4.21)). The fishery is closed to new vessel entry and exit so fishers can only modify their effort and cannot invest in vessel capacity so the number of vessels remains constant. As a result, a change in effort only impacts the variable costs and the fixed costs stay constant. The fishery reaches the MEY when the total fishery net profit (π) is maximised as follows:

$$\pi = \max \left(\sum_k \pi_k \right) \quad (5.3)$$

The model is therefore solved for an optimal level of effort per fleet, $E_{MEY,k}$, which satisfies this economically optimal fishery at the steady state.

5.1.2. Methods to get to the economic equilibria and validation

5.1.2.1. Getting to the BE

In the BE scenario, after calculation of the fleet net profit, fishing effort is adjusted until the BE is reached. It is assumed that higher net profit will lead to larger investment in fleet capacity and effort. Therefore, the change in effort index for each iteration follows a sigmoid curve which is bounded by a maximum (Δ_{max}) and minimum (Δ_{min}) change in effort (Figure 5.1).

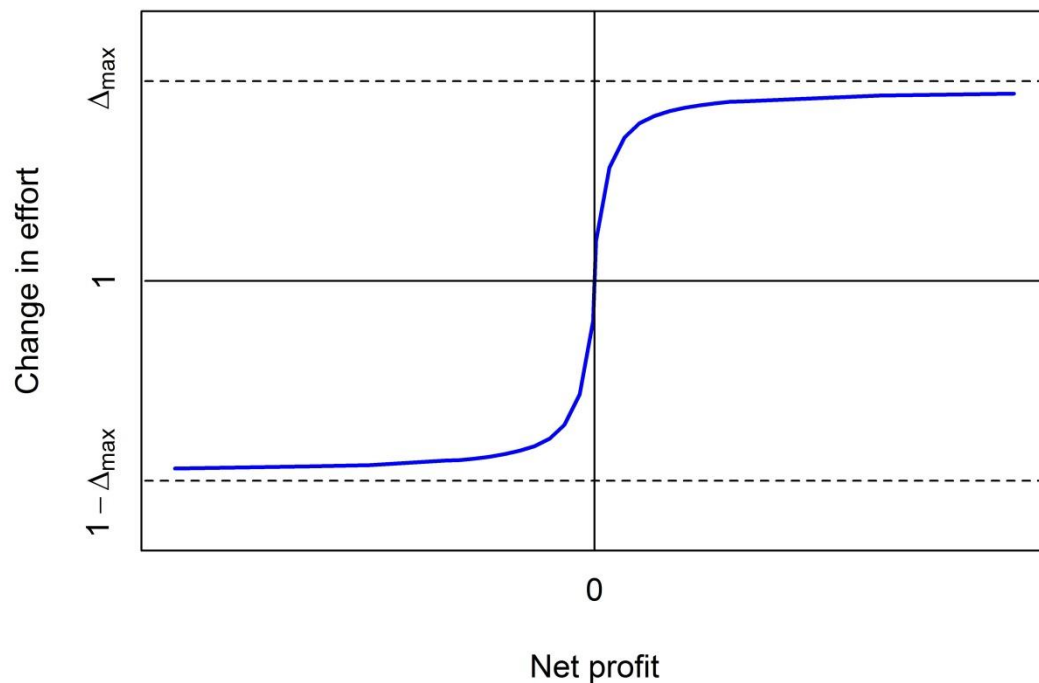


Figure 5.1: Representation of the sigmoid curve defining the change in effort index at each iteration with the change in net profit.

The effort index per fleet is scaled by a factor Δ_k at each iteration (it) following Equation (5.4).

$$\Delta_{k,it+1} = \frac{\Delta_{max}\pi_{k,it}}{\tau C_{*,k,it} + |\pi_{k,it}|} + 1 \quad (5.4)$$

The parameter τ is the steepness of the curve. When there is no change in effort, Δ is equal to 1. If the net profit is negative, Δ is less than 1 and the effort at the next iteration will be reduced, inversely if the net profit is positive.

The BE is reached for a fleet when its net profit is dissipated at the steady state or when the fleet exits the fishery. To enable the model to stop when a fleet exits the fishery and to reduce the number of iterations, it has been assumed that if the revenues are lower than the average aggregated total costs per vessel the fleet will disappear since the revenues cannot cover the function of the last vessel left.

In this study, it is assumed that $\Delta_{max} = 1.5$ and $\tau = 0.2$. This means that, at each iteration, the effort index per fleet can only change by $\pm 50\%$. The choice of these parameters comes from preliminary investigations. For these, different assumptions on change in the effort index with the net profit have been considered. As well as the sigmoid function described in Equation (5.4), two methods of change in effort with the ratio of revenues against costs per fleet were tested. First, the effort is changed by the ratio between revenues and costs in the current iteration as follows:

$$E_{k,it+1} = E_{k,it} \frac{R_{k,it}}{ct_{k,it}} \quad (5.5)$$

Consequently, if the revenues are larger than the costs, the effort index increases and vice-versa. Since this method can induce big jumps in effort, another method considering the square root of the same ratio is also tested to reduce the step of change in effort.

$$E_{k,it+1} = E_{k,it} \sqrt{\frac{R_{k,it}}{ct_{k,it}}} \quad (5.6)$$

These two methods are compared with the method assuming a sigmoid curve for different arbitrary values of Δ_{max} and τ .

Table 5.2: Details of the different simulations tested to evaluate the method to get to the BE. These represent seven cases using a sigmoid change in the effort index (A to G), one case where the effort changes with the ratio of revenues against costs (H) and one case where the effort index changes with the square root of this ratio (I).

Cases	Equation	Details
A		$\Delta_{max} = 1.5$ and $\tau = 0.2$: at each iteration each fleet can only invest or disinvest 50% of its previous effort/capacity (configuration used in the thesis)
B		$\Delta_{max} = 1.5$ and $\tau = 0.3$: the steepness of the sigmoid is reduced compared to A
C	$E_{k,it+1} = E_{k,it} \Delta_{k,it+1}$	$\Delta_{max} = 1.5$ and $\tau = 0.4$: the steepness of the sigmoid is reduced compared to B
D	Where: $\Delta_{k,it+1} = \frac{\Delta_{max} \pi_{k,it}}{\tau c_{*,k,it} + \pi_{k,it} } + 1$	$\Delta_{max} = 1.5$ and $\tau = 0.5$: the steepness of the sigmoid is reduced compared to C
E		$\Delta_{max} = 1.2$ and $\tau = 0.2$: each fleet can only invest or disinvest 20% of its previous effort/capacity
F		$\Delta_{max} = 1.4$ and $\tau = 0.2$: the maximum investment or disinvestment is reduced compared to A
G		$\Delta_{max} = 1.3$ and $\tau = 0.2$: the maximum investment or disinvestment is reduced compared to F
H	$E_{k,it+1} = E_{k,it} \frac{R_{E,it}}{ct_{k,it}}$	The change in effort index follows the ratio of the revenues against the costs
I	$E_{k,it+1} = E_{k,it} \sqrt{\frac{R_{E,it}}{ct_{k,it}}}$	The change in effort index follows the square root of the ratio of the revenues against the costs

The different simulations compared are given in Table 5.2. It was noted in earlier trial runs that the number of iterations to get to the BE can differ depending on the number of seals initially considered. To identify the fastest method, two models were run: the BE simulation for the status quo grey seal predation mortality (P) (current number of seals in VIa) and the BE simulation changing grey seal predation by -10%. Taking the average number of iterations between both simulations provide a good estimate of the mean number of iterations necessary to reach the BE for a particular case scenario (A

to I). Comparing the average number of iterations for all cases enables the identification of the least time consuming method. If the model is not sensitive to the method used then the fleet effort indices at the BE for all cases should be similar.

Table 5.3: Estimated effort index per fleet at the bioeconomic equilibrium and number of iterations to get to the equilibrium for the different methods of change in the effort index (see above) for the simulations where the current seal population in VIa is considered. The number of iterations represents the average number between two simulations (scenario for the current number of seals in VIa and scenario reducing seal population by 10%).

Cases	TR1_10-24	TR1>24	TR2<10	TR2_10-24	Others	Number of iterations
A	5.654089	0.950879	15.91567	0.279272	0.421886	36
B	5.666497	0.970414	15.92275	0.278239	0.414378	46
C	5.684233	0.952359	15.85537	0.283638	0.416301	59
D	5.712435	0.949921	15.96412	0.276193	0.421167	73
E	5.650612	0.961457	15.91190	0.279877	0.421784	82.5
F	5.688022	0.961655	16.00514	0.273965	0.415187	42.5
G	5.687647	0.974262	16.11927	0.266249	0.410936	57
H	5.624107	0.946894	15.92835	0.278612	0.425844	66.5
I	5.635216	0.930864	15.83039	0.285251	0.432913	132

It is clear that, no matter the method used to get to the BE, the estimated effort indices and therefore the estimated revenues and costs for each fleet are similar for large differences in number of iterations (Table 5.3). This demonstrates the robustness of the model to the method used to get to the BE. The small differences observed come from the fact that the model is stochastic and assumed to be at the equilibrium when the difference between average revenues and costs is less than 1%. Consequently, depending on the method the model may stop at different levels of effort which satisfy that assumption.

It is also evident that the sigmoid curve using $\Delta_{max} = 1.5$ and $\tau = 0.2$ (case A) is the method demanding the least number of iterations and was chosen as the preferred method.

5.1.2.2. Getting to the MEY

In the MEY scenario, the model is solved at the steady state to obtain the optimal level of effort per fleet which maximises the total fishery net profit. It is therefore necessary to validate the optimizer used in R to maximise the sum of the fleet net profit (Equation (5.3)).

Three different global optimizers were tested deterministically to determine the best method to use in the study:

- psoptim (in pso package) which corresponds to the global optimization version of optim (local optimization) using particle swarm optimization.
- GenSA (in GenSA package) which is an optimizer able to estimate global optimum using generalised simulated annealing.
- DEoptim (in DEoptim package) which carries out global optimization using differential evolution algorithm.

The particle swarm optimizer (psoptim) was quickly eliminated because it did not reach the global maximum reliably.

The optimizations using the functions GenSA (maximal number of iterations set to 1,000) and DEoptim (default settings so the maximal number of iterations or population generations is 200) estimated the same optimal effort per fleet and net profit at the MEY (Table 5.4). DEoptim stores the different iterations so it is possible to check if the MEY is reached with the default number of iterations or if more runs are necessary. The DEoptim optimizer also enables running the simulation in parallel which explains the large difference in time between the different simulations. Also, no initial values are necessary to perform the optimization. The simulated annealing method necessitates initial values of fleet effort indices. Even if the current optimization results are not sensitive to the initial values used, not having to specify them is an advantage. For these reasons, it has been chosen to use Differential Evolution algorithm optimization to perform the maximisation in the MEY scenario. An important point about testing different optimizers is that it shows that the model is

robust to the choice of optimizer. This means that the global maximum net profit must be correctly identified when performing the optimization.

Table 5.4: Estimated effort index per fleet at the MEY for the current number of seals in the West of Scotland. The estimated total net profit (£) and time (s) for the simulation to run are also given.

Optimizer	TR1_10- 24	TR1>24	TR2<10	TR2_10- 24	Others	Net profit	Time
DEoptim	1	0.401057	1	1	0.889892	11,535,190	7,372
GenSA 1	1	0.401084	1	1	0.889876	11,535,190	40,519

The optimization is done for a specific range in effort index. It is assumed that all vessels are currently fishing at maximum effort and no new vessels can enter the fishery. Therefore the effort index can vary from 0 (fleet stops fishing) to the current level of fishing ($E_{1,k}=1$). This is also motivated by the fact that the number of days at sea are fixed for each fleet in VIa so it seems difficult for a fleet to increase its effort when the fishery is closed except if being rewarded with more days at sea following good performance (cf. part 3.2.2). It has to be noted that if the optimal level of effort for a fleet is 0, its net profit will be negative and will reduce the total sum of net profits (Cissé et al., 2013).

The optimization provides estimated equilibrium fleet effort indices $E_{MEY,k}$ and fleet revenues and costs. This allows the comparison of the fishery revenues and profitability with the values obtained with the “status quo F” and BE models. The goal is therefore to see if considering fleet behaviour via the maximisation of the fishery net profit causes a different effect of grey seal predation on fleet revenues than the effect when the net profits are dissipated.

5.1.3. Changes in seal predation

The role of the study is to evaluate the bioeconomic impacts of grey seal predation on the West of Scotland fisheries. Consequently, fleet revenues can be compared for differences in seal predation (P). To illustrate this, a scaling factor is applied to the

equation of seal predation mortality (4.10) in the three scenarios tested. This constant can take values of 0.7, 0.8, 0.9, 1, 1.1, 1.2 and 1.3. The change is limited to $\pm 30\%$ because the uncertainty around the model outputs increases with large departures from the initial parameters. The parameters have been estimated at the current situation and going too far from this state increases uncertainty in the simulations.

Since P is a product of three components and it is fair to consider seal selectivity for a certain age class constant, applying a scaling factor to P can correspond to a change in predation rate, q , but also to a change in seal population. In this study, the predation rate is assumed constant by default for all scenarios. Since seal dynamics is not modelled within the bioeconomic models, a change in P will be referred as a change in seal population and enables testing scenarios of increase or decrease in seal numbers. An increase can correspond to a population growth and a decline in grey seal numbers can be due to human interventions, disease or removal by natural predators (not likely to be high since killer whales, only natural predators of seals, are only migrating through the area).

5.1.4. Summary

Currently, the West of Scotland mixed demersal fishery is a regulated fishery with restrictions not only on fishing effort and vessel power but also on landings through quotas (Scottish Government, 2015b). Vessels can only enter the fishery if previous vessels leave. So there is also a regulation in terms of fleet capacity. Furthermore, fishing behaviour is difficult to model since it can vary for different reasons. Fishers can change their effort depending on the profit of the previous year but can also change their behaviour on a day to day basis. Therefore it has been chosen to look at simpler cases of fishery equilibrium scenarios which could already give an indication of the direction the fishery would move towards given where it is today. Trophic interactions are less critical in indicating the direction of change resulting from seal impacts on the fisheries. Consequently these models cannot be seen as directly predictive of what would happen in the next hundred years but rather as a way of comparing current seal impacts in different fishery scenarios.

The “status quo F” model is the biological equilibrium model where the economic aspect of the fleets is not taken into account. Fishing mortality is kept constant in this scenario so profit orientated behaviour is not considered. This model estimates the impact of grey seals on the West of Scotland fleet revenues when fishers fish continuously at the same rate.

The dynamic scenarios study grey seal predation impacts for two economic equilibrium scenarios where fishing mortality per fleet is allowed to vary: the bioeconomic equilibrium (BE) and the maximum economic yield (MEY). This enables the evaluation of grey seal impacts when profit orientated fleet behaviour is considered given different fisheries management assumptions. The BE model assumes the fishery is an open-access and that fleet effort and vessel numbers can vary. At the BE, the fleet net profits are dissipated. The MEY scenario assumes the fishery is closed to entry and exit and the fleets can only vary their effort. The total fishery net profit is maximised in this scenario. The BE and MEY models present therefore two economic extremes: the dissipation and the maximisation of the fishery net profit.

The goal of this study is to compare the change in fleet revenues in the three scenarios for different simulations of change in seal numbers. Considering different scenario models enables the comparison of grey seal predation impacts on the fishery for different equilibrium assumptions. This can be seen as sensitivity analysis around the results of grey seal predation impacts on the demersal fishery in VIa.

5.2. Bioeconomic results

5.2.1. Results at status quo seal predation mortality

Figure 5.2 shows the equilibrium stock biomass in the three scenarios, at the current level of seal population. The credible intervals are large for all species which highlights the great variability around the stock-recruitment estimates. This produces large credible intervals around the associated fleet revenues.

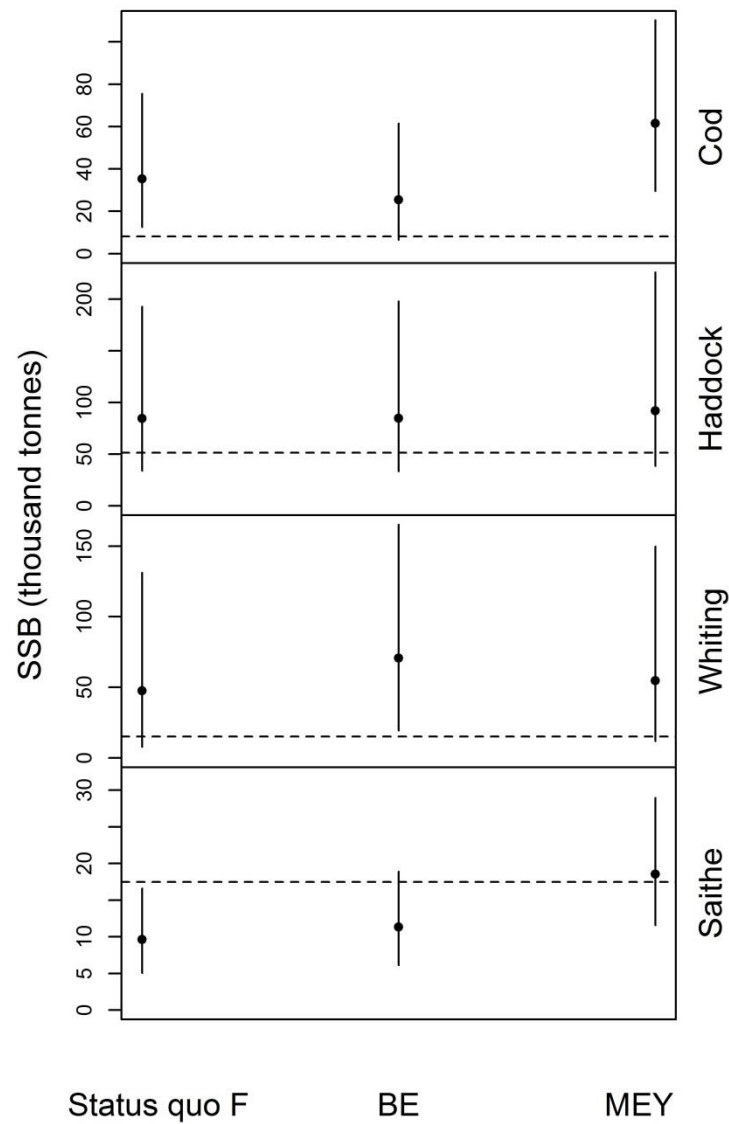


Figure 5.2: Average equilibrium spawning stock biomass (thousand tonnes) at status quo P in the three scenarios. The segment represents the 95% credible interval and the dashed line represents the estimated current SSB.

Except for the saithe stock in the “status quo F” and BE scenarios, the species show an increase in biomass at the equilibrium compared to the current state which seems to show a stock recovery in the long-run. Cod and haddock notably reach levels close to the maximum observed SSB (cf. Figure 4.3) in the “status quo F” scenario and cod goes above it in the MEY scenario.

In all the scenarios the average equilibrium biomass of haddock is similar. The BE model is the one that shows the smallest cod stock but the largest whiting biomass. The fishing mortality being largest for cod, the increase in effort or the entry of vessels to reach the BE induces a smaller cod stock at the equilibrium.

The MEY scenario presents larger stock biomasses than the “status quo F” scenario. A large increase in the cod stock is notably evident. This demonstrates the importance of cod in the maximisation of the fishing net profit.

Comparing the effort index to get to the BE and MEY with the “status quo F” effort index at the current level of seal population gives an idea of the change required by each fleet to currently satisfy the long-run equilibria. The scenario for which the effort changes the most compared to the “status quo F” effort is the BE scenario (Table 5.5).

Table 5.5: Estimated effort indices at the BE and MEY for status quo *P*. The numbers in parenthesis relate to the corresponding change in vessel numbers in the BE scenario assuming that the change in fishing mortality is entirely due to a change in vessel numbers. Since the fishery is assumed closed to entry and exit of vessels in the MEY scenario, the change corresponds only to a change in effort. For comparison, the “status quo F” the effort index for all fleet is 1.

Equilibrium	TR1_10-24	TR1>24	TR2<10	TR2_10-24	Others
BE	4.941 (+35)	0.654 (-4)	16.294 (+474)	0.187 (-123)	1 (=)
MEY	1	0.243	1	0.992	1

When the fishery is assumed to be an open-access, the small trawlers increase their effort while the large trawlers decrease their fishing mortality. The large *Nephrops* trawlers reduce their fishing mortality by more than 80%. The gain on *Nephrops* landings seems to be taken by the small TR2 trawlers instead. It seems that the large trawlers, which are most costly to operate (cf. Figure 3.5), reduce their effort or their capacity which benefits less costly small vessels. The overall fishery gains in small trawlers effort and vessel capacity and loses larger vessels. If considering that the change in fishing mortality is only due to a change in vessel capacity in the BE scenario (only scenario where the number of vessels can vary), overall the fishery increases its vessel capacity, notably of small *Nephrops* trawlers.

To get to the MEY, only the large trawlers decrease their effort, by only few percent for TR2_10-24 but by more than 75% for the large whitefish trawlers. Once again, this seems to be due to the large costs to operate each vessel. The large whitefish trawlers have a cost per vessel 22 times larger than the cost on TR1<10 and 2.8 times greater than the small whitefish trawlers (cf. Table 4.10). Reducing their effort can therefore produce large decreases in fishing costs and increase the fishery net profit. These results highlight the fact that the current total fishing mortality is not economically optimal. This will be presented in more detail in part 5.2.4.

Figure 5.3 shows the fleet revenues and costs for the corresponding effort indices in the “status quo F”, BE and MEY scenarios. The structure of the fishery is completely different between the dynamic equilibria. In the BE scenario, the small trawlers account for most of the revenues whereas the large *Nephrops* trawlers and the foreign vessels are the most profitable in the “status quo F” and MEY scenarios. As shown in Table 5.5, the main difference between the “status quo F” and the MEY is for TR1>24. If the fishing mortality stays the same, the “status quo F” scenario is profitable because it shows positive net profit for all fleets. The maximisation of the total fishery net profit induces however negative net profits for the large whitefish trawlers. This is an anomaly since a fleet making loss is supposed to stop fishing at the equilibrium. The fact that TR1>24 keeps running at loss is due to the assumption of the MEY scenario which says that a fleet can stop fishing but cannot exit the fishery so the net profit is negative if the effort index is 0 due to the fixed costs of the vessels. At the MEY, the total fishery net profit is maximised if TR1>24 keeps fishing with small negative net profit rather than if it stops fishing. It makes sense to have this assumption and to keep this fleet because it is the whitefish fleet presenting the largest revenues currently (Seafish). It is fair to assume that if this would happen in reality, the fleet would exit the fishery, or receive subsidies until a positive net profit is reached.

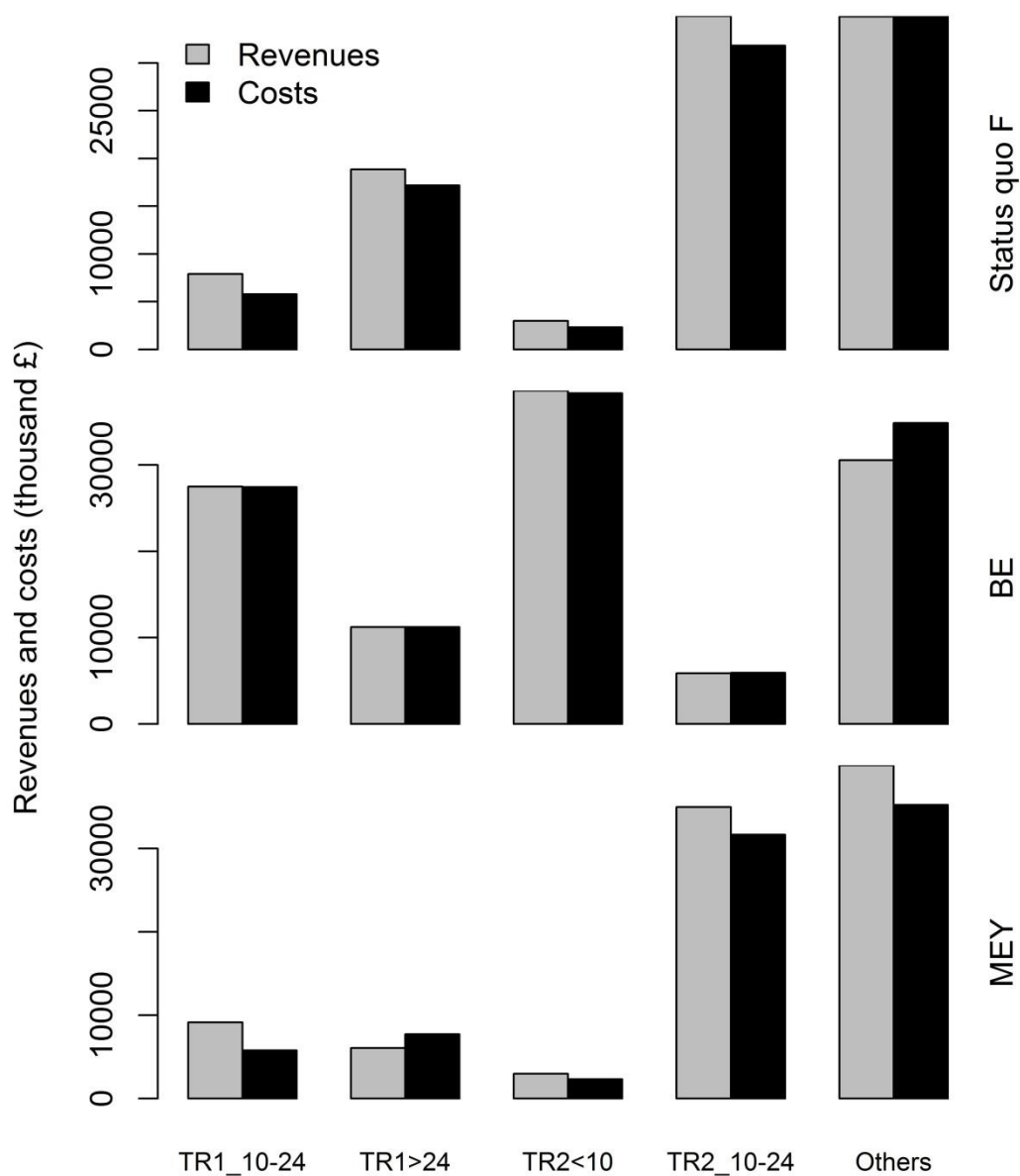


Figure 5.3: Average fleet revenues and costs at status quo *P* in the three scenarios.

Table 5.6: Total fishing revenues and costs (£) at status quo *P* in the different scenarios.

	Status quo F	BE	MEY
Total fishing revenues (£)	99,450,026	113,735,779	93,138,024
Total fishing costs (£)	91,946,590	117,800,100	82,706,030

As regards to the entire fishery, the BE scenario is the one bringing the largest revenues and the MEY scenario the smallest (Table 5.6). The “status quo F” scenario is situated in between both. However, at the BE the net profit is dissipated (except for the “Others” fleet because its effort is kept constant hence the larger costs at the BE) but they are maximised at the MEY. Larger revenues at the BE could for instance reflect a fishery with more fishers but it also implies a major change in the current fishery configuration. However, the MEY seems easier to reach and the net profits are maximal and induce an optimal fishery in the long-run.

5.2.2. Grey seal impacts on fish stocks

Before looking at the economic impact of grey seal predation, it is useful to consider the biological impacts of seals on the three stocks of interest (Figure 5.4). As expected, the credible intervals are large for all species due to the high variability around the stock-recruitment relationship.

It is clear that despite a difference in SSB values, the trend in the change in SSB with seal numbers is similar in the three scenarios. Cod is the fish the most sensitive to an increase in grey seal numbers with a steeper decrease in SSB for an increase in seal numbers compared to the other species. Surprisingly, despite a weight of haddock consumed by seals in 1985 and 2002 of the same order of magnitude as the weight of cod consumed (Harris, 2007), the haddock SSB is largely stable for this species even for large changes in the seal population. A decreasing trend in whiting SSB is clearly visible when grey seal predation is increased but the slope is less steep than for cod.

The cod stock seems more sensitive to a decrease in seal numbers than to an increase. Indeed, a decrease in seal numbers induces a bigger change in SSB than an increase in seal numbers of the same amount does (Table 5.7). This is also seen in Figure 5.4 where the slope is slightly steeper between -30 and 0% than between 0 and +30%. The large size of the credible intervals may however mean that these differences are not significant.

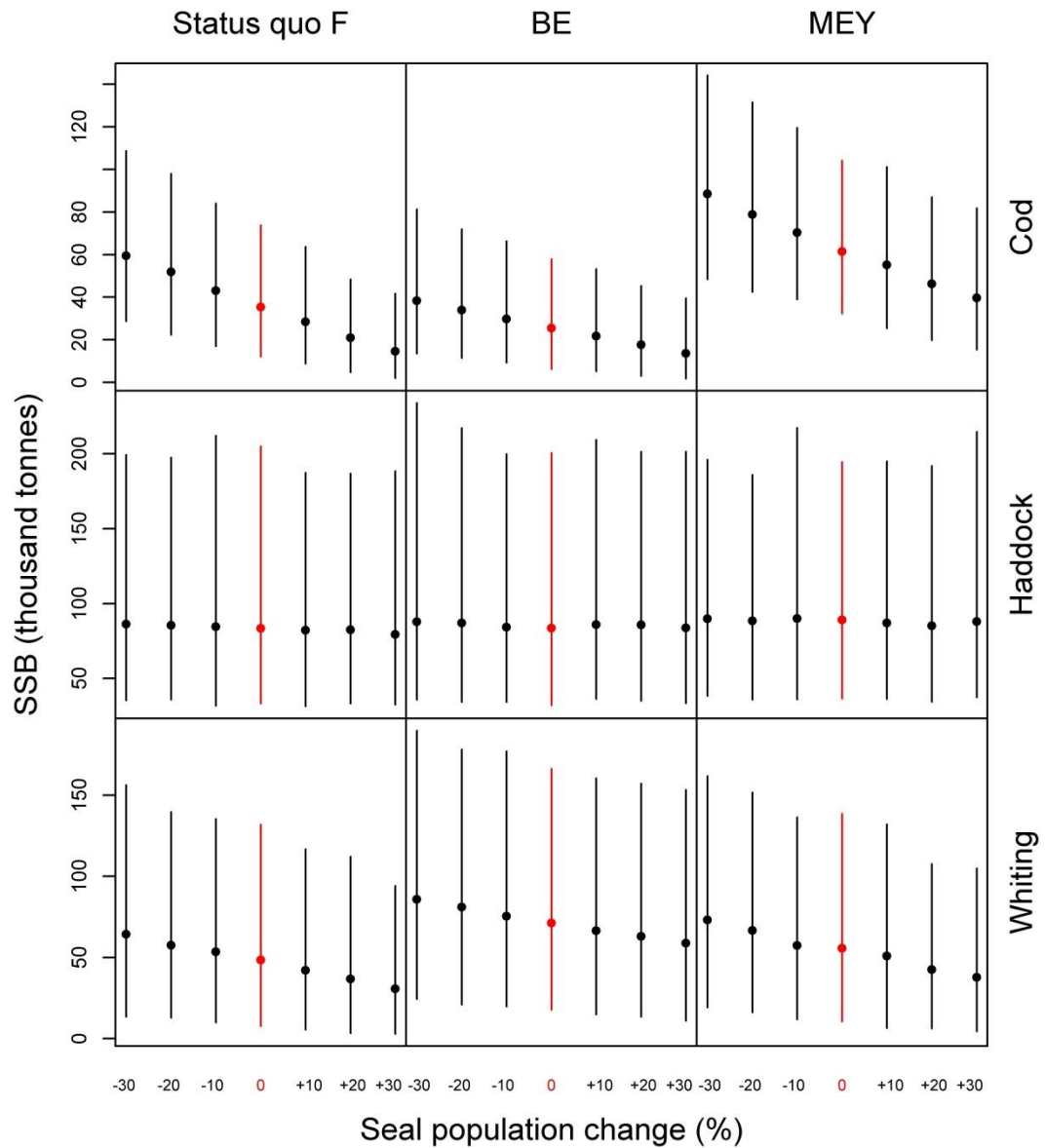


Figure 5.4: Average SSB (dots) and 95% credible interval (segment) for the three species of interest and in the three different equilibrium scenarios for a change in seal population between -30% and +30%.

For whiting, the change in SSB is more or less similar no matter the direction of the change in seal numbers (Table 5.7) and an almost perfect straight line can be drawn between -30% SSB and +30% SSB in Figure 5.4.

In the “status quo F” simulation, an increase in seal population of 30% pushes the cod and whiting stocks at risk of extinction with a lower limit of the credible interval around 2,000 tonnes.

Table 5.7: Change in cod and whiting SSB (%) for an increase or a decrease in seal numbers of 30% compared to the SSB at the current level of seal population.

Scenario	Cod		Whiting	
	-30%	+30%	-30%	+30%
Status quo F	+68	-59	+33	-37
BE	+51	-46	+21	-17
MEY	+44	-36	+32	-32

In the dynamic scenarios (BE and MEY) fleet effort can change so the impact of seal predation on SSB may not only be due to seal predation directly but also to the change in fleet behaviour with fish abundance. The BE scenario estimates smaller SSB for cod and larger for whiting for all changes in seal population, similar to that observed at the current seal population level (Figure 5.2). In the MEY scenario, the levels of SSB for whiting are slightly larger than for the “status quo F” scenario. However there is larger cod stock at MEY compared to the other scenarios which highlights again the importance of the cod stock in the maximisation of fishing net profit.

The equilibrium whiting biomass goes beyond the maximum observed values at the BE only for two cases of seal population change (-30% and -20%). However, for cod at the MEY, all the average SSB, except for a change in seal population of +30%, are larger than the observed one. In the “status quo F” scenario, cod SSB is also larger for any decrease in seal numbers. Knowing the possible overcompensation effect of the Ricker stock-recruitment assumption when SSB goes beyond the observed values, these results may be uncertain. This will be discussed in more detail in the next chapter.

5.2.3. Grey seal impacts on fishing revenues

After considering the biological impacts of grey seal predation on fish stocks and showing that the impact is most important for cod, less so for whiting and is minor for haddock, it is necessary to translate these changes into economic terms by looking at the impact of grey seal predation on fleet revenues and net profits.

The change in fleet revenues is not completely symmetrical depending on the direction of the change in seal population (Figure 5.5). Similarly to what was visible for cod SSB in the previous part, a decrease in seal population has overall a larger impact than an increase in seal numbers.

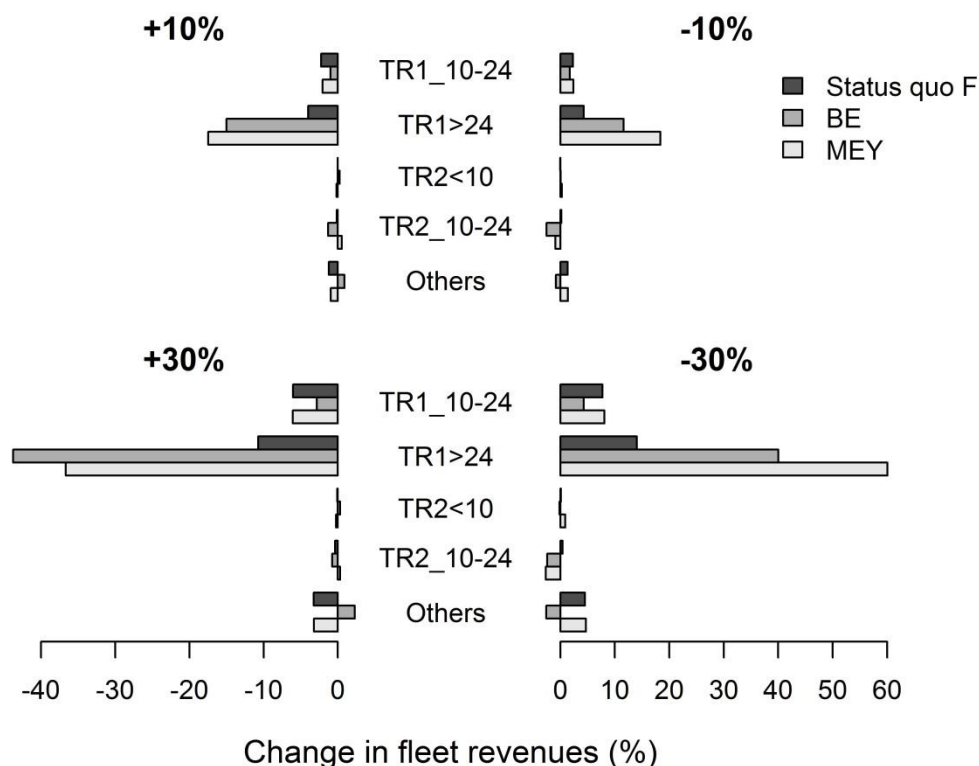


Figure 5.5: Change in fleet revenues (%) in the three different equilibrium scenarios for a small (10%) and large (30%) change in seal population.

The large whitefish trawl fleet (TR1>24) is the most impacted by a change in grey seal population in the three scenarios. The “status quo F” scenario is the one showing the smallest impact for this fleet with a maximum change in the revenues of around 14% when the seal population is reduced by 30%. The MEY scenario is the one having largest impacts with an important increase in TR1>24 revenues of 60% when the seal population is reduced by 30%. The increase at the BE is of 40%.

If this decrease in predation mortality is related to a change in seal numbers this would correspond to a change of more than 9,600 individuals which could seem large in the short-term even if considering human interventions, predator removal or disease. A change of $\pm 10\%$ may be more realistic and corresponds to a change of around 3,200

individuals. In this case, the impact is reduced to 4% for TR1>24 in the “status quo F” scenario, 12% at the BE and 18% at the MEY. Consequently, if the fishery is at the BE or MEY, a 10% decrease in seal population can produce a larger increase in the revenues of TR1>24. However, the impacts for the rest of the fleets are minimal.

After the large whitefish trawlers, the small whitefish fleet (TR1_10-24) and the “Others” fleet are the most impacted by grey seal predation. As expected, the *Nephrops* trawlers are the least impacted since cod, haddock and whiting are caught as bycatch and not directly targeted.

It has been mentioned in part 4.3.2 that it is possible to obtain revenue distributions resulting from the stochastic nature of recruitment. The average fleet revenues differ significantly for changes in levels of seal population. However, the comparison of the 95% intervals at the steady state in the different scenarios highlights the large range of values the revenues can take for the different seal population scenarios (Figure 5.6). Indeed all the credible intervals for the different seal population changes are overlapping indicating that even if the average revenues are different, the changes in revenues due to the change in grey seal predation at the steady state is small compared to the size of the credible intervals. The large credible intervals demonstrate again the great uncertainty around the stock-recruitment relationship which was already highlighted in Figure 5.4.

The TR1 fleets present a clear decreasing trend in average revenues with an increase in seal predation. The inverse trend at the BE for the “Others” fleet that targets whitefish is an artefact due to its effort being kept constant. This fleet’s landings depends mainly on what the other fleets are catching and do not respond to the change in seal predation. The change in revenues for the *Nephrops* fleets presents no clear trends in line with the small change in bycaught landings of the three species for which grey seal predation is modelled.

While the “status quo F” scenario is the one presenting the smallest impacts of seal predation for the TR1>24 fleet, it is also the one presenting the largest revenues for this fleet. The MEY scenario which had the largest impacts on the revenues is the one estimating the smallest revenues for this fleet. This could be the reason why the change

is larger when the revenues are small. The proportion of each fleet in the total revenues changes with the scenarios. Indeed the “Others” fleet presents the largest revenues in the “status quo F” and at the MEY, followed by TR2_10-24, TR1>24, TR1_10-24 and TR2<10. At the BE, the fleet bringing the most revenues to the fishery is TR2<10 followed by TR1_10-24, “Others”, TR1>24 and TR2_10-24.

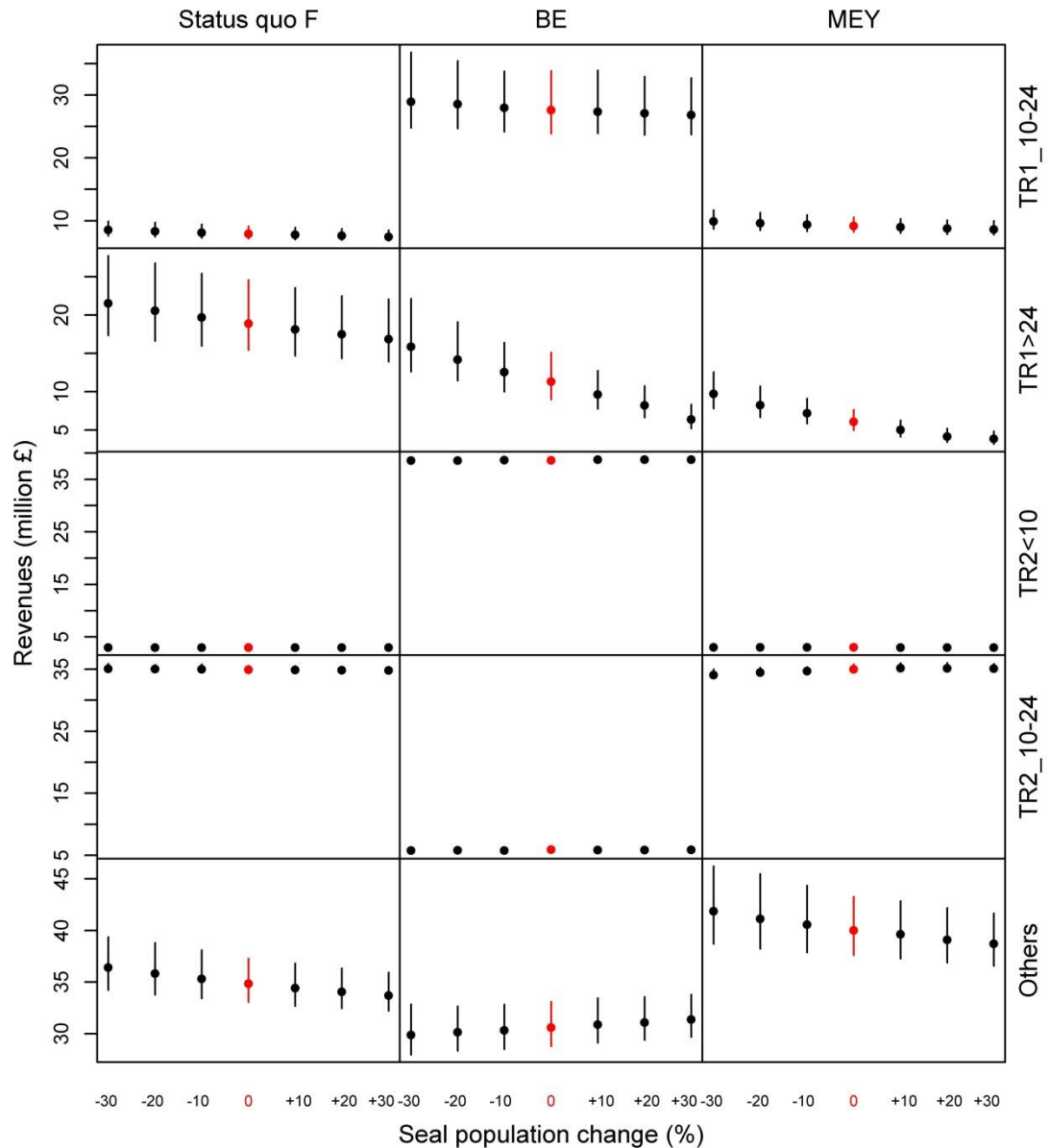


Figure 5.6: Average fleet revenues (dots) and 95% credible interval (segment) for the three species of interest and in the three different scenarios for a change in seal population between -30% and +30%. The credible intervals for the TR2 fleets do not appear on the figure because they are too small compared to the scale of the y-axis which is common to the three equilibrium scenarios.

The MEY is the scenario where the total fishing net profit is maximised. It is therefore also interesting to see the impacts of grey seal predation on the fleet net profits. The impacts on the net profits are smaller than the impacts on the fleet revenues for the five fleets with a maximum impact of 37.2% for TR1>24 (Table 5.8). As observed for the revenues, the large whitefish trawlers are the most impacted and the *Nephrops* trawlers the least. These results seem to show that when the total fishery net profit is maximised the impacts of grey seal predation may be large on fleet revenues but they are reduced on fleet net profits.

Table 5.8: Change in the fleet net profits (%) in the MEY scenario following a change in seal population between -30% and +30%.

Fleet	-30%	-20%	-10%	10%	20%	30%
TR1_10-24	8.1	4.9	2.4	-2.1	-4.6	-6.1
TR1>24	37.2	23.0	12.2	-12.3	-23.7	-28.1
TR2<10	0.9	0.5	0.3	-0.2	-0.2	-0.2
TR2_10-24	-0.1	0.0	-0.1	0.0	-0.1	-0.2
Others	4.7	2.8	1.4	-0.9	-2.3	-3.2

When looking at the scale of the entire fishery, the change in seal predation results in a change in the total fishery revenues and net profit between -4.3% and +5.7% (Table 5.9). In the “status quo F” the changes in revenues and net profit are identical because, the effort being constant, the costs are the same for all simulations. The change in net profit at the BE are not presented here because by definition the net profits are dissipated at the equilibrium.

For the three scenarios, the direction of the change in the total fishery revenues is consistent, with an increase in revenues and net profit with a decrease in grey seal population. When the fishery is assumed to maximise its net profit, a change in grey seal population has a slightly larger impacts on the revenues than on the net profit.

While large changes in fleet revenues were observed in the three scenarios, notably for TR1>24, at the fishery scale, even large changes in seal population have relatively small effects on the total fishery revenues and net profits. The impacts are also less variable

between the scenarios. This is due to the fact that, in the three scenarios, the TR1<24 fleet only accounts for a small part of the total revenues (Figure 5.6).

Table 5.9: Change in the total fishery revenues and net profit (%) in the three different equilibrium scenarios following a change in seal population between -30% and +30%.

Scenario	Type of change	-30%	-20%	-10%	10%	20%	30%
Status quo F	Change in revenues and net profit	5.0	3.2	1.5	-1.4	-2.6	-3.8
BE	Change in revenues	4.3	2.8	1.1	-1.4	-2.7	-4.3
MEY	Change in revenues	5.7	3.5	1.7	-1.5	-3.3	-4.3
	Change in net profit	5.2	3.1	1.5	-1.2	-2.6	-3.4

Consequently these results shows that, no matter the equilibrium considered, the impacts of grey seal predation on fishing revenues differ depending on the fleet and are minimal at the level of the entire fishery.

Table 5.10 shows the change in revenues for a small change in seal population of $\pm 10\%$ at the level of the entire fishery, at the level of one vessel but also what this 10% change in revenues represents per seal. At the BE, it is assumed that the change in fishing mortality is entirely due to a change in the number of boats and not to a change in effort, assuming all the vessels are identical. As a result, the change at the fishery level is divided by the total number of vessels to get the revenues per vessel. The number of boats at the BE is larger than in the other scenarios where the fishery has limited access. This is an over-simplification but it gives an idea of the costs scaled to the number of vessels in the fishery. To get the change in revenues per seal the change in the total fishery is divided by the number of seals that represents 10% of the population hence 3,204 individuals.

The results are of the same order of magnitude for all scenarios at the fishery and seal levels. As expected, the MEY presents the highest change in revenues at the fishery level because the impacts were the largest in this scenario (Table 5.9). Assuming an open-access fishery produces a large number of boats and reduces the change in fishing

revenues per vessel compared to the other two scenarios. The change in fishing revenues per vessel following a change in seal numbers are the largest at the MEY.

Table 5.10: Change in annual fishing revenues (£) following an increase or decrease in seal population of 10% (3,204 individuals) at the level of the entire fishery, one vessel and one seal in the three different equilibrium scenarios.

Scenario	+10% seals			-10% seals		
	Fishery	Vessel	Seal	Fishery	Vessel	Seal
Status quo F	-1,391,139	-6,323	-434	1,570,350	7,138	490
BE	-1,408,721	-2,348	-440	1,430,484	2,372	446
MEY	-1,441,673	-6,553	-450	1,586,755	7,213	495

Converting the change in fishing revenue to what it would mean per seal gives an overall cost of seal predation between £434 and £495 per seal depending on the scenario considered.

5.2.4. Sustainability of the VIa fishery

5.2.4.1. Fishing mortality and revenues per species

Conventionally, the effort (or fishing mortality in this study since selectivity and predation rate are constant) at the BE is always larger than the effort at the MEY. When the fishing mortality goes beyond the one at the BE (F_{BE}), the fishery net profit becomes negative and, on average, fishing is not economically sustainable. Consequently, from a management point of view, the fishing mortality on a fish species should be at or below F_{BE} for the catch to be economically viable.

It is interesting to compare the average fishing mortality for the three species of interest at the different equilibria and compare it with the status quo fishing mortality in the West of Scotland to determine the economic sustainability of the fishery. Also, it is interesting to study how this sustainability window varies with seal population changes. Figure 5.7 shows the values the total fishing revenues can take with changes in

seal population as a function of average fishing mortality. First, as expected, for all species, the fishing mortality and revenues at the BE are the largest compared to the MEY results. Also, at the BE, a large decrease in the total fishing revenues necessitates a large decrease in F . However, for MEY where F is generally low, a large decrease in revenues occurs for a small decrease in F . Similarly, changing the grey seal population has a larger impact on fishing mortality at the BE than at the MEY.

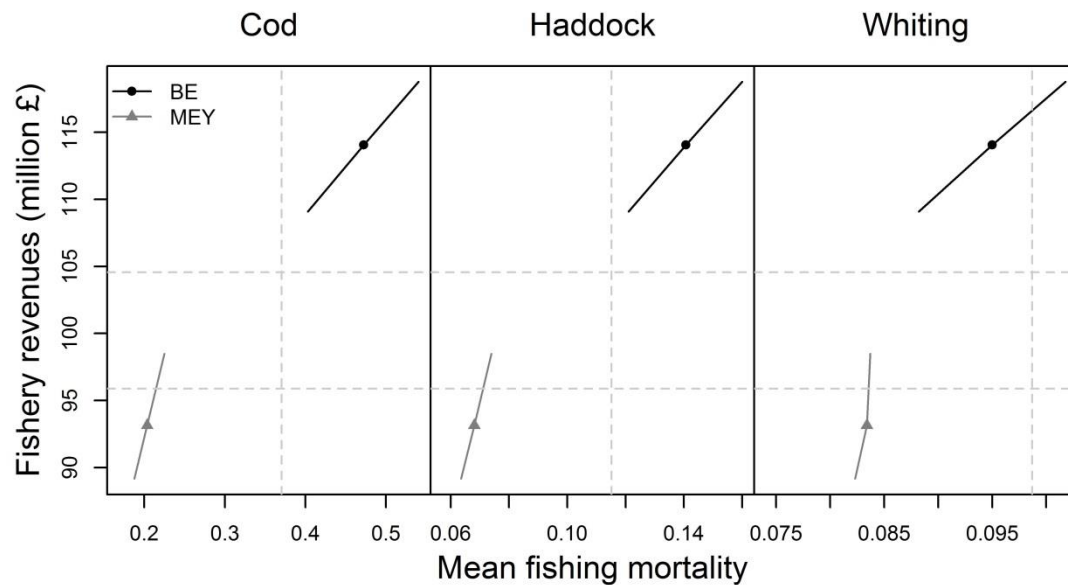


Figure 5.7: Average total fishery revenues and fishing mortality at the BE (dots) and MEY (triangles). The segments represent the range of change in fishing revenues as a function of mean fishing mortality for seal population changes between -30% and +30%. The dashed vertical grey line corresponds to the average status quo fishing mortality and the dashed horizontal grey lines give the range of fishing revenues in the “status quo F” scenario. The age range used to take the mean fishing mortality follows ICES (2013b).

For cod and haddock, the current fishing mortality is economically sustainable because it is lower than F_{BE} within the range of grey seal population considered. However, for whiting the current fishing mortality is larger than F_{BE} and a reduction in fishing or grey seal mortality is necessary to fish at economically sustainable levels despite the really small fishing mortality values.

Despite the economic viability of the fishery in the “status quo F” scenario with only positive profits for all fleets (Figure 5.3), fishing is not economically sustainable on the whiting stock. This could be resolved by reducing the current fishing mortality by 4% if

the seal population stays stable. Nevertheless, the fishery being mixed the profitability of individual stocks is not critical.

5.2.4.2. Change in total fishing mortality required to obtain an economically optimal fishery

In the MEY scenario, each fleet can change its effort independently from the others following the conventional method used in multifleet models. However it is interesting to know where the current fishery is compared to the economically optimal case where the fishery net profit is maximised, given the current configuration of the fishery. Therefore a new MEY scenario is tested but this time it is assumed that the proportion of each fleet in the total fishing mortality cannot change. In other words, the change in fleet effort index is the same for all fleets and the optimal level of effort is a single constant E_{MEY} . This enables the comparison of the current effort index with the optimal level of effort which maximised the fishery net profit keeping the proportion of each fleet in the total fishing mortality constant. By default, as for the MEY scenario, the upper bound on effort index is set to be the current fishing effort index, i.e. assuming that the fleets fish already at the maximum effort or fishing mortality level.

Figure 5.8 shows the proportion by which the current fishing effort or mortality in the West of Scotland should be reduced to maximise the total fishery net profit without changing the composition of the fleets. At the current level of seal population, the current fishing mortality should be reduced by about 19.6%. Increasing seal numbers induces a decrease in the current fishing effort but overall the effort reduction is about the same regardless of the level of seals.

The results when fleet effort indices can vary between 0 and twice the current effort give the same results. This may be evidence of the necessity to reduce the current fishing mortality to maximise the fishing net profit in VIa.

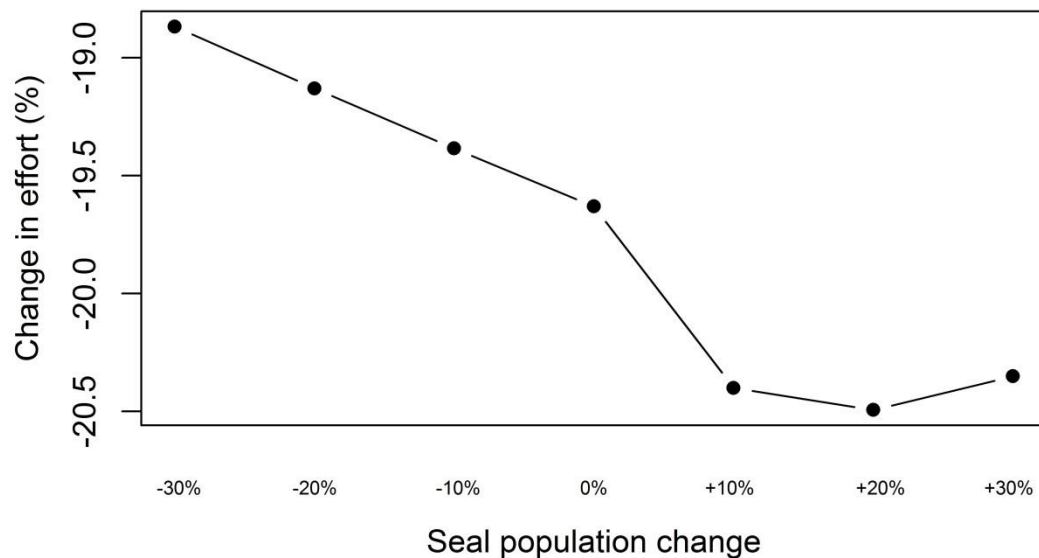


Figure 5.8: Change in fishing effort index (or mortality) necessary to maximise the fishery net profit compared to the current fishing effort index and keeping the current fishery configuration.

5.2.5. The importance of cod in grey seal impacts

It has been seen in part 4.2.1.1.6 that the grey seal predation mortality on cod estimated by the state-space model is larger than that on haddock and whiting making cod the fish that is likely to be the most impacted by grey seal predation. The simulation study of seal impacts on fish stocks seems also to validate this assumption (Figure 5.4). Also, TR1>24, which is most impacted in all scenarios, is also the fleet that lands the greatest weight of cod given the status quo fishing mortality (Figure 5.9). This motivates the investigation of the role of cod in grey seal impacts on fishery.

To investigate the importance of cod in grey seal impacts, a fixed F simulation was run forcing the collapse of cod by setting the recruitment to be 0 every year. The corresponding grey seal impact on fleet revenues is compared to the “status quo F ” simulation which uses the initial stock-recruitment relationship (Figure 5.10). It is clear that grey seal impacts on all fleet revenues are substantially reduced when the cod stock collapses. Even reducing the seal population by 30% only increase the revenues of TR1>24, the most impacted fleet, by less than 3%.

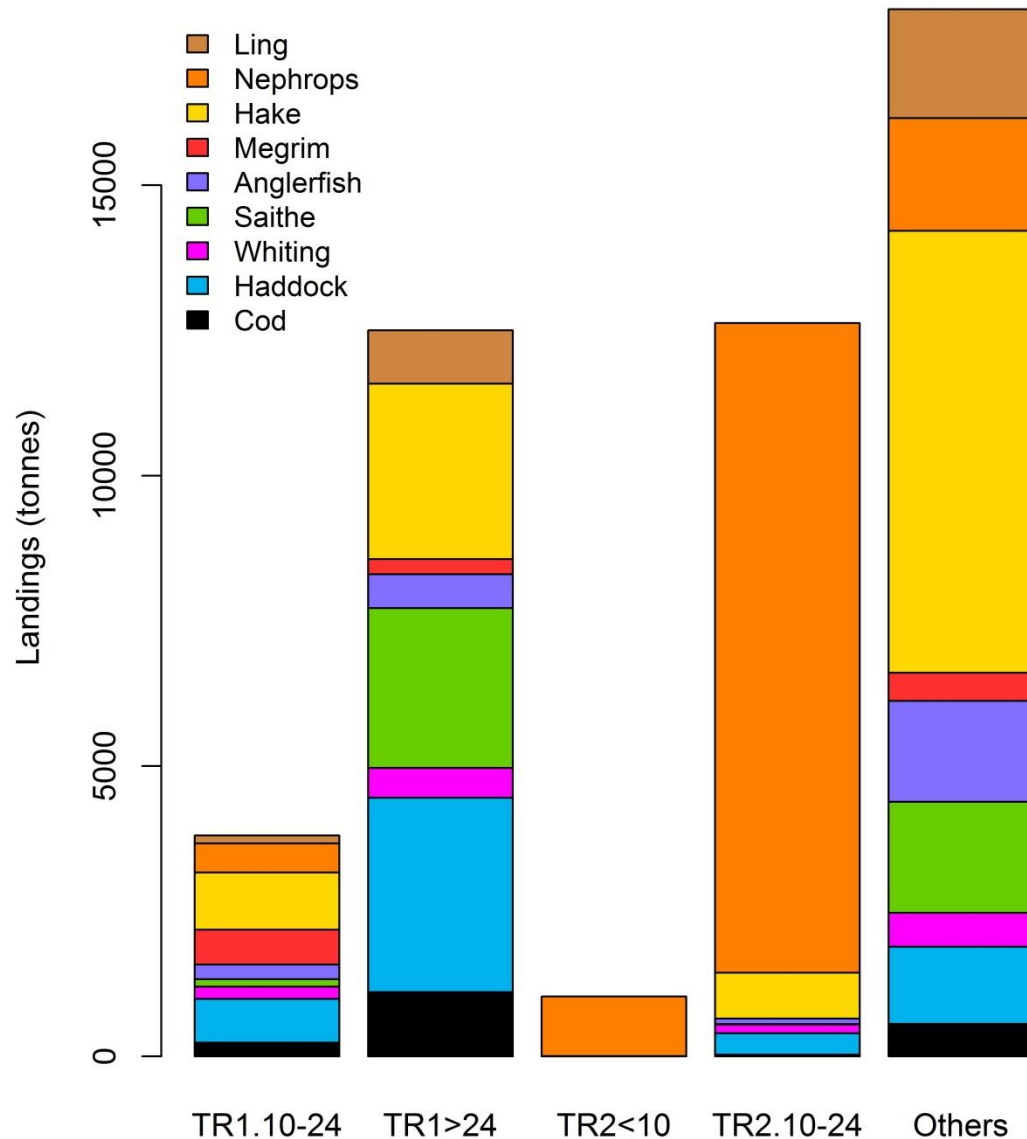


Figure 5.9: Landings per species and fleet in the “status quo F” scenario and for the current seal population level.

This emphasizes two points:

- From part 4.2.2.1.3 we know that grey seal predation is larger on cod than haddock and whiting and seal predation mortality on haddock and whiting is the smallest mortality. This makes cod the fish the most impacted by grey seal predation and the economic impacts on fishing revenues from the predation on the other species are minimal.

- There is little economic impact of grey seal predation on the West of Scotland fishery when the cod stock collapses. Avoiding the collapse of cod should be the main goal of fisheries regulations. A reduction in seal population, even drastic, will be ineffective if cod disappears.

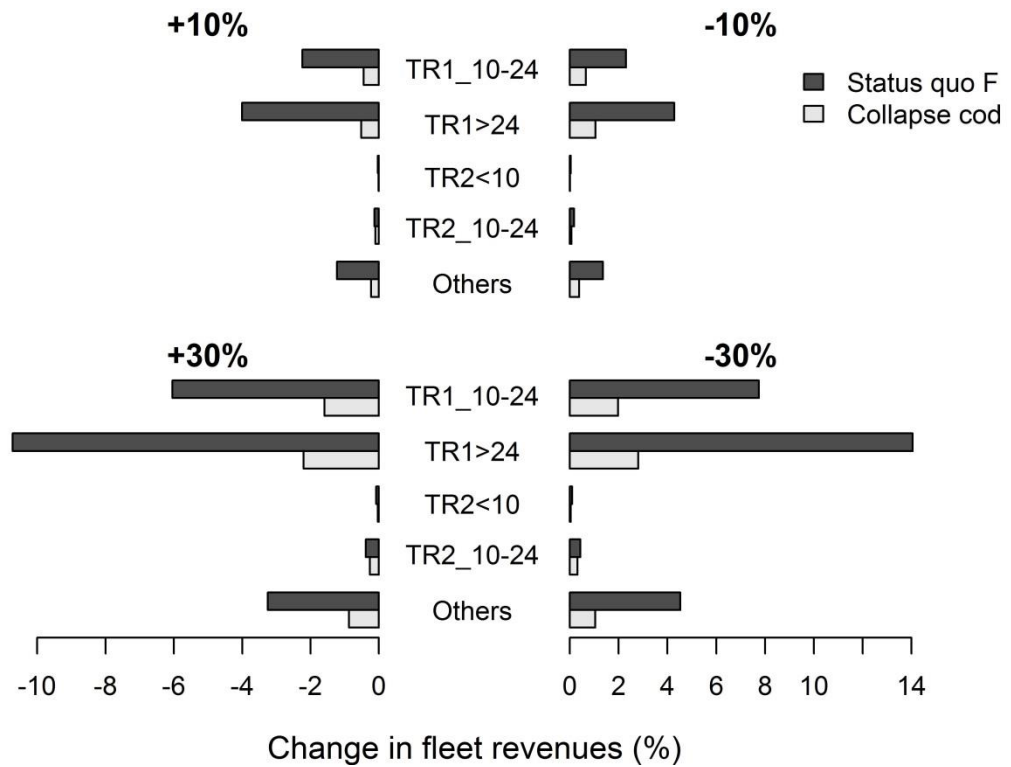


Figure 5.10: Change in fleet revenues (%) for a small (10%) and large (30%) change in seal population in the “status quo F” scenario and when the recruitment for cod is set to 0.

The next chapter studies the sensitivity around grey seal impacts on fishing revenues.

Chapter 6

Sensitivity analysis

It is important to study the sensitivity of the bioeconomic simulation models to the different assumptions taken in this study. This evaluates the robustness of the results or highlights the limitations of the models that need to be kept in mind for the discussion of the results (Figure 6.1).

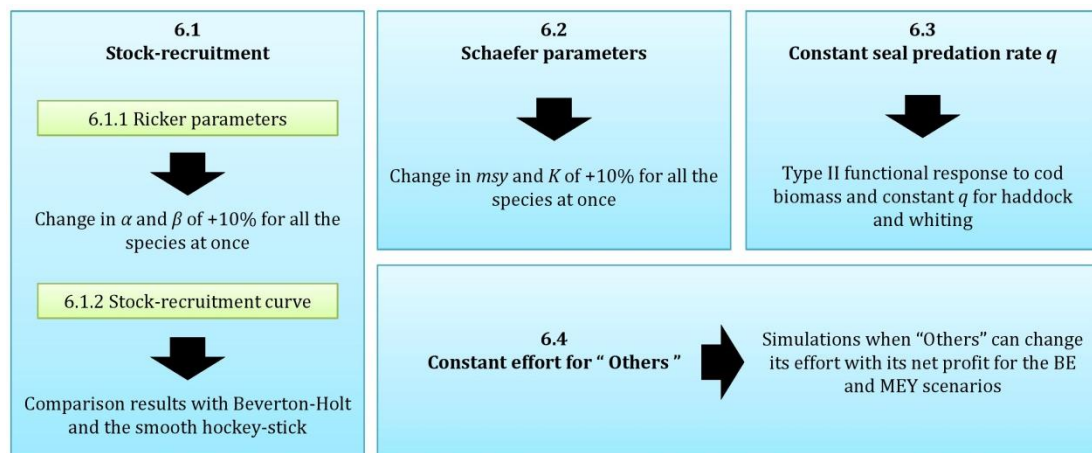


Figure 6.1: Schematic diagram of the different sensitivity analyses done in this chapter.

The robustness of the bioeconomic results to the stock-recruitment relationship is investigated in the first part. Sensitivity around the Schaefer parameters is also tested in part 6.2. The different scenarios assumed a constant seal predation rate; the sensitivity around this assumption is discussed in part 6.3. Finally, the effort of the “Others” fleet is assumed constant in the dynamic scenarios, it is also necessary to see if the models are sensitive to this assumption.

6.1. Sensitivity around the stock-recruitment assumptions

The different bioeconomic models assumed a Ricker stock-recruitment relationship (Ricker, 1954). Two different aspects need therefore to be tested. The sensitivity of the model to the parameter estimates of the Ricker curve related to the measurement errors which affect the shape of the curve. But also the sensitivity around the choice of the curve by comparing the results with the two other commonly used curves: Beverton-Holt (Beverton and Holt, 1957) and the smooth hockey-stick (Froese, 2008).

6.1.1. Sensitivity around the stock-recruitment parameter estimates

A stock-recruitment curve could be mainly sensitive to two aspects: the slope at the origin and the maximum recruitment. The larger the slope at the origin, the faster the fish stock will reach the maximum recruitment value and vice-versa. Also a shallow slope may make the stock more vulnerable to collapse (e.g. when the replacement line lies above the stock-recruitment curve). The maximum recruitment is also important since for the Beverton-Holt and smooth hockey-stick curves it is constant at high SSB. For the Ricker curve, the maximum is the value at which the recruitment starts to decrease for larger values of SSB.

It is important for the bioeconomic models to have stock-recruitment parameters that are reliable and lead to robust bioeconomic results. However, the reliability of the estimates is limited by the short time series of stock-recruitment data and the fact that the parameters are themselves estimated from estimates of recruitment and SSB resulting from stock assessment models. Testing the robustness of the simulation model to the stock-recruitment parameters is therefore necessary.

To analyse the overall sensitivity of the models to the Ricker parameters, the experimental scenarios are run for different simulations changing each stock-

recruitment parameter, α and β (Equation (4.3)) by +10% for all fish species. This value is used to simulate the local sensitivity at the initial parameter values which were estimated at the current state of the fishery. The models being non-linear changing the parameters by more than 10% may not be representative of the global sensitivity to these parameters.

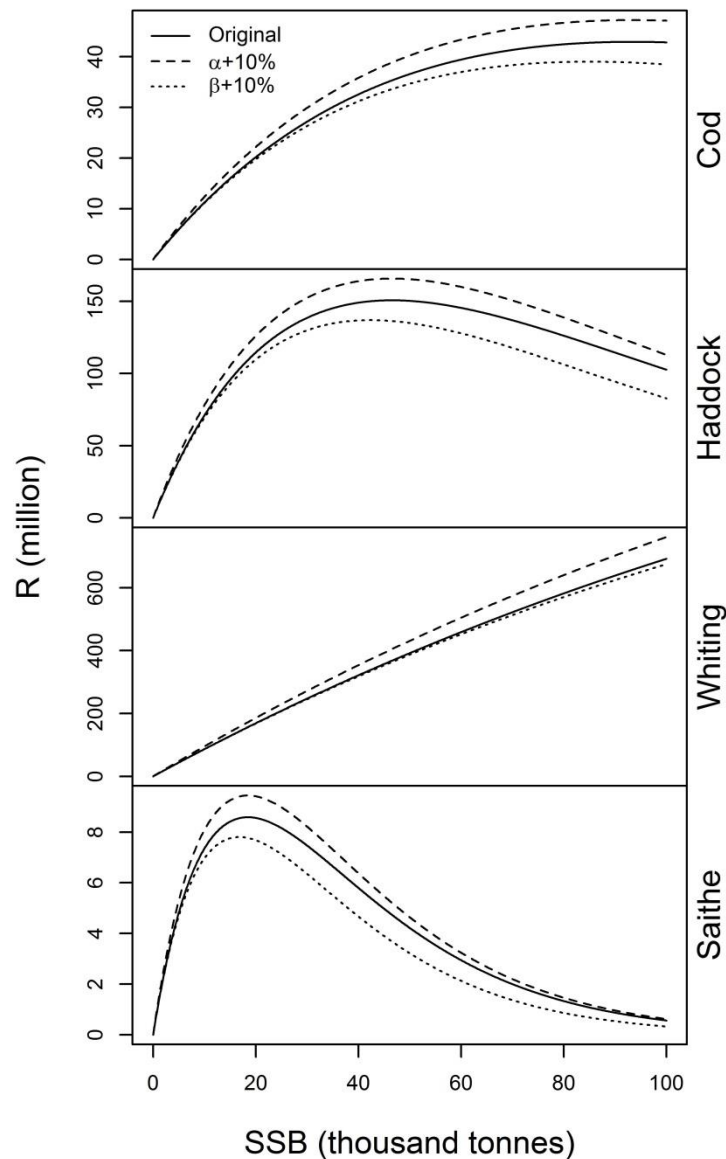


Figure 6.2: Stock-recruitment curves changing one parameter at a time by +10% used to analyse sensitivity of the equilibrium models to the Ricker stock-recruitment parameters.

With the Ricker assumption, increasing β decreases the maximum recruitment and changing α increases both the slope at the origin and the maximum recruitment (Figure 6.2). The parameterisation does not allow variation of the slope and the maximum recruitment independently.

The fish species most affected by the change in the stock-recruitment parameters is whiting which shows large changes in average SSB in all equilibrium scenarios (Table 6.1). Overall, an increase in α induces an increase in SSB while an increase in β induces a decrease in SSB. This is expected since increasing α by 10% increase the slope at the origin and the maximum recruitment while increasing β decrease the maximum recruitment. Therefore, the impact is overall larger when α is increased than when β is.

Table 6.1: Change in average equilibrium SSB (%) at status quo P when the Ricker parameters are changed by +10% compared to the results obtained with the initial stock-recruitment parameters in the three equilibrium scenarios.

Scenario	Case	Cod	Haddock	Whiting	Saithe
Status quo F	$\alpha+10\%$	+26	+8	+81	+17
	$\beta+10\%$	-10	-7	-11	-9
BE	$\alpha+10\%$	+13	+4	+50	-5
	$\beta+10\%$	+8	-9	-7	7
MEY	$\alpha+10\%$	+8	+6	+69	+2
	$\beta+10\%$	-5	-9	-11	-7

Table 6.2 shows the change in fleet revenues for a +10% change in α or β compared to the initial run with the original stock-recruitment parameters at status quo P . The revenues for the *Nephrops* fleets (TR2) are not sensitive except in the BE model for TR2_10-24. This was expected since cod, haddock, whiting and saithe are caught as bycatch by these fleets. The importance of the impact is due to the large change in effort index for the large *Nephrops* trawlers at the BE as shown in Table 5.5 in the previous chapter. Unsurprisingly, the most impacted fleet is again TR1>24 and, in the dynamic scenarios, changing the stock-recruitment parameters can induce a large change in revenues for this fleet at status quo P . The impact of changing α and β for the other fleets is minimal.

The increase in the change in revenues when α is modified seems to show that the model is sensitive to both a change in the slope at the origin and in the maximum recruitment when a Ricker relationship is assumed. Overall, an increase in α causes an increase in fish stocks so an increase in the fleet revenues and an increase in β , a decrease in stocks and the fleet revenues.

Table 6.2: Change in fleet revenues (%) at status quo P when the Ricker parameters are changed by +10% compared to the results obtained with the initial stock-recruitment parameters in the three equilibrium scenarios.

Scenario	Case	TR1_10-24	TR1>24	TR2<10	TR2_10-24	Others
Status quo F	$\alpha+10\%$	+5	+9	0	0	+3
	$\beta+10\%$	-2	-4	0	0	-1
BE	$\alpha+10\%$	+3	+31	-1	+4	-1
	$\beta+10\%$	+1	-26	0	-6	+1
MEY	$\alpha+10\%$	+3	+53	0	-1	+1
	$\beta+10\%$	-2	-17	0	0	-1

Rather than the actual value of the revenues for each fleet, the study is mainly concerned with the impact of seal predation on fleet revenues. As the TR1>24 is the fleet most affected, the sensitivity around the stock-recruitment parameters for different changes in seal population is studied just for this fleet.

Figure 6.3 shows the difference in seal impacts on TR1>24 when the stock-recruitment parameters are changed by +10% compared to the initial results obtained with the initial parameters. In the “status quo F” scenario changing the stock-recruitment parameters only induces a change in grey seal impacts of less than 1%; this model is therefore not sensitive to the stock-recruitment parameters. However, the change is more important in the dynamic scenarios and can reach 20% for large changes in seal population (30%). Also, the direction of the change differs with the scenario considered. Increasing α almost always produces a decrease in grey seal impacts on TR1>24 revenues. This is similar to the increase in the fleet revenues previously observed (Table 6.2). Indeed, the increase in recruitment produces larger revenues. A given predation mortality therefore has a smaller impact on larger revenues than

smaller revenues. An increase in β generally produces an increase in grey seal impacts (except in the “status quo F” scenario when the change is almost 0) because the maximum recruitment is reduced and the revenues decrease also compared to the initial simulation. Since the simulations are run for identical grey seal predation mortality, increasing β increases grey seal impacts on TR1>24.

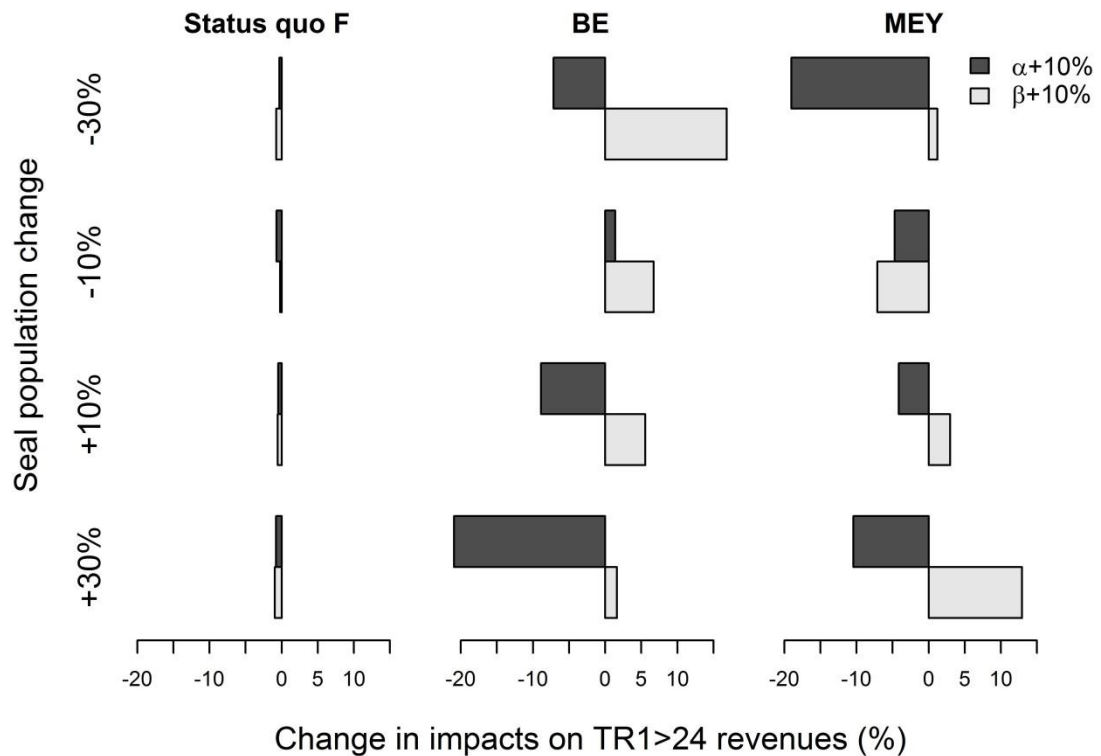


Figure 6.3: Change in grey seal impacts on TR1>24 revenues (%) for a +10% change in α and β compared to the impacts with the initial stock-recruitment parameters.

The larger the seal population change, the larger the change in grey seal impacts becomes. When seal numbers are changed by a small amount (10%), the change in the impacts is less than 9%. Consequently, the sensitivity around the stock-recruitment parameters increases with the magnitude of the change in seal population. The stock-recruitment being highly variable, the bioeconomic results for the largest changes in seal population may be more uncertain since they are more sensitive to the stock-recruitment parameters.

For extreme cases of change in seal population ($\pm 30\%$), the dynamic scenarios show opposite sensitivity. At the BE, the -30% case is more sensitive to β and the +30% case

to α . The contrary is observed at the MEY. This can be related to the effect of the change in seal population on the replacement line, the stock-recruitment curve and on the size of the fish stocks. Decreasing grey seal mortality induces a decrease in the slope of the replacement line and the inverse occurs by increasing grey seal population. Since only the maximum recruitment is modified by changing β , this parameter is not important at low SSB. The parameter α is on the contrary, since increasing it induces an increase in recruitment even when the SSB is low. The results at the BE confirm this. The SSB is low when seal population is increased by 30% so the model is mainly sensitive to α and the inverse is shown for the +30% case. However, this is not seen in the MEY scenario. This can be explained by the value of cod SSB in the different cases. Indeed, the cod biomass is larger than the observed SSB no matter the number of seals in this scenario. This means that the stock-recruitment curve for the $\beta + 10\%$ case already differs from the original stock-recruitment curve. At high SSB both α and β are important and the difference depends on where the replacement line crosses the stock-recruitment curve.

6.1.2. Sensitivity around the choice of stock-recruitment curve

The results presented in Chapter 5 assumed a Ricker stock-recruitment relationship. Even if commonly used for cod and haddock in ICES assessments (ICES, 2013b), it is necessary to see if the models are sensitive to this assumption by running the simulations with two other common stock-recruitment curves: Beverton-Holt and the smooth hockey-stick.

Figure 6.4 shows the difference in seal impacts on TR1>24 when a Beverton-Holt or hockey-stick stock-recruitment is assumed compared to the initial results obtained with the Ricker assumption. In the “status quo F” simulation, the change in grey seal impacts on TR1>24 for the different changes in seal population is small when the Beverton-Holt and hockey-stick curves are assumed, the maximal change being of 3% for a large decrease in seal numbers of 30%.

Similarly to what was observed in the previous part for the sensitivity to the stock-recruitment parameters, the dynamic models are more sensitive to the stock-recruitment assumption. The largest changes in grey seal impacts are observed for a large decrease in seal population and the sensitivity is smaller for smaller changes in seal numbers. This is expected since the differences between the three curves occur at high SSB (cf. Figure 4.12). At large SSB, Ricker assumes an overcompensation effect and the two other curves assume a high constant recruitment. Therefore, the difference in the estimated stocks happens when the SSB goes outside the range of observed data. This can happen when the total mortality on fish is reduced such as in the extreme case where seal predation mortality is decreased by 30%. That is why the difference in grey seal impacts is the largest in the -30% case.

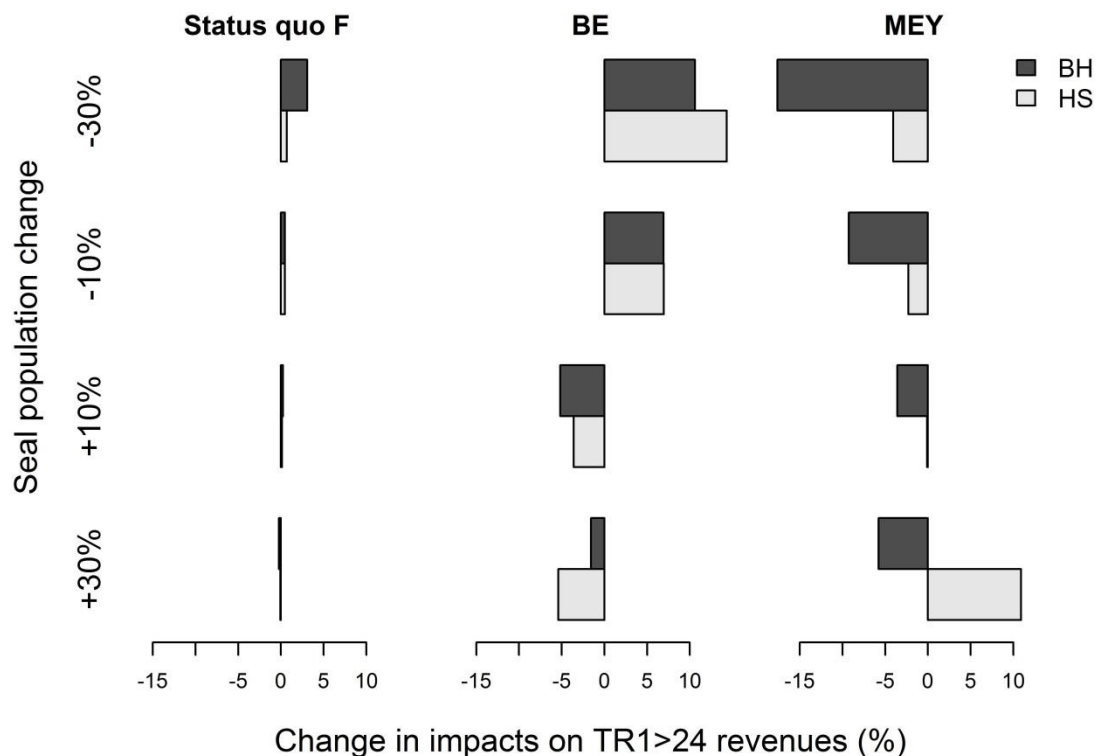


Figure 6.4: Change in grey seal impacts on TR1>24 revenues (%) assuming a Beverton-Holt (BH) and a smooth hockey-stick (HS) compared to the impacts assuming a Ricker stock-assessment relationship.

It seems that, overall, the simulation assuming a smooth hockey-stick curve presents smaller differences in impacts on TR1>24 revenues than the Beverton-Holt assumption. This certainly comes from the fact that for cod, the most impacted fish, the hockey-stick curve is closer to the Ricker than the Beverton-Holt curve. Also, the BE

model is slightly less sensitive than the MEY model. This is expected since the cod biomass at the MEY is the largest and more difference exists between the curves at high SSB.

6.1.3. Summary of the sensitivity analysis around the stock-recruitment assumptions

The sensitivity analysis on the stock-recruitment relationship enables to draw some conclusions about the bioeconomic models:

- The “status quo F” scenario is not sensitive to a small change in the stock recruitment parameters or to the choice of the stock-recruitment curve.
- The BE and the MEY models are more sensitive to both aspects. The fact that the fleet fishing mortality can change in the dynamic scenarios seems to be responsible for larger changes in the stocks which add sensitivity to the bioeconomic results.

The estimation of the stock-recruitment cannot be improved with the few years of data available and it is believed that the original estimates are the best estimates within the bounds of observed data. This means that, when the estimated SSB goes outside these bounds, the uncertainty around the fish dynamics increases, notably for high SSB. This happens for cod in the “status quo F” scenario when seal population is decreased by more than 10% and in the MEY scenario when seal population changes between -30 to +20% (Figure 5.4). It also happens for whiting at the BE when the number of seals is decreased by more than 20%. Cod is therefore the fish the most affected by the sensitivity around the stock-recruitment. The MEY results, for which the cod stock is the largest, need therefore to be considered with great care.

6.2. Sensitivity analysis around the Schaefer surplus production function

For the species where there is no age-structured data, a Schaefer surplus production function was used in the models. The function depends on preliminary estimation for the parameters msy and K (Equation (4.17)). A sensitivity analysis is performed on these parameters to see if the model outputs differ with a change of +10% in each parameter for all species.

Overall, increasing msy by 10% induces an increase in the estimated equilibrium biomass and landings (Figure 6.5). Increasing K induces an increase in biomass and landings at low fishing mortality but a decrease at high fishing mortality. The impacts of changing the Schaefer parameters are larger at high fishing mortality. Hake is the species for which changing the Schaefer parameters have different consequences. Increasing msy decreases the hake biomass at low fishing mortality, increasing K produces higher biomass for all values of fishing mortality and, the landings are always increased compared to the original case with the initial parameters. These differences for hake are due to the fact that the stock biomass is large so the maximum sustainable yield is not reached and the surplus production curve for a change in msy is always below the original curve. The surplus production function for the other species goes beyond MSY. When K is reduced, the biomass is therefore below the original biomass for high fishing mortality.

The fleet revenues at status quo P are compared in the different scenarios (Table 6.3). The estimated revenues are sensitive to the change in the Schaefer parameters with a change going from 1 to 45%.

Depending on the change, the most impacted fleet differs but overall, the *Nephrops* trawlers, and more importantly the large trawlers (TR2_10-24), are the most impacted by the change in the Schaefer parameters. Also, the TR2 fleets are more sensitive to a change in K than in msy . This is expected because in all the scenarios the fishing

mortality on *Nephrops* is less than the fishing mortality at maximum sustainable yield (F_{MSY}).

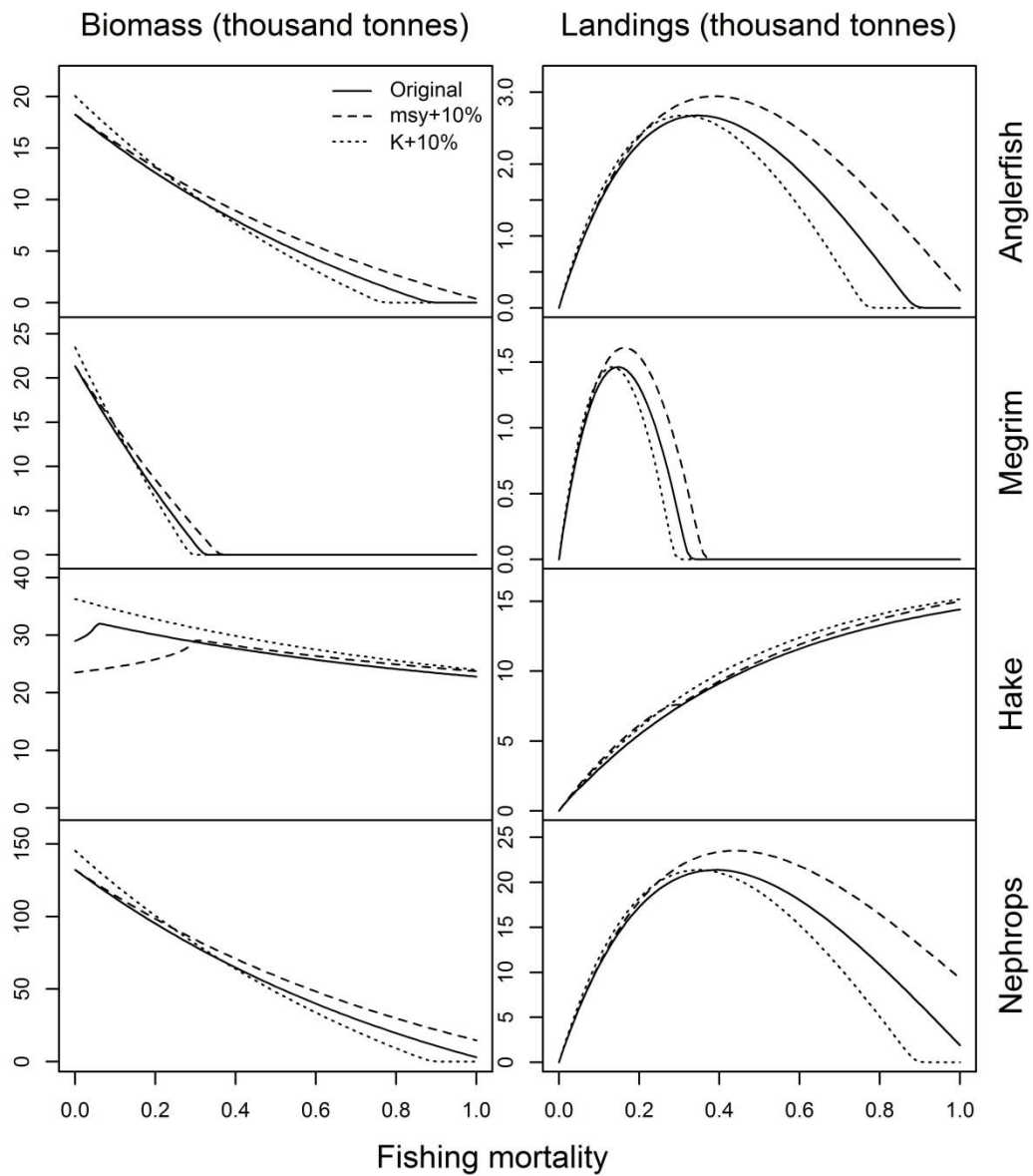


Figure 6.5: Change in the equilibrium biomass and landings as a function of fishing mortality for a +10% change in the Schaefer parameters: msy and K .

The most impacted whitefish fleet is TR1>24 and it is overall more sensitive to a change in msy than K . This is also expected because in the simulations, anglerfish and megrim are fished at a level of fishing mortality close to F_{MSY} . The msy parameter is therefore the most important for the whitefish trawls.

Table 6.3: Change in fleet revenues (%) at status quo P when the Schaefer parameters are changed by +10% for all other species compared to the results obtained with the initial Schaefer parameters in the three equilibrium scenarios.

Scenario	Case	TR1_10-24	TR1>24	TR2<10	TR2_10-24	Others
Status quo F	$msy+10\%$	+3	+2	+3	+3	+4
	$K+10\%$	+4	+3	+7	+7	+4
BE	$msy+10\%$	+15	-14	+5	+43	+2
	$K+10\%$	-7	+4	+5	+45	+2
MEY	$msy+10\%$	+1	+21	+2	+3	+2
	$K+10\%$	+4	-5	+7	+7	+4

Since the principal interest is on the impact of grey seal predation on cod, haddock and whiting, the change in impacts with changes in seal population is studied for TR1>24 (Figure 6.6). As observed before with the stock-recruitment, the “status quo F” simulation is not sensitive to a small change in the Schaefer parameters since the change in grey seal impacts on TR1>24 revenues is less than 1%.

The dynamic scenarios are slightly more sensitive with a maximum change of around 10% at the BE and MEY for a 30% change in grey seal numbers. When a smaller change in grey seal population is simulated, the change in impacts is reduced to less than 5%. The change in sensitivity between msy and K for the different seal population changes is related to the fishing mortality and its position regarding F_{MSY} on the surplus production curve.

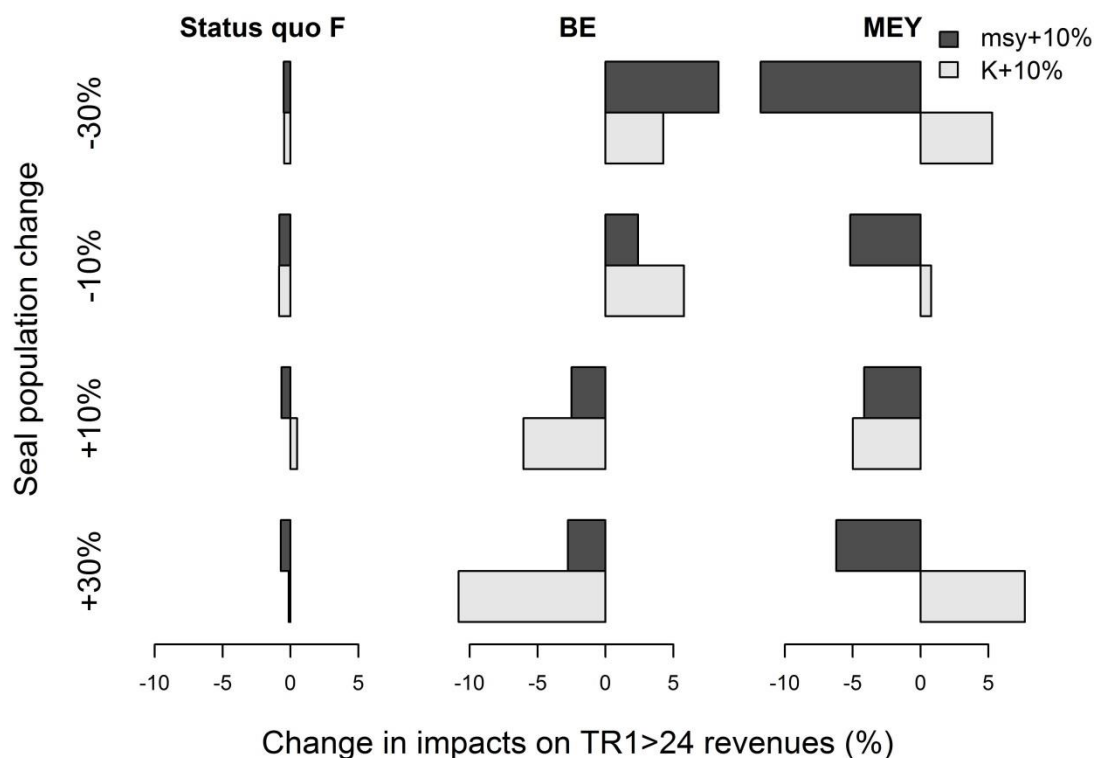


Figure 6.6: Change in grey seal impacts on TR1>24 revenues (%) for a +10% change in msy and K for all other species compared to the impacts with the initial Schaefer parameters.

6.3. Sensitivity around the assumption of constant seal predation rate

Although the variable seal predation rate (q) outputs from the state-space model were chosen to parameterise the simulation model for cod and haddock, a constant rate is considered by default within the models. Classical foraging theory considers that the ability of seals to catch fish would vary with fish biomass. This underlies the concept of functional response of a predator to the prey biomass where the weight of prey consumed varies with the prey abundance. This variation has different shapes according to Holling (1959). The type I assumes that the functional response is linear and proportional to the stock of prey. The type II functional response reflects the situation where the predation increases with the abundance of prey but is limited by predator satiation/saturation and its capacity to process food so the shape is

asymptotic. Finally, the type III functional response is close to the type II response except that the predator only consumes a small proportion of prey when they are present at low density and switch to another species which is more abundant. The curve has therefore an “S” shape.

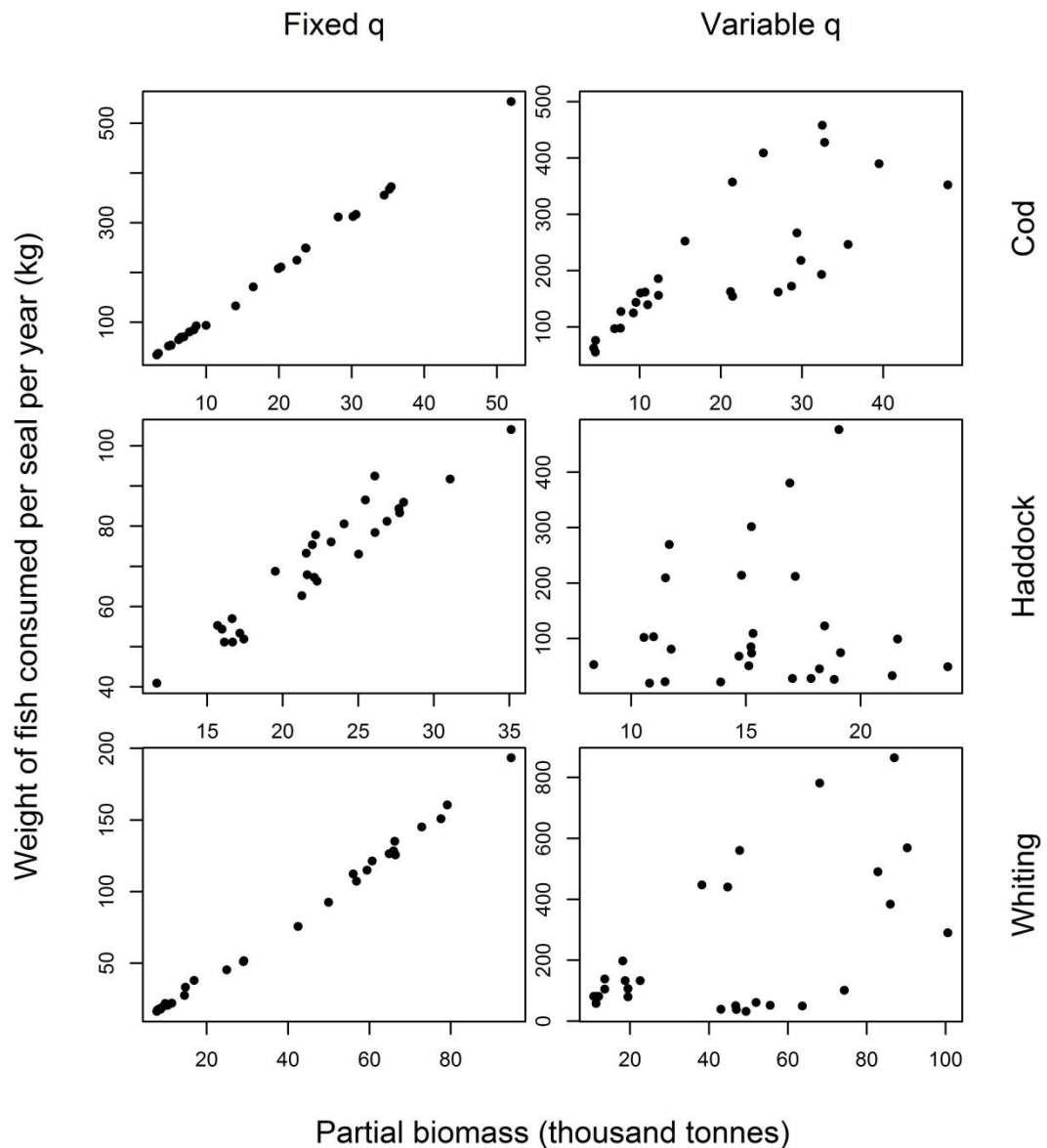


Figure 6.7: Comparison of the estimated functional response for a fixed and variable predation rate assumption for the three fish species of interest. The partial biomass corresponds to the biomass available to seals.

The functional response for the three species of interest was studied using the state-space outputs for the fixed and variable q simulations (Figure 6.7). As expected, in the

case of a fixed predation rate, the functional response is linear and would correspond to a Holling type I functional response. Indeed the seal predation rate is constant so there is a proportional relationship between the biomass of fish available and the weight of fish consumed. This assumption can be problematic at larger partial biomass (biomass available to seal predation) because the model predicts a constant increase in seal catches as long as the biomass increases. The functional response for a variable rate is unclear. Indeed a possible type II or III functional response seems to appear in the case of cod which would correspond to a seal predation rate which is a function of the cod partial biomass. However, for haddock and whiting, the dots are more spread and the relationship is less obvious.

The type II and III functional responses mean that q can varies with fish partial biomass. The Bayesian analysis was considering only two years of seal diet data and, as mentioned in Chapter 4, the outputs outside these years are highly uncertain. It is therefore extremely speculative to fit a type III response to the data which necessitates estimating three parameters.

A type II functional response was fitted to the variable seal predation rate and partial biomass data obtained from the state-space model using the Equation (6.1). This estimates the seal predation rate (q) as a function of fish partial biomass (PB) (Figure 6.8).

$$q_y = \frac{\chi}{1 + \chi\omega PB_y} \quad (6.1)$$

Where χ and ω are constants to be estimated and represent in foraging theory the rate of search (or attack rate) and the handling time respectively. The partial biomass is calculated as follows:

$$PB_y = \sum_a (N_{a,y} w_{a,y} sel_a) \quad (6.2)$$

Here the partial biomass is an estimate of the fish biomass available to the seals. It represents the total biomass discounted by size selectivity by seals.

Following Equation (6.1), the seal predation rate decreases with an increase in fish biomass. At low partial biomass seals spend more time searching for prey and less time is allocated to prey consumption.

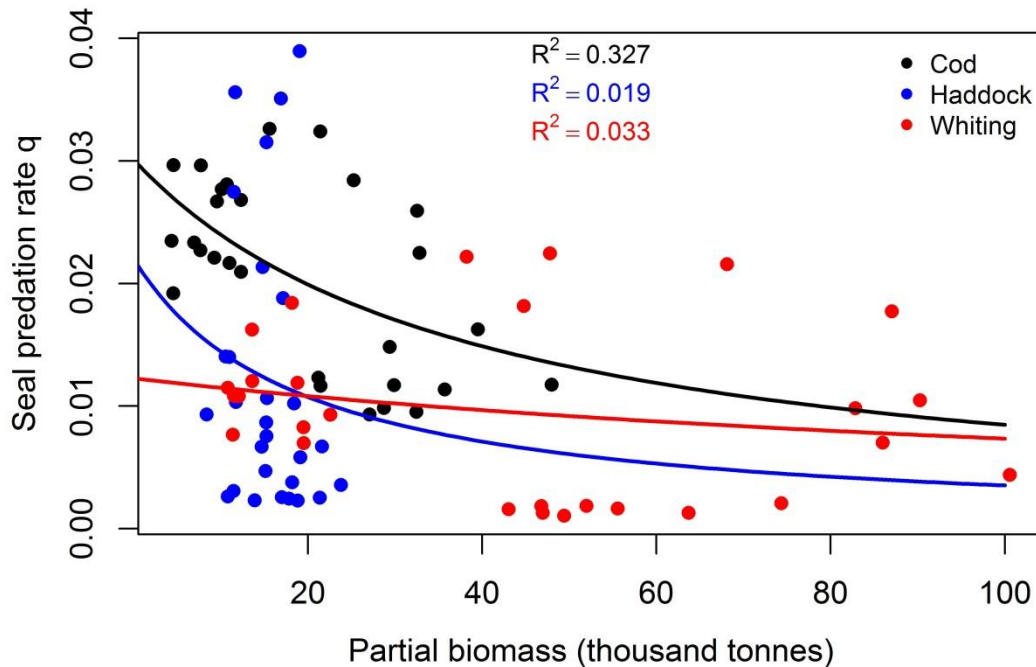


Figure 6.8: Fit of the type II functional response for cod, haddock and whiting where the seal predation rate varies with the partial biomass and corresponding coefficient of determination.

The coefficient of determination is calculated for each fit and the values of the parameters are given in Table 6.4. For cod, the R-squared is relatively high with 33% of the variability in q being explained by the type II functional response model. However this is not the case for haddock and whiting where the proportion of variance explained is very low. This means it is difficult to fit a useful seal functional response model to the haddock and whiting data and a fixed predation rate seems more reliable in the absence of information to support a more complicated model. This motivated the assumption of constant seal predation in the bioeconomic models. However, since earlier analysis shows that cod is a key stock in evaluating seal impacts and there is some evidence for a type II response, sensitivity to an alternative predation model is considered for this species.

To investigate this sensitivity, the results in Chapter 5 can be compared with what is obtained when a functional response of seals to cod biomass is assumed. To do so, simulations were run where q varies deterministically with cod partial biomass using Equations (6.1) and (6.2) and the estimates in Table 6.4. The fit being poor for haddock and whiting, the original seal predation rate is used and kept constant for these species.

Table 6.4: Estimated parameters for the functional response of seals to fish biomass. The corresponding standard errors are given in parenthesis.

Species	χ	ω
Cod	0.03008906 (± 0.00386)	0.8485748 (± 0.28609)
Haddock	0.0219914 (± 0.02755)	2.3811486 (± 3.94261)
Whiting	0.0122622 (± 0.00339)	0.5453473 (± 0.58314)

It is clear that considering a type II functional response of seals to cod biomass changes the estimates of cod SSB in the different equilibrium scenarios and for different changes in seal population (Figure 6.9). The biomass for haddock and whiting is unchanged compared to what was presented in Figure 5.4 with a constant predation rate scenario. This was expected for the “status quo F” simulation since the fishing mortality is constant; however it is surprising for the two dynamic scenarios. Indeed since the fleet can change their effort with a change in stock biomass to get to the dynamic equilibria, a change in haddock and whiting SSB can be expected. The absence of impact on the two stocks comes from the fact that the equilibrium fishing effort index per fleet between the functional response and the constant predation rate simulations are really close. This means that assuming a variable predation rate does not impact the estimates of fishing mortality at the BE and MEY and only impacts seal mortality on cod so the trend in cod SSB. The cod stock is therefore the stock the most impacted by considering a type II seal functional response.

In the “status quo F” scenario, considering a functional response increases the impacts on the cod stock compared to the constant q assumption. An increase in seal population induces a larger decrease in cod SSB and vice-versa. Considering a functional response in the BE scenario is mainly responsible for a decrease in cod biomass compared to the

estimates with a constant q assumption. A large increase in seal population (+30%) is responsible for the collapse of the cod stock in both scenarios. At the MEY, however, the estimated cod biomass is increased compared to the results assuming a constant predation rate, no matter the change in grey seal numbers. This is further evidence that cod is important in the maximisation of the net profit in VIa.

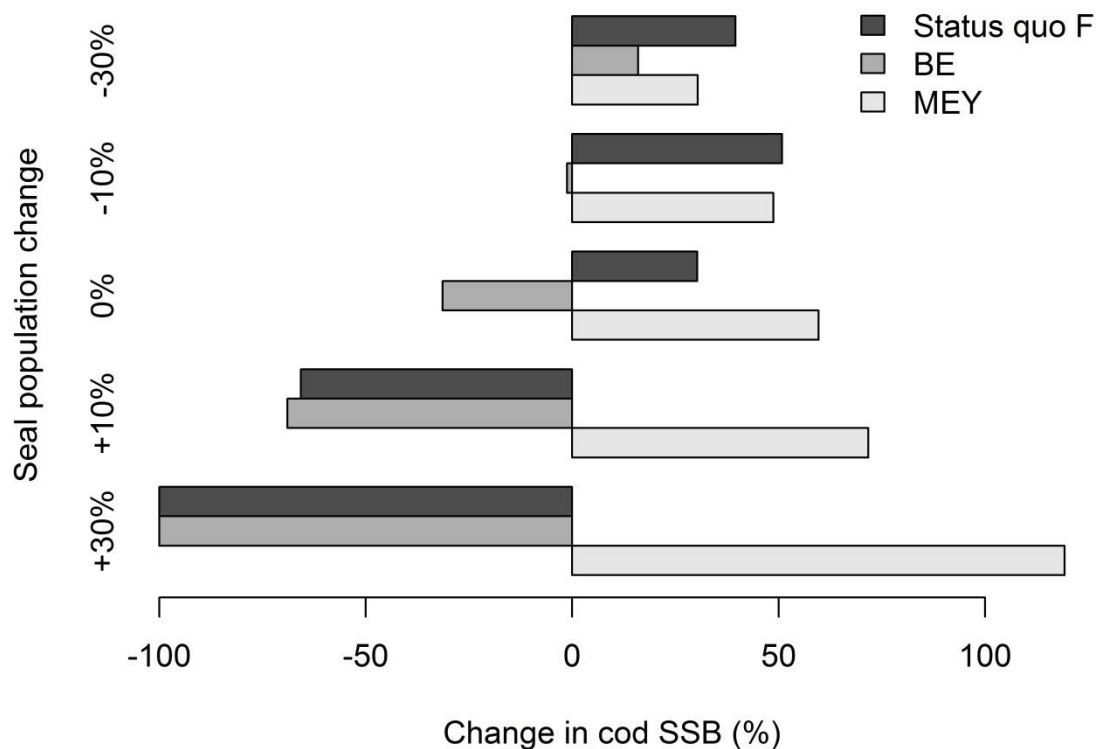


Figure 6.9: Change in average cod SSB (%) when a type II functional response of seals to cod biomass is assumed compared to the SSB estimated with the constant predation rate in the three equilibrium scenarios.

Consequently, the cod stock is highly sensitive to the seal predation rate assumption in all the scenarios. The cod SSB estimated with the constant q assumption is really close to the maximum observed SSB in the “status quo F” and BE scenarios and above maximum SSB at MEY. Considering a type II seal functional response induces an estimated stock that goes largely beyond the observed cod biomass when the seal population is decreased and no matter the change in seal numbers at the MEY. This also means that this model is more sensitive to the stock-recruitment assumptions.

The large increase in cod SSB can be explained by the value of the seal predation rate in the three scenarios since seal selectivity is constant (Figure 6.10). Indeed in the three

scenarios, q increases with the increase in seal population. This makes sense since an increase in seal numbers induces a decrease in the cod partial biomass and therefore an increase in q according to the Equation (6.1). When the seal predation rate value is below the constant q value (dashed line), the estimated equilibrium cod SSB is larger than what was estimated with the constant q assumption and vice-versa. The value of q at the MEY is much smaller than the constant q value and explains the large increase in the cod stock when a type II response is assumed.

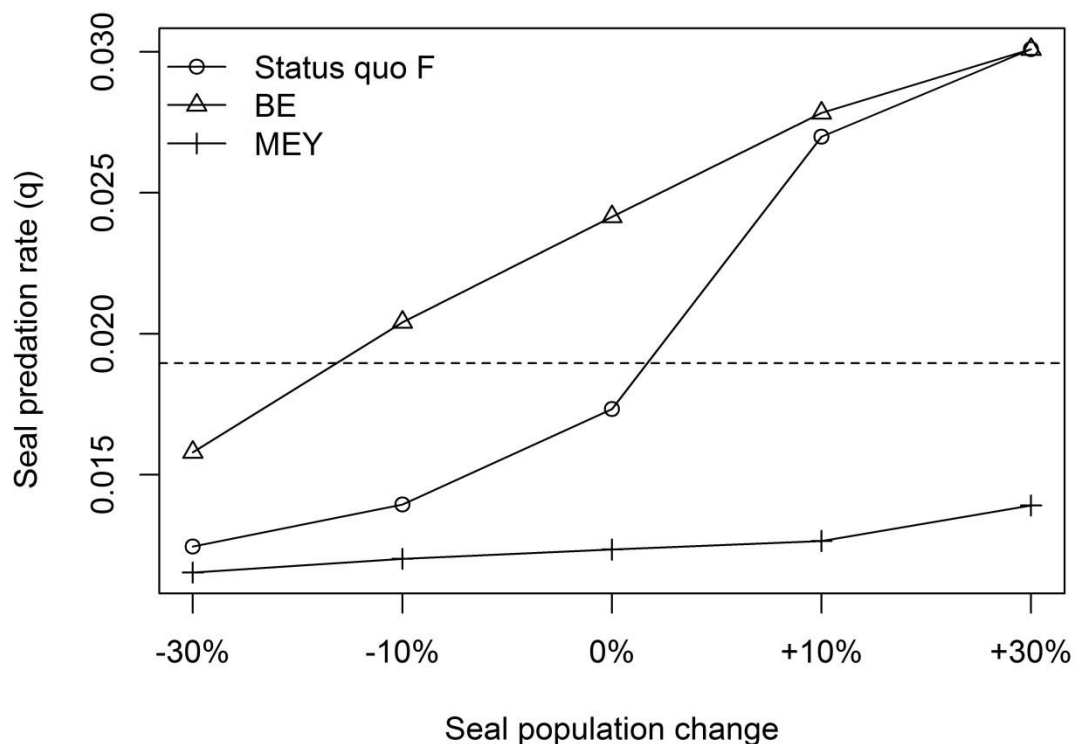


Figure 6.10: Change in seal predation rate (q) on cod with change in seal population when a type II functional response of seals to cod biomass is assumed in the three experimental scenarios. The horizontal dashed line corresponds to the value of q when it is assumed constant.

Consequently, considering a type II seal functional response to cod implies more severe changes in SSB than considering a constant predation rate. Also, the cod stock is more sensitive to an increase in grey seal population and can rapidly go to collapse in two of the scenarios.

The large differences in cod biomass when a functional response is considered compared to the results for a constant seal predation rate are expected to make large changes in the whitefish revenues compared to what was visible in Figure 5.5. That is

indeed the case in Figure 6.11 which shows changes in revenues of more than 60% for TR1>24 in the dynamic scenarios when seal population is changed by 30%.

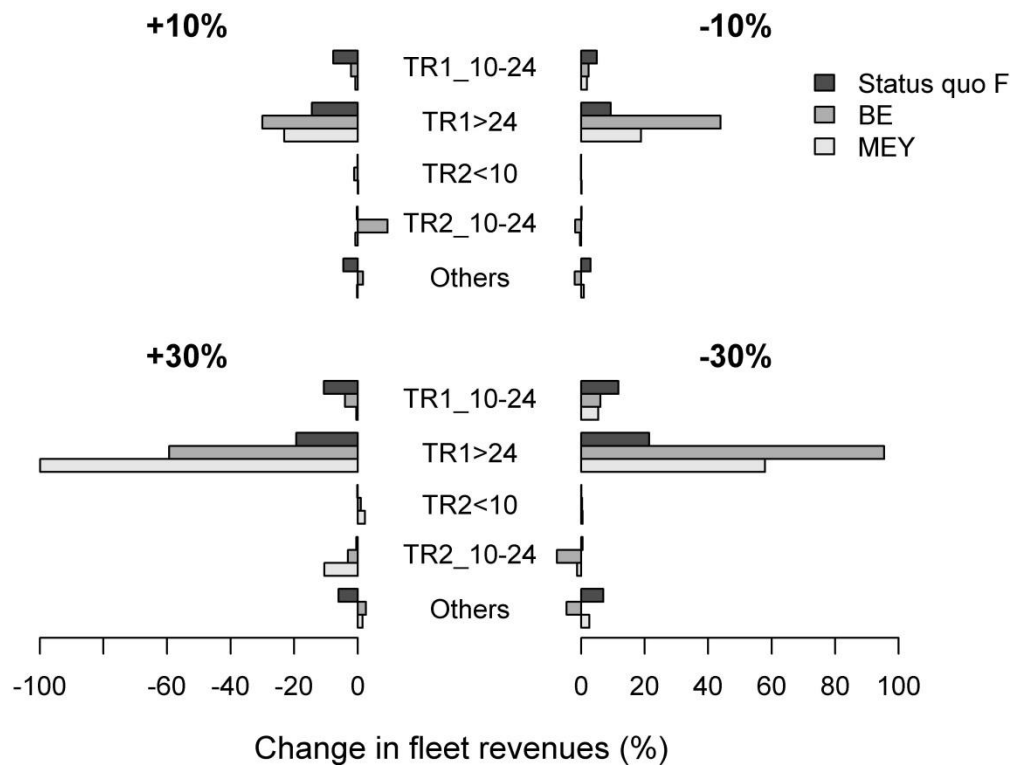


Figure 6.11: Change in fleet revenues (%) in the three different equilibrium scenarios for a small (10%) and large (30%) change in seal population when a type II functional response of seals to cod biomass is assumed.

Similarly to that observed for a constant seal predation rate scenario, the large whitefish trawlers, which land the largest quantity of cod, are the most impacted by grey seal predation but this time the magnitude of the change in revenues is larger. An increase in seal numbers of 30% leads to the elimination of TR1>24 at the MEY.

If the impacts on TR1>24 revenues when a functional response is assumed are compared to the impacts when a constant q is assumed, as expected, the impacts on the revenues are larger than what was observed before, and this is the case for all scenarios (Table 6.5). This means that the results are sensitive to the seal foraging model. Given the absence of a robust foraging model, the estimates of seal impacts on TR1>24 are subject to substantial uncertainty.

At the level of the entire fishery, grey seal predation impacts on revenues are slightly larger in the three scenarios when a functional response is considered (Table 6.6) but the magnitude of the change is small. This can be related to the small contribution of TR1>24 in the total fishing revenues. At the MEY, the change in impacts on the fishery net profit is minor indicating that the grey seal predation may alter the fishery performance but does not impact the net profit. This is certainly due to a parallel increase in fishing costs which balances the increase in revenues.

Table 6.5: Change in grey seal impacts on TR1>24 revenues (%) when a type II functional response of seals to cod biomass is assumed compared to the results obtained with the constant predation rate in the three equilibrium scenarios.

Scenario	-30%	-10%	+10%	+30%
Status quo F	+7	+5	+10	+9
BE	+55	+32	+15	+16
MEY	-2	0	+6	+63

Table 6.6: Change in the grey seal impacts on total fishery revenues and net profit (%) in the three different equilibrium scenarios when a type II functional response of seals to cod biomass is assumed.

Scenario	Type of change	-30%	-20%	-10%	10%	20%	30%
Status quo F	Change in revenues and net profit	+2.8	+2.5	+1.8	+3.7	+4	+3.2
BE	Change in revenues	+3.4	+3.2	+2.4	+1	+1.4	+0.7
MEY	Change in revenues	+0.7	+1.1	+0.4	+1	+2.2	+7.3
	Change in net profit	-0.5	+0.4	0	+0.1	-0.1	+1.2

In conclusion, the models are sensitive to the assumption of constant seal predation rate and the impacts of grey seal predation on the whitefish trawlers may be underestimated if the constant q assumption is unrealistic. This seems to concern mainly TR1>24 since this is the fleet that lands the largest quantity of cod in VIa. However, even if more realistic, assuming a functional response of seals to cod biomass leads to uncertain results due to high levels of estimated cod SSB.

6.4. Sensitivity analysis around the cost assumptions for the “Others” fleet

Because no cost data is available for the “Others” fleet, it has been chosen to consider this fleet has an externality in the dynamic scenarios; BE and MEY. This means the effort index for this fleet is constant and does not vary with its net profit. The fleet is considered at the BE at the beginning of the simulations so that the costs equal the average revenues at the status quo F and P . This assumption is made because the UK fleets are currently close to the break-even point (Seafish, Figure 3.6) and it is likely other fleets are in a similar state. However, this may not be the case in reality. Consequently, it is necessary to see if the dynamic models are sensitive to this assumption.

The BE and MEY scenarios are run allowing the fleet “Others” to vary its effort index at each iteration such as the other fleets. It means that the effort for this fleet is no longer constant and can vary with changes in fish stocks. This change is responsible for a modification of the equilibrium effort index per fleet at the status quo seal population, notably for TR1>24 and “Others” (Table 6.7). However, the total fishing revenues and net profit do not change much by allowing “Others” to vary its effort. Since TR1>24 is the most impacted fleet in both scenarios and is one of the fleet of interest, the change in grey seal predation impacts is considered for this fleet only (Table 6.8).

Table 6.7: Change in the equilibrium status quo P fleet effort index (%) when the “Others” fleet is allow to vary its effort compared to the estimated effort index when its effort is kept constant. The change in total fishing revenues and net profit is also given.

Scenario	TR1_10-24	TR1>24	TR2<10	TR2_10-24	Others	Revenues	Net profit
BE	+14	+45	-2	+50	-58	-4	0
MEY	0	+35	0	+1	-10	-1	+2

Grey seal impacts on TR1>24 revenues is sensitive to a small change in seal population but the difference is more important when the change in seal numbers is larger.

Overall, allowing the “Others” fleet to vary its effort despite the uncertainty around the cost function for this fleet induces a decrease in grey seal impacts on TR1>24.

Table 6.8: Change in grey seal impacts on TR1>24 revenues (%) when the “Others” fleet is allow to vary its effort compared to the results obtained when its effort is kept constant in the two dynamic scenarios.

Scenario	-30%	-10%	+10%	+30%
BE	-5	3	-8	-19
MEY	-24	-9	-10	-15

Consequently, the assumption of constant effort for “Others” may overestimate grey seal impacts on TR1>24. Because this fleet accounts for a small part of the total fishing revenues at the equilibrium in the dynamic scenarios, the impact on the fishery revenues and net profit is minor.

6.5. Summary

This chapter investigated the sensitivity around the different assumptions taken in this study and how this impacts the bioeconomic results presented in Chapter 5. A summary of the sensitivity for the most impacted fleet, TR1>24, is presented in Table 6.9. Different conclusions can be drawn from this analysis:

- The “status quo F” model is robust to all the assumptions except the assumption of constant seal predation rate for which the impact on TR1>24 revenues can be underestimated due to a decrease in q and an increase in the cod biomass when a functional response of seals to cod is considered.
- The dynamic models, BE and MEY, are sensitive to all the assumptions tested in the analysis. The largest sensitivity is for the foraging model assumption for which considering a constant seal predation rate may underestimate seal impacts, but also for the assumption of constant effort for “Others” where the impacts could be overestimated by considering this fleet as an externality.

Table 6.9: Sensitivity of the three bioeconomic scenarios expressed as the change in seal impacts on TR1>24 revenues (%) for a +10% change in seal population compared to the initial simulation results.

Sensitivity to the	Change considered	Status quo F	BE	MEY
Stock-recruitment parameters	$\alpha + 10\%$	-0.5	-8.9	-4.1
	$\beta + 10\%$	-0.6	+5.5	+3.0
Ricker assumption on stock-recruitment	Beverton-Holt	+0.2	-5.2	-3.6
	Hockey-stick	+0.1	-3.6	-0.1
Schaefer parameters	$msy + 10\%$	-0.7	-2.5	-4.2
	$K + 10\%$	+0.5	-6.0	-5.0
Constant seal predation rate	Type II seal functional response to cod biomass	+10.4	+15.0	+5.6
Constant effort for "Others"	Variable effort	None	-7.8	-9.6

The dynamic models for which fleet efforts can change are the most sensitive. It seems that this sensitivity occurs when the fleets can change their effort index independently from one another since some investigative work showed that changing the effort index of all the fleets by the same amount does not make the MEY model sensitive.

The results assuming a type II functional response are highly uncertain. Indeed the decrease in q in the models induces a large cod biomass which goes beyond the bounds of observed data. Yet, the models are sensitive to the choice of stock-recruitment relationship for high SSB values. Also, the functional response is fitted using the results from the state-space model. However, only two years of grey seal diet data exist and this increases the uncertainty around the fitted curve. The assumption of fixed seal predation rate may therefore be more robust than the type II simulations.

The scenarios are sensitive to the assumption of constant effort for "Others". However, the sensitivity run was done assuming the fleet starts the simulation at the break-even point. The fleet is currently operating so positive net profits, even small, are expected. The results of the sensitivity analysis may be not only due to the assumption of constant effort but also on the assumption of dissipated net profit at the start of the

runs. Nevertheless, since assuming a constant effort index may overestimate grey seal impacts, the bioeconomic results may be seen as worst case scenario.

Even if the models are sensitive to certain assumptions, this affects mainly the most impacted fleet, TR1>24, and the impact for the total fishery is minimal. Also, the sensitivity of the models increases with the increase in the change in seal numbers. This comes from the fact that this corresponds to large changes in initial parameters which were estimated at the current state of the VIa fishery. Important changes in grey seal population are also responsible for larger changes in fish stocks and larger sensitivity around the stock-recruitment curves. The sensitivity is relatively minor for changes in seal population of $\pm 10\%$. These results can be considered as more robust than the results for $\pm 30\%$ change in seal numbers.

Chapter 7

Discussion and conclusions

7.1. Grey seal impacts on fisheries

The increase in grey seal population in the North Atlantic (Bowen et al., 2003; Thomas et al., 2011; Thomas, 2014) and the decrease in groundfish landings since the mid-1900s (Christensen et al., 2003) are responsible for a rising controversy between fishers and conservationists. Around the UK, grey seals are protected under the Conservation of Seals Act since 1970 (HM Government, 1970) and more recently under the Marine Act (Scottish Parliament, 2010) and the public is very reluctant to cull seals (Minister of Supply and Services Canada, 1986; Lambert, 2002). Among the scientific community the opinions are also divided. While it is broadly accepted that seals are responsible for the non-recovery of the demersal stocks on the east coast of Canada (Mohn and Bowen, 1996; Chouinard et al., 2005; Trzcinski et al., 2006), the situation around the UK is less clear. Some papers suggest a similar effect on cod (Cook et al., 2015; Cook and Trijoulet, 2016) but others take the conservationists' view (Boyd and Hammond, 2010). It is currently difficult to determine the importance of grey seal predation in the decline of the fish stocks. Despite this, the fishers still seek the return to seal regulation (Lavigne, 2003; Read, 2008) and this emphasizes the need for further investigation.

Studying the impact of seal predation on the fish stocks and comparing the weight of fish consumed with fishing landings, which is often considered in the literature (Bjørge et al., 2002; Lundström, 2012), is not sufficient to conclude on seal impacts on fisheries. Because fishing is a commercial activity, it is necessary to consider the economic

impact of seal predation. However, despite a large literature on the economic impacts of depredation (Bjørge et al., 1981; Moore, 2003; Kauppinen et al., 2005; Königson et al., 2005; Jounela et al., 2006; Butler et al., 2011), i.e. seal damage to the fishing gears and fish, the impact of seal predation is hardly examined and there is to our knowledge no paper looking at the bioeconomic impacts of grey seal predation on fisheries. This study modelling the bioeconomic of seal predation on the West of Scotland demersal fisheries within multifleet fishery models is consequently an important contribution to the literature in the field. These models are applicable to any fishery as long as age-structured data is available for the fish species of interest.

The study considered grey seal predation mortality on the three main traditional demersal species in the West of Scotland mixed fishery, cod, haddock and whiting, whose landings have decreased since the mid-1900s (ICES, 2011) while the seal population has increased (Thomas, 2014). While grey seal predation on cod had already been estimated in the West of Scotland (Holmes, 2008; Holmes and Fryer, 2011; Cook et al., 2015; Cook and Trijoulet, 2016), the Baltic Sea (Gårdmark et al., 2012) and the eastern Canada (Mohn and Bowen, 1996; Trzcinski et al., 2006; O'Boyle and Sinclair, 2012), this study presented the first estimates for haddock and whiting, species which represent also an essential part of grey seal diet in the Division VIa (Hammond et al., 2006; Harris, 2007).

Grey seal predation mortality was estimated through Bayesian parameter estimation using a common single species state-space stock assessment model which, unlike ICES stock assessments, explicitly accounts for grey seal predation. The impacts of grey seal predation on fish stocks and fleet revenues were then studied using these predation mortality estimates within a bioeconomic simulation model. Different bioeconomic scenarios were tested and this enabled a comparison of the impacts for different fisheries configurations. Applying a scaling factor on seal predation enabled simulating an increase or decrease in seal population which could correspond to population growth or decline due to diseases, human interventions or predator removal. It means that seal dynamics (Flaaten and Stollery, 1996; Thompson et al., 2005) is not modelled as a function of prey biomass. Grey seals are considered as generalist predators (Hammond and Grellier, 2006; Brown et al., 2012; Gosch et al., 2014) that can switch from one species to another if the prey abundance is low (Smout et al., 2013).

Consequently, the number of seals should not be impacted by fish biomass. The grey seal population has increased between 1985 and 2002 (Thomas, 2014) and seal consumption levels of cod in 1985 and 2002 are similar (Hammond et al., 2006; Harris, 2007) despite a significant decline in the cod stock (ICES, 2013b). This is evidence that grey seal population does not vary directly with cod biomass. Also, even if the three species of interest represent 23% of grey seal diet in 2002 (Harris, 2007), the main prey is sandeel, a species of low commercial value which is not modelled in the study. Applying a scaling factor to the grey seal mortality to simulate a change in grey seal population independent of the whitefish biomass was consequently considered as a reasonable option.

The results at the current rate of fishing and for the current seal population level estimate an increase in the three stocks of interest at the different equilibria showing a possible recovery of the stocks. For cod, this is in contradiction with Cook et al. (2015) who argue the unlikely recovery of cod in the near future. This may come from the fact that in Cook et al. (2015) the analysis is done until 2005 while this study estimates a small increase in cod SSB from 2005 onwards. This is supported by Cook and Trijoulet (2016) who used recent values of fishing mortality and concluded on a possible recovery of the stock which remains, however, fragile to small increases in total mortality.

Seal predation mortality is large on cod but smaller than the other mortalities (fishing and natural mortality) for haddock and whiting. This is surprising because haddock represents the same proportion as cod in grey seal diet (10% in 2002) and whiting is one of the fish the most numerous in the diet even if in terms of weight it represents a proportion of only 3% (Harris, 2007). The sum of cod natural mortality and seal predation mortality is larger than the current natural mortality in the ICES VIa cod assessment for which seal predation is subsumed within the natural mortality (ICES, 2014c), no matter the assumption on grey seal predation rate. This means that cod natural mortality may be currently underestimated and this would affect fisheries management and notably the estimation of management reference points. This is confirmed by a parallel study (Appendix H) which shows that considering seal predation in single species stock assessments can affect the perception of the stocks and impacts the values of management reference points such as fishing mortality at

maximum sustainable yield. The results present large confidence intervals but the median measurement is clearly affected by the consideration of grey seals in the assessments even for haddock and whiting for which the seal predation mortality is low. While the importance of grey seal predation on the recovery of the cod stock was already studied in Cook and Trijoulet (2016), this new study highlights how the state-space model can support fisheries management in the West of Scotland.

Previous average grey seal predation estimates in the West of Scotland (Holmes and Fryer, 2011) and in Canada (Trzcinski et al., 2006) are of a similar order of magnitude to this study (Table 7.1). The estimates of this study are slightly larger than the Canadian ones but the assumption in the models were different. Trzcinski et al. (2006) calculated grey seal predation mortality based on seal energetic requirements. Cod represented less than 5% of the Canadian grey seal diet in 2002 while it represents 10% in the West of Scotland (Harris, 2007). The growth rate of cod in Canada is slower so comparing the average mortality over ages 1 to 5 will refer to a different size range. Unlike recent studies in the North Atlantic where seal predation was considered as insignificant compared to the total mortality on fish stocks (Boyd and Hammond, 2010; MacKenzie et al., 2011; Alexander et al., 2014) these values seem of sufficient magnitude to matter in evaluating stock status for fishery management.

Table 7.1: Average grey seal predation mortality estimates on cod (between ages 1 and 5) compared with the literature. The estimates correspond to the results obtained for both seal predation rate scenarios.

Year	State-space model	Holmes and Fryer (2011)	Trzcinski et al. (2006)
1985	0.12-0.2	0.22-0.23	0.09
2002	0.28-0.47	0.27-0.32	0.32

Grey seal predation mortality at the age of highest selectivity in the eastern Canada was recently estimated to be around 0.25 in 2002 (O'Boyle and Sinclair, 2012). In this study, the estimate at age 2 is 0.82 and was 0.71-0.83 in Holmes and Fryer (2011). However, O'Boyle and Sinclair (2012) assumed an asymptotic seal selectivity with the maximum reached from age 2 while here selectivity has a domed shape and decreases after age 2.

Mohn and Bowen (1996) estimated a seal predation mortality of 0.08 at maximum selectivity (age 1) in 1985. The 1985 estimate is 0.24 at age 2 in this study.

The estimates of seal predation mortality for haddock and whiting are much lower than those for cod. While it may be indicative of a species preference, it may in part be an effect of size. Haddock and whiting have much lower size at age and the highest predation mortality is on the oldest fish (ages 6-7) while for cod it reaches a maximum at ages 2-3. These ages correspond to a similar mean length where a two year old cod has a mean length of 45.8 cm while six year old haddock and whiting have mean lengths of 43.4 cm and 38.5 cm respectively. It is suggestive of a size preference by seals since fish below and above this size have lower mortality rates, although for large fish this is only discernible in cod. The consequence of the apparent size preference is that, for cod, seals remove smaller fish before the size of maximum selection by the fishery hence removing them before the fishery leading to sequential competition. For haddock and whiting size selection increases along with the fishery and is closer to “scramble” competition.

An increase in grey seal predation induced a clear decrease in the cod and whiting stocks, the decline being more important for cod certainly due to the larger grey seal predation mortality for this species. However, changes in grey seal predation, even severe, have no clear impact on the haddock biomass and this, despite the fact that the weight of haddock consumed is the largest compared to the other species (Harris, 2007) and the estimates of seal predation are similar than those for whiting. This seems to emphasize the small impact of grey seal predation on the haddock stock in the West of Scotland and is confirmed by the stock assessment analysis (Appendix H) which shows that a change in grey seal predation does not affect the values of management reference points. This could be due to the better condition of the haddock stock with an estimated SSB of 33,663 tonnes in 2012 while cod and whiting biomasses are estimated to be 1,835 and 8,028 tonnes respectively (ICES, 2013b). This could make cod and whiting more sensitive to grey seal predation or large values of fishing mortality. This can also come from a difference in the stock-recruitment. However, recruitment for whiting is more variable than for haddock. A difference in natural mortality values for the three species seems to be a more realistic reason. Indeed, the values of natural mortality on haddock are the smallest and it is the species presenting

therefore the smallest total mortality. Consequently it is also the largest fish stock at the equilibrium. Despite presenting similar values of average fishing and seal predation mortalities, whiting is subject to a larger natural mortality than haddock and this may explain the difference of impacts between the two species. These results for haddock demonstrate the limits of comparing seal consumption with fishing landings to assess the impact of grey seal predation. Indeed, while the weight of haddock consumed by seals was 7,952 tonnes in 2002; 7,115 tonnes of haddock were landed by the fishery. These figures alone may lead to the conclusion of a large impact of grey seal predation on haddock catches. However, this study demonstrates the absence of significant impacts on this species.

A recent study considering a multispecies Ecopath with Ecosim model concluded that grey seals are not responsible for the recent decline (1985-2014) in cod, haddock and whiting in the West of Scotland (Alexander et al., 2014). However, this does not suggest grey seal predation has no impact on the stocks currently. Indeed, the study showed that reducing the grey seal population to zero in VIa induces a slight increase in the three stocks and mainly in cod. This seems consistent with the results of this present study for which the impacts are the largest on cod. However, the impacts are more important in the current study since decreasing seal population by 30% is enough to induce large impacts on the cod stock. This difference may be explained by the fact that the number of seals in Alexander et al. (2014) is limited to the 1987 level while the population has increased by 23% since then (Thomas, 2013). Even if the study considered two classes of fish (mature and immature) it does not take into account seal selectivity at age from the seal diet data. This study may be therefore more reliable regarding the consideration of grey seal diet. However, the study of Alexander et al. (2014) considers trophic interactions which are not considered in our study and these may change the directions of the grey seal impacts if seals consume also the predators of the species of interest (Yodzis, 2001).

Cod is the key stock in evaluating the impacts of seal predation on the demersal fishery. The large grey seal predation mortality on the stock and its poor condition make it the fish the most impacted by grey seal predation. This seems to confirm the conclusions of Cook et al. (2015) and Cook and Trijoulet (2016) about the high estimated seal predation on cod. This similarity is expected since the studies used very similar state-

space models but this study shows also that cod recovery is possible at the current seal and fishing mortalities and that the impacts are small on the two other species of interest, comparison that was not possible before. However this result is in contradiction with a previous study suggesting that grey seal predation on cod is not substantial enough to be included in VIa cod assessment (Holmes, 2008). However, the argument of this latter study is that considering seal predation on cod makes little difference to the estimated SSB in the final years (2005-2007) and the model is too uncertain to conclude on the incorporation of seals in stock assessments. Also, the natural mortality on cod in this paper is assumed to be 0.1 or 0.2. Our models assumed a mortality that varies by age following Lorenzen (1996) and this results in different partition of the total mortality into the three types of mortality. The paper points out however that it makes a difference in estimated fishing mortality, as demonstrated in this study, and that may impact management reference points (Appendix H). Similarly to Holmes (2008), our study also highlights the uncertainty around the results. Even if considering grey seals in cod stock assessment changes the perception of the stock and the values of management reference points, the large confidence intervals estimated around the reference points impede the conclusion on the importance of considering grey seal predation in cod stock assessment.

There seems to be evidence that preserving the cod stock would help maximising the fishery net profit in the long-run since the cod biomass is the largest in the MEY scenario. It is therefore important to focus on cod management in VIa to achieve larger profits. Even if grey seal predation impacts on fleet revenues are moderate when the cod stock recovers, they are close to zero when the stock collapses. This does not mean grey seal impact on cod is substantial but rather that its bioeconomic impact on haddock and whiting is minor. This is unexpected given the proportion of both species in grey seal diet (Harris, 2007). This seems likely to be due to the small predation mortality on these species. This could also be due to the vulnerability of cod to seal predation given the state of the stock. However, the status quo fishing mortality results show a recovery of the cod stock even for large increases in grey seal population and this may contradict the poor condition assumption. Cod presents however low values of recruitment compared to haddock and whiting. Cook et al. (2015) demonstrated that grey seal predation on cod in VIa may threaten the recovery of the stock in the long-run. Cook and Trijoulet (2016) concluded that cod recovery in VIa is fragile and

sensitive to an increase in both fishing and seal predation mortality. Likewise, on the Canadian east coast, grey seals are believed to contribute to the non-recovery of the stocks despite the closure of the fishery in 1993 (Chouinard et al., 2005; Trzcinski et al., 2006; O'Boyle and Sinclair, 2012). The importance of cod in grey seal impacts can also be due to a difference in selectivity pattern for seals and fishing vessels. Indeed, grey seals predate on younger cod and may reduce the portion of older cod available for fishing vessels the following years. Preventing cod collapse may be the most important management goal to focus on in the West of Scotland since a change in grey seal numbers would not bring any benefit to the fishery if the cod stock collapses.

Grey seal impacts are unequal between the fleets with some being almost not impacted such as the *Nephrops* trawlers, which land whitefish as bycatch, and others showing large changes in revenues such as the vessels targeting cod, haddock and whiting (TR1). A substantial change in grey seal predation could induce a drastic change in the whitefish trawlers' revenues but these changes are relatively small when aggregated at the fishery level. The biological impacts of seals on the fish stocks are therefore potentially more important than the economic ones. For all scenarios, the fleet of large whitefish trawlers (TR1>24), which currently lands the largest quantity of cod in VIa, is the fleet the most affected by a change in grey seal population. This fleet is consequently the key to understand seal effects on the fishery.

Grey seal impacts differ depending on the scenario with larger impacts in the dynamic scenarios (BE and MEY) but the sensitivity of the models to the input parameters increases for these models, and this brings greater uncertainty to the results. The decrease in effort index at the BE and MEY may also seem very large for the bigger trawlers. The estimated large values of cod SSB in the MEY scenario increases the uncertainty around seal impacts due to the high uncertainty around the recruitment estimates beyond the bounds of observed data. The stock-recruitment relationship could therefore be important in evaluating seal impacts in the dynamic scenarios.

The MEY scenario presents more regulations than the extreme unregulated open-access and overall, grey seal impacts are larger at the MEY. It can be therefore argued that if seal reduction can slightly increase the fishery revenues, its success may be improved by fisheries regulations. This demonstrates the importance of fisheries

management and its effect on the fish stocks (Clark, 2006; Anderson and Seijo, 2011; Chakraborty and Kar, 2012; Hutniczak, 2012; Cissé et al., 2013).

In the case of multifleet fisheries models, the MEY scenario corresponds to the conventional MEY equilibrium where all fleets can vary their effort independently under a specific constraint in effort. However, the maximisation can advantage certain fleets at the expense of the others as it is observed in the literature (Brasao et al., 2000; Cissé et al., 2013; Guillen et al., 2013). Indeed since it is the sum of the fleet net profits which is maximised, theoretically, it may be more beneficial to decrease the effort of the least profitable fleets and to allocate the maximum level of fishing to the most profitable ones. Even if theoretically correct, this scenario may seem unrealistic from a management point of view since there must be clear policy reasons to ask some vessels to reduce their effort or stop fishing for fisheries management purposes. This illustrates the difficulty to choose the best management option in fisheries regulations. This mainly depends on the goal that managers want to reach. If the fishery is open-access the effort and the revenues are maximised (Armstrong and Skonhøft, 2006; Clark, 2006). If the fishery is at the MEY, the net profit is maximised but this may disadvantage fleets with the highest costs ($TR_{1>24}$ in this study) (Cissé et al., 2013; Guillen et al., 2013). While the net profits are not maximised, the “status quo F” simulation shows only positive profits but a larger effort than MEY which may be detrimental for the stocks in the long-run (Brasao et al., 2000; Hutniczak, 2012). The MEY scenario with a reduction in the fishing mortality of the large whitefish trawlers may be more favourable to the cod stock than the current fishing mortality in the West of Scotland but will decrease $TR_{1>24}$ revenues. It may be therefore difficult to implement in the reality.

The fact that grey seal population has stabilized in the West of Scotland in the past ten years (Thomas, 2014), the low probability of having a large decline in seal population (except if due to large scale epidemic events) and the increase in uncertainty for large changes in seal numbers highlight the use of small changes in grey seal predation in the models as the best representation of possible changes in seal population (i.e. $\pm 10\%$ scenarios or $\pm 3,204$ individuals). A realistic change in grey seal population of $\pm 10\%$ did not show substantial impacts on fleet revenues for all scenarios. The impacts are increased by the consideration of a seal functional response to cod biomass but the

uncertainty of the results is also amplified. Indeed, the functional response is fitted from the state-space model outputs which were estimated with only two years of seal diet data (1985 and 2002). It is clear that this may not be enough to fit a realistic functional response curve (Matthiopoulos et al., 2003; Middlemas et al., 2006; Smout et al., 2014). The assumption of constant seal predation rate presents therefore results which may be more reliable but this assumption may underestimate the impact of seal predation at low fish biomass. This represents the situation of interest since the stocks are currently at their lowest estimated levels. However, both assumptions do not take into account the switching behaviour of seals that may occur at low biomass. To model this, a type III functional response is necessary (Smout et al., 2014) and this would reduce the impact of seals on the stocks when the biomass is low. Nevertheless, this relationship necessitates the estimation of a third parameter compared to the type II response and the paucity of seal diet data prevents its estimation.

There is reason to believe the BE scenario is the dynamic scenario closest to reality. Indeed even if restricted entry exists in the West of Scotland fishery, it was effectively closed after the bioeconomic equilibrium was reached and the current net profit for the fleets is relatively small (Seafish). The current fishery configuration is therefore close to the BE. The comparison of the dynamic models showed a slightly smaller impact of seal predation on the total fishery revenues when the fishery is unregulated (open-access). This stresses that, with the current fishery structure in VIa, the bioeconomic impact of grey seal predation may be minor.

The simulation model is not a complete fisheries model so management conclusions cannot be drawn with precision from this model. However, comparison of seal impacts in the different simulation scenarios enables to have some insights into the consequences for management in the area. According to the results of the model, the current VIa fisheries are not maximising their current net profit and a reduction in the fleet effort is necessary to reach this goal. From the study, it is clear that cod is the key species for management in the West of Scotland and needs to be carefully managed to prevent its collapse because it is the fish the most impacted by grey seal predation but also because it supports high fishing revenues in the area, notably for the whitefish trawlers. Also the impact of seal predation increases with the consideration of fisheries

regulations within the model (MEY vs. BE) which may be evidence that a regulated fisheries may be more vulnerable to seal predation because bringing larger net profits.

There exist to our knowledge, no paper estimating grey seal predation impacts on fishing revenues. It is consequently not possible to compare the results to direct values in the literature. Flaaten and Stollery (1996), however, estimated the cost of Minke whale predation in the North Atlantic. They concluded that a 10% increase in the number of whales would cost \$19 million to the Atlantic fisheries so \$219 per whale. In this study a 10% increase in grey seal population in the West of Scotland would cost around 10% of that value to the demersal fishery but the cost per seal is larger. However, the difference in fisheries and sea mammal species makes the comparison between both studies difficult.

Depredation impacts have already been quantified and even if they do not represent the same measure it could be interesting to compare the costs of depredation with the cost of predation. Bjørge et al. (1981) estimated a cost of depredation due to grey seals in Norway of maximum £3,300 per vessel and an average cost of £200-300. A 10% increase in grey seal population in VIa costs can cost more than the maximum depredation cost estimated in the Norwegian fishery. In the Moray Firth, harbour and grey seal depredation impacts on the salmon fisheries can cost more than £30,000 per year (Butler et al., 2011). With 2,028 seals in the Moray Firth in 2011 (Duck and Morris, 2013) this would correspond to a cost of £15 per seal. The cost of predation in the West of Scotland is estimated between £434 and £495 per seal which is much larger. Of course this is an over-simplification because not all the seals present in the Moray Firth are responsible for depredation impacts in the salmon fishery and this could be easily due to “problem” individuals as it is often observed at the netting stations (Bosetti and Pearce, 2003; Lehtonen and Suuronen, 2010; Graham et al., 2011; Konigson et al., 2013; Harris et al., 2014). The cost per seal estimated for the salmon fisheries is therefore certainly underestimated. The Cornish fishery is estimated to lose £100,000 per year due to grey seal depredation impacts (Bosetti and Pearce, 2003). The seal population counting around 350-400 individuals in this area, this represented a cost of £250-286 per seal. This is still smaller than the costs estimated in this study. This may be evidence that grey seal predation impacts may be larger than depredation impacts. However, the study presents results that are more qualitative than quantitative so this

should be considered just as an indication. Also, the results may not be directly comparable with other fisheries and areas.

The study does not take into account the benefit of ecotourism activities. The cost of seal predation could be compared to the benefit of grey seal presence in the West of Scotland. Grey seals could attract tourists who would come specially to see wildlife on the Scottish coast and they would bring income to other tourist attractions such as hotels or restaurants. The best way to estimate the benefit of grey seals in VIa is to study the benefits of whale-watching activities. Even, if not entirely dedicated to seal-watching, grey seals are the third most popular wildlife attraction in Scotland after cetaceans and seabirds (Woods-Ballard et al., 2003). Whale-watching represents currently \$1 billion of incomes in the world (Fennell, 2014) whose \$133 million are spent around the Atlantic islands (Hoyt, 2005). In Scotland, the gains from tourism reach £2.5 billion per year and in rural areas whale-watching can represent 12% of these incomes (Woods-Ballard et al., 2003). In the West of Scotland, tourism gains from whale-watching have been estimated around £1.8 million per year and the indirect incomes from other tourism attractions during the touristic trip can reach £7.8 million per year (Warburton et al., 2001). It has been around ten years that grey seal population has stabilized in VIa (Thomas, 2014). This means that grey seal predation pressure may not increase in the short-term. It can be consequently argued that even if grey seals represent only one portion of the £1.8 million that were estimated in 2001, grey seal presence may be more beneficial than harmful to the Scottish industry.

It is also important to keep in mind, that if fishers may be impacted by seals the contrary is also true. The impact of fisheries on marine mammals is used by conservationists to highlight the negative impact that fisheries also have on marine mammals. Fishers compete with seals for the same resources (Harwood, 1984; DeMaster et al., 2001; Furness, 2002). Also, the legal shooting of seals in many places in the North Atlantic may influence the growth rate of grey seal population. The population of harbour seals in the UK, for instance, has been severely impacted by previous culling and virus infection and seems to have not completely recovered (Thompson et al., 2005). Furthermore, grey seals can be victim of incidental catches in fishing nets (Read, 2008). By stealing fish from the nets and foraging around trap nets, grey seals are vulnerable to accidental captures (Morizur et al., 1999). Also, the

restoration of management measures such as human interventions could have a negative impact on tourism and conservation economics (Parsons, 2003). There are therefore many aspects to consider in planning management strategies and governments are often confronted with the situation where people demand the removal of a protected population (grey seals) to ensure the recovery of an endangered population (fish outside biological limits) (Sinclair et al., 1998; Courchamp et al., 2003). Further research needs to be done to inform managers with the importance of the impacts in both directions to lead to sustainable fisheries management.

7.2. Main conclusions

The state-space model is important for comparison with current single species assessment in VIa. It shows that considering seal predation in the assessments changes the perception of the three stocks and affects management reference points even for whiting where seal predation mortality is low. This may be highly important since these assessments are used to inform fisheries management. However, the uncertainty around the estimates is large. Grey seal predation costs can be large at individual level compared to depredation impacts but represent a small part of the total fishery revenues (often less than 2% for a change of $\pm 3,200$ seals). Seal predation is therefore not important at the fishery level but some fleets are more sensitive than others. Cod and the large whitefish trawlers ($TR1 > 24$) are crucial in understanding grey seal impacts and are likely to be mainly affected by a reduction in seal population. However, the efficiency of marine mammal culls has never been proven (Minister of Supply and Services Canada, 1986; Yodzis, 2001; Morissette et al., 2012; Bowen and Lidgard, 2013) and seal reduction has a cost. Trade of seal products is banned in Europe (European Commission, 1983; 1985; 1989) so no benefit is possible from the seal carcasses. Few seals are already shot each year by licensed fishers and are also victims of fishing bycatch (Morizur et al., 1999). Grey seal presence brings also incomes to the ecotourism industry. A simple cost-benefit comparison seems to highlight that seal reduction may not be beneficial in the West of Scotland. However, the study does not take into account seal impacts on small local fisheries which may be more affected by

grey seal predation (Perring, 2001). This needs to be studied in more detail to be fully understood.

7.3. Limitations and future directions

This study made the assumption that the fish population is homogenous and equally available to seals and fishers. This is obviously an over-simplification and is certainly not realistic. Indeed, the trawlers may not fish in the same areas as grey seals so seals may predate on fish not directly available to fishers. The grey seal breeding colony is notably close to a rocky untrawlable shelf (Marine Environmental Mapping Programme, 2015) which may mean seals forage in areas away from the fishery. However, the absence of overlap between fishing and foraging zones does not mean the absence of competition if the fish stocks in VIa are well mixed. Indeed the entire system is dynamic, seals and fish move and some studies have suggested that the cod stock in VIa is not differentiable from the stocks in the North Sea (Wright et al., 2006; Holmes et al., 2008; Heath et al., 2014b). Certain studies investigated the possible overlap between fishing and seal grounds (Cronin et al., 2012; Gruber, 2014; Oksanen et al., 2014). However, overlap does not mean competition. Usage maps (Jones et al., 2013; STECF, 2015b) represent an average picture of the situation and may not be illustrative of actual grey seals and vessels movements. Seals can notably forage hundreds of kilometres away from the haul-out sites (Cronin et al., 2013; Klimova et al., 2014). Adding spatiality to the simulation model would need careful study of VMS and telemetry data but it would become difficult to predict fleet and seal repartition when running to the equilibrium. A possibility would be to create a spatial game theory model where fishers and seals are players and choose where to fish following the maximisation of their utility (Holland and Sutinen, 1999; Wilen et al., 2002; Hutton et al., 2004; Andersen et al., 2010). However, this does not take into account fish movements and adds more sources of uncertainty around the model. For considering spatiality in the model, the perfect study would be to follow all seals and vessels in the West of Scotland, to record where they fish and to see if competition between them exists in real time. This is obviously impossible to carry out. Consequently, it is very difficult to study grey seal impact spatially and a good understanding of movement and

responses to changes in prey distribution would be essential to the consideration of a spatial simulation model. Taking the assumption of homogenous fish population equally available to fishers and seals may therefore be a respectable assumption. Varying seal numbers and fishing mortality may be used to represent the different regions in VIa where grey seal predation and fishing mortality are variable. This could for instance resolve the problem of heterogeneity in the area.

The simulation model did not account for trophic interactions between fish and other predators than grey seals and fishers. The model assumed that this other predation is subsumed within the natural mortality component of the total fish mortality. The natural mortality is kept constant in the model. Grey seals are not the only predator of commercial fish. Indeed, seabirds and cetaceans are also responsible for removal of large quantities of commercial fish (Overholtz and Link, 2007). The largest predation on demersal fish comes from predatory fish themselves (Boyd and Hammond, 2010; Engelhard et al., 2014). Intraspecific cannibalism and interspecific predation of old fish on young fish notably occur in demersal species (Sparholt, 1994). The models also considered only grey seal predation on cod, haddock and whiting. This highlights the problem of the trophic cascades. Indeed, grey seals can be the predator of a target commercial species, but can also feed on their piscivorous predators. In that case, the removal of seals may generate in the long-term the decrease of the target species due to the increase of their piscivorous predators (DeMaster et al., 2001; Yodzis, 2001; Lavigne, 2003). Or inversely, the increase in grey seal population may have a positive impact on commercial fish by predateding on their piscivorous predators (Trzcinski et al., 2006). This could result in a situation where a decrease in seal predation may not induce an increase in fishing catches and sometimes may have the opposite consequence. The way the models are currently written cannot quantify these indirect grey seal predation impacts. It is therefore difficult to reliably conclude on grey seal impacts on the fishery (Gazit et al., 2013). This means that the results presented in this study inform about the direction of grey seal impacts in the short-term and for the initial assumptions of the model but cannot predict what would happen in the long-term. Indeed, the non-linear effects produced by trophic interactions are not discernible in the short-term so the absence of trophic interactions is not critical in short-term projections. Most importantly the results give the relative impact of grey seals on the fleets and demonstrate that the large whitefish trawlers is the fleet the

most impacted compared to the others. Considering multispecies modelling can induce different conclusions about grey seal impacts (Alexander et al., 2014) but currently, no age-structured multispecies models exists to assess grey seal impacts on the demersal fish around the UK. Incorporating grey seal predation in an age-structured multispecies model for the West of Scotland fisheries would be an interesting direction of improvement for this work.

The main uncertainty about this study comes from the errors associated with the input data. Indeed, both the state-space stock assessment model and the simulation model are parameterised using empirical data that are already uncertain. For instance, grey seal diet estimates are highly uncertain and present large confidence intervals (Harris, 2007). Data from the literature such as the length to weight conversion parameters (Coull et al., 1989) were estimated from experiments and are therefore subject to measurement errors. The stock-recruitment relationship is subject to both measurement and process errors. This brings high uncertainty around the stock estimates and therefore around grey seal impacts. This is highlighted by very large credible intervals for the results presented in this study. This uncertainty around the stock-recruitment is a very important point because the stock-recruitment curve gives the size of the fish stocks and an incorrect relationship may lead to completely different results of grey seal impacts. Also, the simulation outputs are sensitive to the estimates from the state-space model used to parameterise the biological part of the model where grey seal predation is taken into account. Depending on the assumption around the seal predation rate, the outputs from the state-space model are different. Fortunately, in this study, runs done with the new seal diet data validated the state-space model in the recent years and the seal estimates for 1985 and 2002 are similar for both seal predation rate assumptions and are the ones used in the simulation model. Despite being uncertain, the seal parameters in this study seem therefore well estimated. The assumption of constant price may also affect the results of this study. While this assumption was justified for the whitefish, it is less definite for *Nephrops*. Despite the fact that the price of *Nephrops* has been relatively constant in the past 30 years, the simulations allow a change in *Nephrops* landings and this may impacts its price in the real market. This assumption affects therefore the economic component of the model so TR2 trawlers' revenues. All these examples show that errors are accumulated within the simulation model and add to its uncertainty. This highlights the fact that this study

is maybe just a first step in the comprehension of grey seal impacts on the West of Scotland fisheries and this may limit its use for management in the area.

Even if the seal functional response to cod biomass is very uncertain given the paucity of seal diet data it represents a concept broadly accepted (Holling, 1959). Grey seal impacts are sensitive to the foraging model so the predator response is important. It may be interesting to consider the stochasticity around the response curve. The stock-recruitment uncertainty being considered, it would be possible to study the uncertainty around the functional response in a similar way by adding variability around the curve using the residual variance. New grey seal diet data for the years 2010-2011 will be published soon. The consideration of this data is likely to improve the fit of the functional response. The stochastic seal functional response is worth further investigation in the future.

The study of grey seal predation impacts in the West of Scotland is limited by the lack of grey seal diet data (Hammond et al., 2006; Harris, 2007). Two years (1985 and 2002) are not enough to estimate grey seal predation mortality along the time series of 28 years (1985-2012) and the state-space model sometimes estimated improbable changes in mortality for the years grey seal diet data was not available for. This explains the consideration of an average mortality between 1985 and 2002 as the best estimate of current seal predation mortality in the study. Even if the mortality was scaled to the current seal predation population this can bias the current grey seal predation estimates. The use of the new seal diet data would improve the Bayesian parameter estimates and enable the use of recent estimates of grey seal predation mortality as representative of the current seal mortality in the West of Scotland. This may reduce the bias of considering average predation mortality on old diet data. The studies on grey seal predation impacts on fisheries in the West of Scotland would certainly be improved by the continuous collection of seal diet data; this is consequently highly advised in the future.

Appendices

Appendix A: Summary of the simulation model

The following table summarises the equations used in the simulation model. The input parameter values for the model are available at the DOI [10.15129/ba3baf8c-17f6-471a-a84b-b15346642388](https://doi.org/10.15129/ba3baf8c-17f6-471a-a84b-b15346642388).

Table A.1: Equations used in the simulation model.

Equation number	Equation	Description
(4.1)	$N_{a,y,j} = N_{a-1,y-1,j} e^{-Z_{a-1,y-1,j}}$	The population N at age a and year y for the species j (cod, haddock, whiting or saithe) decays exponentially as a result of the total mortality Z
(4.3)	$N_{1,y,j} = (\alpha_j SSB_{y-1,j} e^{-\beta_j SSB_{y-1,j}}) e^{\varepsilon_j}$	The stock-recruitment follows a Ricker relationship where α and β are constants. The spawning stock biomass SSB corresponds to the population of mature fish so that $SSB_{y,j} = \sum_a (N_{a,y,j} m_{a,j} w_{a,j})$. Stochasticity is added to the stock recruitment to account for process errors with $\varepsilon_j \sim Normal(0, \sigma^2)$
(4.8)	$Z_{a,y,j} = M_{a,y,j} + F_{a,y,j} + P_{a,y,j}$	The total mortality Z is partitioned between natural mortality M , fishing mortality F and seal predation mortality P
(4.9)	$M_{a,y,j} = \gamma_j w_{a,y,j}^{-\delta_j}$	M is estimated following Lorenzen (1996) and depends of the fish weight w . The parameters γ and δ are constants

Table A.1 (continued): Equations used in the simulation model.

Equation number	Equation	Description
(4.10)	$P_{a,y,j} = sel_{a,j} q_j G_y$	P is function of seal selectivity sel for a certain age class, the ability to catch fish or seal predation rate q and the number of seals G , the two latter being constant
(4.11)	$sel_{a,j} = \left(\frac{l_{a,j}}{(\zeta_j - 1) \left(\frac{\eta_j}{\zeta_j - 1} \right)} \right)^{(\zeta_j - 1)} e^{(\zeta_j - 1) - \frac{l_{a,j}(\zeta_j - 1)}{\eta_j}}$	sel follows a gamma curve assuming a preference for certain fish length l and with ζ and η being constants
(4.12)	$F_{a,y,j,k} = s_{a,j,k} E_{y,k}$	F for the fleet k is the product of an age component or selectivity s and a year effect or fishing effort index E . The total fishing mortality on a fish species j is therefore $F_{a,y,j} = \sum_k F_{a,y,j,k}$
(4.14)	$C_{a,y,j} = \frac{F_{a,y,j}}{Z_{a,y,j}} N_{a,y,j} (1 - e^{-Z_{a,y,j}})$	The catch C is calculated using the Baranov equation
(4.15)	$L_{a,j,k} = \lambda_{a,j,k} C_{a,j}$	Landings L are estimated using the proportion (λ) of landings in the total catch
(4.17)	$B_{y+1,j} = B_{y,j} + \frac{4msy_j}{K_j} B_y \left(1 - \frac{B_{y,j}}{K_j} \right) - L_{y,j}$	The biomass B for the other species (anglerfish, megrims, hake, <i>Nephrops</i> and ling) is calculated using a Schaefer surplus production function where msy is the maximum sustainable yield and K the carrying capacity

Table A.1 (continued): Equations used in the simulation model.

Equation number	Equation	Description
(4.18)	$L_{y,j} = (1 - e^{-F_{y,j}})B_{y,j}$	Landings for the other species are assumed to be function of F and B
(4.19)	$R_{y,k} = \sum_j (p_j L_{y,j,k})$	The revenues R are the product of fish landings with the price p of this specific fish
(4.21)	$ct_k = v(cv_k + cf_k)$	The total cost ct of a fleet k is the sum of the variable costs cv and the fixed costs cf per vessel multiplied by the number of boats v . The variable costs are given as proportional to the fishing effort index following a constant ρ such as $ct_k = \rho_k E_k$

Appendix B: List of symbols used in the study

Table B.1: Biological parameters used in the study. The parameter values are available at the DOI 10.15129/ba3baf8c-17f6-471a-a84b-b15346642388.

Symbol	Parameter	Equation	Unit	Comments
a	Subscript for age			
B	Fish biomass	(4.17)	t	Schaefer production function
C	Fishing catch	(4.14)	number of fish	Baranov equation
E	Fishing effort index	(4.12), (4.20)		To estimate fishing mortality and variable costs
ε	Multiplicative random effect	(4.7)		Lognormal random effect on stock-recruitment and on q in Bayesian analysis
F	Fishing mortality	(4.12), (4.13)	y^{-1}	
G	Seal number	(4.10)	seals in thousands	
gr	Subscript for aggregated fleet groups	(4.27)		TR1, TR2 and Others fleets
GW	Gutted weight	(4.22)	g	From Coull et al. (1989)
it	Subscript for iteration number			Used in the BE scenario
j	Subscript for species			
k	Subscript for fleet			
K	Fish carrying capacity	(4.5), (4.17)	number of fish in (4.5), t in (4.17)	Schaefer surplus production function and smooth hockey-stick stock-recruitment curve
l	Length of fish	(4.11), (4.23)	cm	Weight to length conversion (Coull et al., 1989) and estimation of seal selectivity
L	Landings	(4.15), (4.18)	t	At age for cod, haddock, whiting and saithe and aggregated for the other species
m	Proportion of mature fish	(4.2)		
M	Fish natural mortality	(4.9)	y^{-1}	

Table B.1 (continued): Biological parameters used in the study. The parameter values are available at the DOI 10.15129/ba3baf8c-17f6-471a-a84b-b15346642388.

Symbol	Parameter	Equation	Unit	Comments
<i>msy</i>	Maximum sustainable yield	(4.17)	t	Schaefer surplus production function
<i>N</i>	Fish number	(4.1)	number of fish	
<i>N₁</i>	Recruitment	(4.3)-(4.5)	number of fish	Fish number at age 1
<i>P</i>	Seal predation mortality	(4.10)	y ⁻¹	
<i>PB</i>	Fish partial biomass	(6.2)	t	To estimate <i>q</i> when a seal functional response to cod biomass is considered
<i>q</i>	Seal predation rate	(4.10), (4.24), (6.2)	seal ⁻¹ y ⁻¹	
<i>RF</i>	Raising factor	(4.22)		Weight to length conversion
<i>s</i>	Fishing selectivity	(4.12)	y ⁻¹	
<i>sel</i>	Seal selectivity	(4.11)		
<i>SSB</i>	Spawning stock biomass	(4.2)	t	
<i>w</i>	Weight of fish	(4.2), (4.9), (4.22), (6.2)	kg, g in (4.22)	
<i>y</i>	Subscript for years			
<i>Z</i>	Total mortality on fish	(4.8)	y ⁻¹	
<i>α</i>	1 st stock-recruitment parameter	(4.3)-(4.5)	recruits. t ⁻¹	For Ricker, Beverton-Holt and hockey-stick
<i>β</i>	2 nd stock-recruitment parameter	(4.3), (4.4)		For Ricker and Beverton-Holt
<i>γ</i>	Allometric scaling factor	(4.9)	y ⁻¹	To estimate natural mortality

Table B.1 (continued): Biological parameters used in the study. The parameter values are available at the DOI 10.15129/ba3baf8c-17f6-471a-a84b-b15346642388.

Symbol	Parameter	Equation	Unit	Comments
δ	Rate at unit weight	(4.9)		To estimate natural mortality
Δ	Change in effort index	(5.4)		For BE scenario at each iteration
ζ	Shape parameter of seal selectivity curve	(4.11)		
η	Mode of seal selectivity curve	(4.11)	cm	
θ_1	1 st constant weight to length conversion	(4.23)	g.cm ⁻¹	Coull et al. (1989)
θ_2	2 nd constant weight to length conversion	(4.23)		Coull et al. (1989)
λ	Proportion of landings in total catch	(4.15)		
σ	Standard deviation of stock-recruitment estimates	(4.7)		
τ	Steepness of sigmoid curve	(5.4)		For estimation change in effort index in BE scenario
φ	Proportion of aggregated fleet in total catch at age	(4.27)		TR1, TR2 and Others fleets (<i>gr</i>)
χ	Seal attack rate	(6.2)	t.seal ⁻¹	Type II functional response
ψ	Fleet proportion in total landings	(4.28)		For the five fleets considered
ω	Seal handling time	(6.2)	y	Type II functional response

Table B.2: Economic parameters used in the study. The parameter values are available at the DOI [10.15129/ba3baf8c-17f6-471a-a84b-b15346642388](https://doi.org/10.15129/ba3baf8c-17f6-471a-a84b-b15346642388).

Symbol	Parameter	Equation	Unit	Comments
c	Initial total cost per fleet	(5.2)	£	When effort index is 1 in the BE scenario
ct	Fleet total costs	(4.21), (5.2)	£	
cf	Fleet fixed costs	(4.21)	£	
cv	Fleet variable costs	(4.20)	£	
p	Price of fish	(4.19)	£	In real terms, taking 2012 as reference
R	Fleet revenues	(4.19)	£	
v	Number of vessels	(4.21)	numbers	
π	Net profit	(5.1)	£	
ρ	Proportionality constant	(4.20)		Estimation of variable costs

Appendix C: Input data used to parameterise the state-space stock assessment and simulation models

This section assembles the data used for the parameterisation of the state-space and simulation models. The values of the inputs of the simulation model and the empirical data from Marine Scotland and Seafish are available at the DOI [10.15129/ba3baf8c-17f6-471a-a84b-b15346642388](https://doi.org/10.15129/ba3baf8c-17f6-471a-a84b-b15346642388). Table C.1 presents the empirical data used to parameterise the state-space stock assessment model in the Bayesian parameter estimation.

Table C.1: Summary of empirical data used for the state-space model in the Bayesian analysis.

Type of data	Empirical data	Years	Reference
Fish data	Proportion of mature fish at age	1985-2012	ICES (2013b)
	Mean weight at age in the total catch	1985-2012	ICES (2013b)
	Weight to length conversion parameters		Coull et al. (1989)
Fishing data	Landings at age	1985-2012	ICES (2013b)
	Discards at age	1985-2012	ICES (2013b)
	Indices of abundance from research vessel surveys	1985-2012	ICES (2013b)
Seal diet data	Average per capita consumption rates	1985 and 2002	Harris (2007)
	Numbers of fish consumed at age	1985 and 2002	Length-structured data (Harris, 2007) converted to age-structured data by Marine Scotland
Seal data	Seal numbers	1985-2011	Thomas (2012). Following Thomas (2013; 2014) the estimate in 2012 was assumed equal to the 2011 value

The empirical data used in the estimation of the Schaefer surplus production parameters and of the landing index for ling are given in Table C.2. Table C.3 collects the outputs from the state-space model that were used as input parameters for the biological part of the simulation model. The empirical data from the literature used for the biological part of the simulation model is presented in Table C.4 and in Table C.5 for the economic part of the model.

Table C.2: Empirical data available (biomass, landings and years) and used (B and F and msy and K) to estimate Schaefer surplus production function parameters and the landing index for ling.

Species	Biomass	Landings	Years	B and F	msy and K	Reference
Anglerfish	V1a	V1a	2005-2012	2007-2011	2005-2012	ICES (2013b)
Megrim	IVa+V1a	V1a	1985-2012	2007-2011	1985-2012	ICES (2013b)
Hake	Northern stock	V1a	1978-2012	2007-2011	2003-2012	ICES (2014d)
<i>Nephrops</i>	V1a	V1a	1995-2012	2007-2011	1995-2012	ICES (2013b)
Ling		V1a	1988-2012	2007-2011		ICES (2013c)

Table C.3: Summary of outputs of the state-space model used to parameterise the simulation model for cod, haddock and whiting.

Type of data	Symbol	Parameter	Years	Purpose
Fish data	N_1	Recruitment	2007-2011	Calculate the initial numbers of fish at age
	Z_a	Total mortality at age	2007-2011	
	SSB	Spawning stock biomass	1985-2012	Calculate the stock-recruitment parameters
	N_1	Recruitment	1985-2012	
	γ	Allometric scaling factor		Calculate the natural mortality as a function of fish weight
	δ	Natural mortality rate at unit weight		
Fishing data	F_a	Fishing mortality at age	2007-2011	Used as initial fishing mortality
Seal data	η	Mode of the seal selectivity distribution		Calculate seal selectivity on fish
	ζ	Shape parameter of the seal selectivity distribution		
	q	Seal predation rate	1985, 2002	Average for the 2 years

Table C.4: Empirical data used to parameterise the biological part of the simulation model.

Symbol	Parameter	Years	Equation	Reference	Comments
G	Seal number	2007-2011	(4.10)	Thomas (2012)	
γ	Allometric scaling factor		(4.9)	Lorenzen (1996)	For saithe only
δ	Natural mortality rate at unit weight		(4.9)		
m_a	Proportion of mature fish at age		(4.2)	ICES (2013b; 2013d)	
l	Length of fish	2007-2011	(4.11), (4.23)	Coull et al. (1989)	
w_L w_D	Fish weight in landings and discards	2007-2011	(4.15)	ICES (2013b; 2013d)	
w	Fish weight in the stock		(4.2)	ICES (2013b; 2013d)	
$C_{a,gr}$	Catch at age (landings and discards)	2012-2014	(4.26)	Marine Scotland	Given for TR1 and TR2 for cod, haddock and whiting
C_a	Catch at age	2012-2013	(4.14), (4.15), (4.16)	ICES (2013b; 2013d; 2014c)	
\bar{F}	Fishing mortality	2007-2011	(4.27)	ICES (2013d)	For saithe only

Table C.5: Empirical data used to parameterise the economic part of the simulation model.

Symbol	Parameter	Years	Equation	Reference	Comments
p	Fish price	2007-2011		Marine Management Organisation (2012)	Real price using 2012 as reference year
v	Number of vessels	2007-2012		Seafish	
cv	Variable costs	2007-2012		Seafish	
cf	Fixed costs	2007-2012		Seafish	
L_k	Fleet landings	2007-2011		Marine Scotland	Used to calculate TR2_10-24 costs

Appendix D: Description of the state-space stock assessment model

This appendix describes in detail the state-space model used to estimate the biological parameters of the bioeconomic models for cod, haddock and whiting. The following description is taken from Cook et al. (2015).

Structural model

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

$$N_{a,y} = N_{a-1,y-1} e^{-Z_{a-1,y-1}}$$

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

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

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

$$F_{a,y} = s_{a,y} E_y$$

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

$$E_y = E_{y-1} e^{\varepsilon_{E,y}} \quad \varepsilon_{E,y} \sim \text{Normal}(0, \sigma_E^2), y \neq 1$$

$$s_{a,y} = s_{a,y-1} e^{\varepsilon_{s,a,y}} \quad \varepsilon_{s,a,y} \sim \text{Normal}(0, \sigma_s^2), y \neq 1$$

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

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

$$M_{a,y} = c(\bar{w}_{a,y})^b$$

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

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

$$P_{a,y} = s_{seal,a,y}q_{seal,y}G_y$$

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

$$s_{seal,a,y} = \left(\frac{\bar{l}_{a,y}}{(\alpha - 1)\beta} \right)^{\alpha-1} e^{-\alpha-1-\frac{\bar{l}_{a,y}}{\beta}}$$

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

$$q_{seal} = q_{seal,y-1}e^{\varepsilon_{qseal,y}} \quad \varepsilon_{qseal,y} \sim Normal(0, \sigma_{qseal}^2), y \neq 1$$

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

Observation equations

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

$$U_{k,a,y} = s_{k,a} q_k N_{a,y} e^{-\rho_k Z_{a,y}}$$

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

$$\ln\left(\frac{s_{k,a}}{1 - s_{k,a}}\right) = \frac{\ln(9)(a - A_{50,k})}{SR_k}$$

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

$$\hat{U}_{k,a,y} \sim Normal(\ln(U_{k,a,y}), \sigma_{k,a}^2)$$

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

$$C_{a,y} = \frac{F_{a,y}}{Z_{a,y}} N_{a,y} (1 - e^{-Z_{a,y}})$$

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

$$\ln\left(\frac{r_{a,y}}{1 - r_{a,y}}\right) = \frac{\ln(9)(\bar{l}_{a,y} - D_{50})}{SR_D}$$

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

$$L_{a,y} = r_{a,y}C_{a,y}$$

$$D_{a,y} = (1 - r_{a,y})C_{a,y}$$

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

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

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

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

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

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

$$H_{a,y} = \frac{P_{a,y}}{Z_{a,y}} N_{a,y} (1 - e^{-Z_{a,y}})$$

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

$$h_{a,y}, a = 1 \dots A \sim Multinomial(n_y, p_{seal,1,y}, p_{seal,2,y}, \dots, p_{seal,A,y})$$

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

$$Y_{seal,y} = \sum_a H_{a,y} \bar{w}_{a,y}$$

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

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

Appendix E: Priors used in the Bayesian analysis

The Table E.1 below gives the details of the priors used in the state-space model for the Bayesian analysis. Most of them come from Cook et al. (2015) and have been updated to be applicable to the two new species, haddock and whiting.

Table E.1: Prior distributions on the parameters to estimate.

Type of data	Parameter	Prior	Comment
Survey data	Catchability	Uniform(-12,3)	
	Selection range	Uniform(0.01,2)	
	Age at which 50% of fish are retained by the survey	Uniform(-1,6)	
	Standard deviation of measurement error	Gamma(0.01,0.01)	Non-informative prior on precision
Fish data	Proportionality constant for natural mortality function	Normal(3.69,4)	From Lorenzen (1996)
	Exponent constant for natural mortality function	Normal(-0.305,1250)	From Lorenzen (1996)
	Initial population at age in the 1st year	Age a: Normal(x[a]+1.6,0.3)	For cod x=c(6.98,6.8,6.1,5.0,3.7,2.6) For haddock x=c(9.6,9.4,8.5,7.5,6.7,6.4,4.9) For whiting x=c(10.5,9.6,8.6,7.5,6.3,5.4) The mean is the average catch at age scaled up by 1.6
	Recruitment in each year	Normal(x[1]+1.6,0.3)	

Table D.1 (continued): Prior distributions on the parameters to estimate.

Type of data	Parameter	Prior	Comment
Fishery data	Initial fishing mortality	Uniform(-3,0.5)	
	Process error on selectivity	Uniform(1e-5,100)	
	Process error on effort	Uniform(0,100)	
	Selectivity at age in initial year	Age 1: Uniform(0.1,0.8)	Age 3 is the reference age so selectivity=1. Age 7 only concerns haddock
		Age 2: Uniform(0.2,1.5)	
		Age 4+: Uniform(0.2,2)	
	Standard deviation of measurement error on landings, discards and catch	Gamma(0.01,0.01)	Non-informative prior on precision. Catch used just for cod after 2005
	Discard retention ogive	Normal(6,0.5)	From Cook (2013)
50% retention length for the discards	Normal(mls,0.01667)	mls is the minimum landing size for each species, 35 cm, 30 cm and 27 cm for cod, haddock and whiting respectively	
Misreporting	Beta(2,0.5)	The mode of the distribution is 1 so misreporting is considered rare	
Seal data	Seal predation rate	Uniform(-10,5)	
	Process error on seal predation rate	Uniform(1e-6,100)	
	Shape parameter for selectivity curve	Uniform(1,30)	Large range to reduce information on the prior
	Mode of the selectivity curve	Normal(45,0.01)	Mean is the midpoint of the observed length distributions. Precision larger than in Cook et al. (2015) to make the prior not too informative and usable for the 3 species
	Standard deviation of measurement error on seal consumption	Gamma(4,0.33)	Gives mean precision for seal catch equal to the reciprocal of sample variance with 50% coefficient variation

Appendix F: Outputs from the state-space model

Outputs for cod

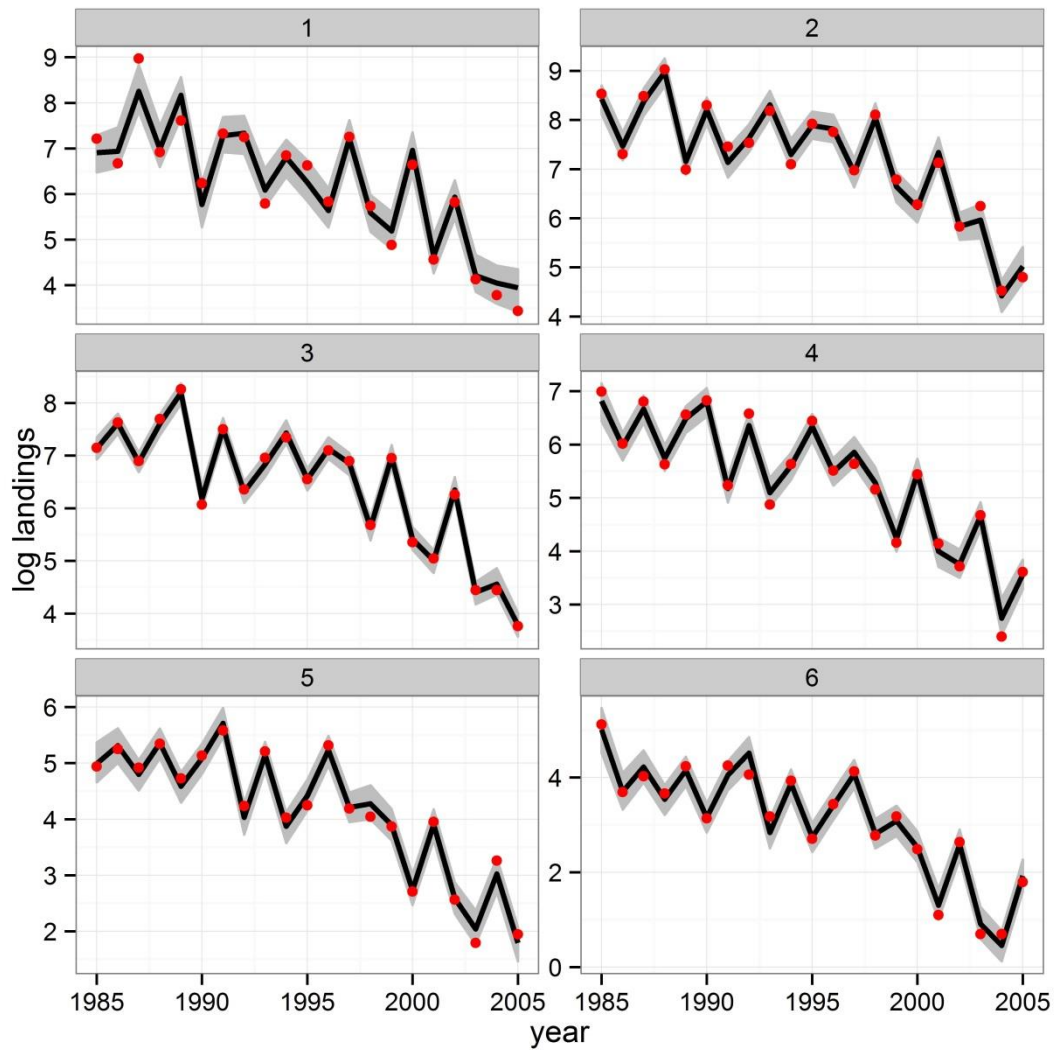


Figure F.1: Time series log landings (in numbers) for the fixed seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

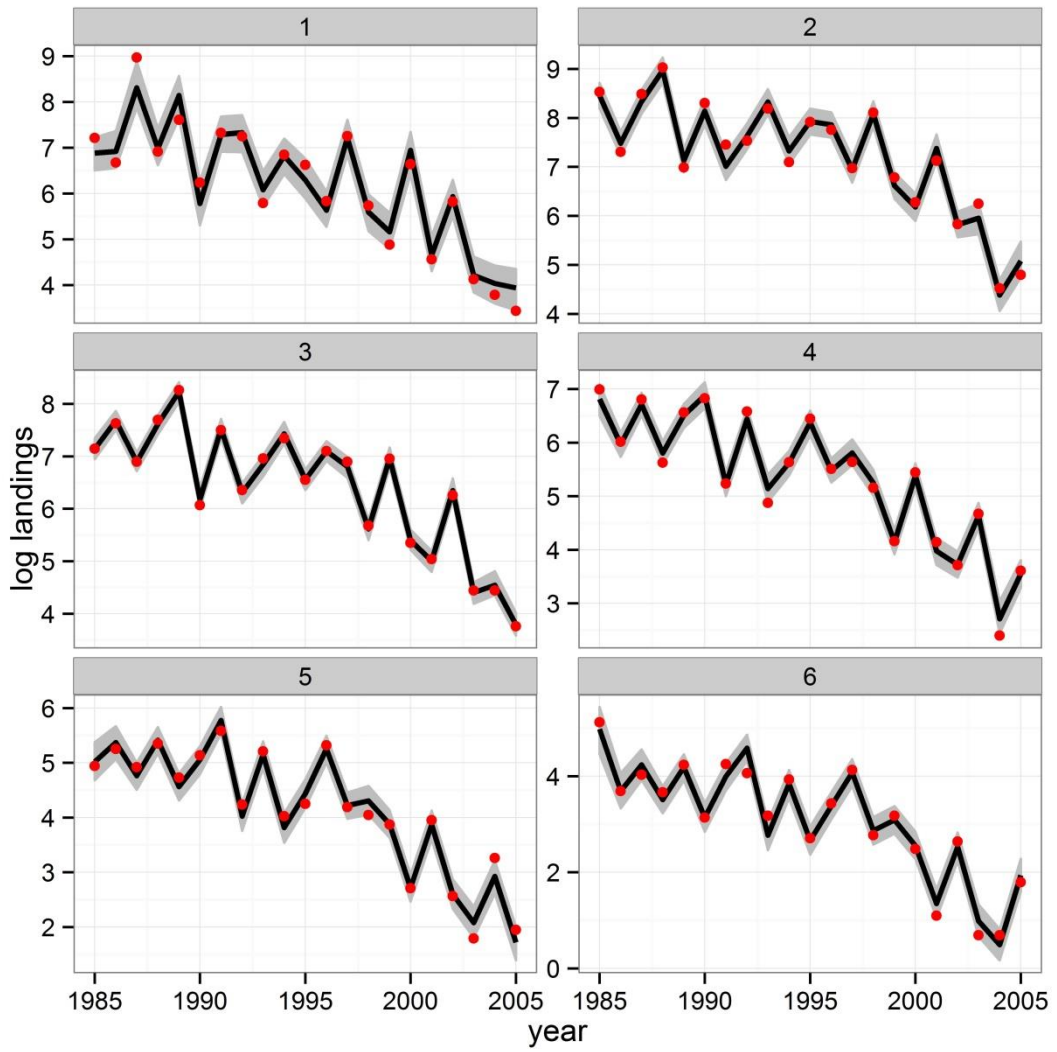


Figure F.2: Time series log landings (in numbers) for the variable seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

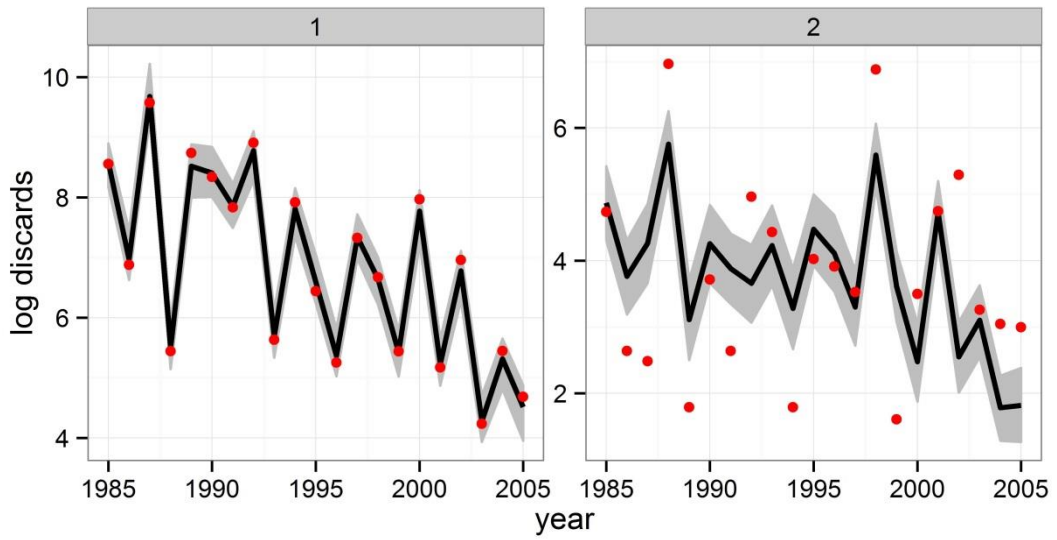


Figure F.3: Time series log discards (in numbers) for the fixed seal predation rate model given by fish age (1 and 2). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

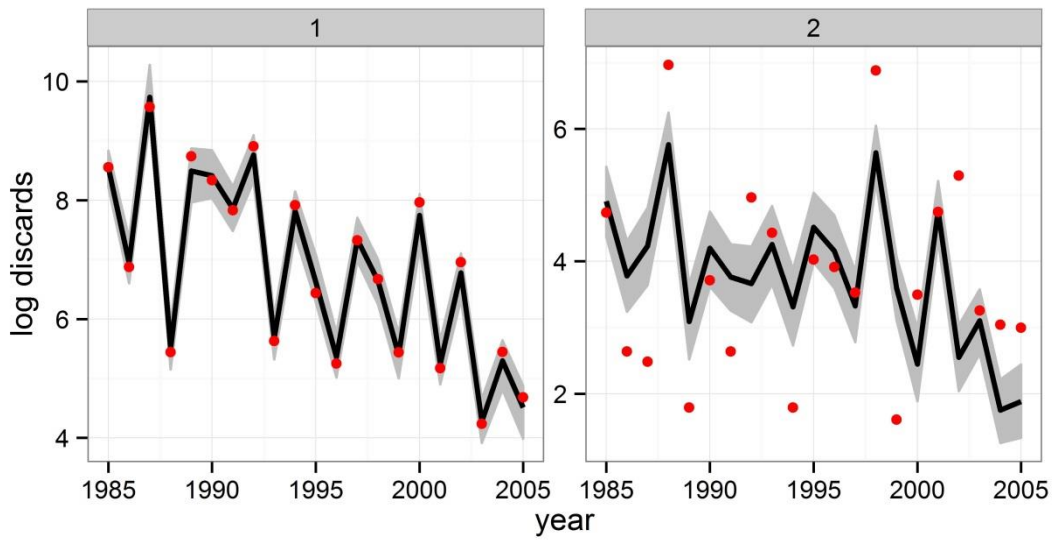


Figure F.4: Time series log discards (in numbers) for the variable seal predation rate model given by fish age (1 and 2). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

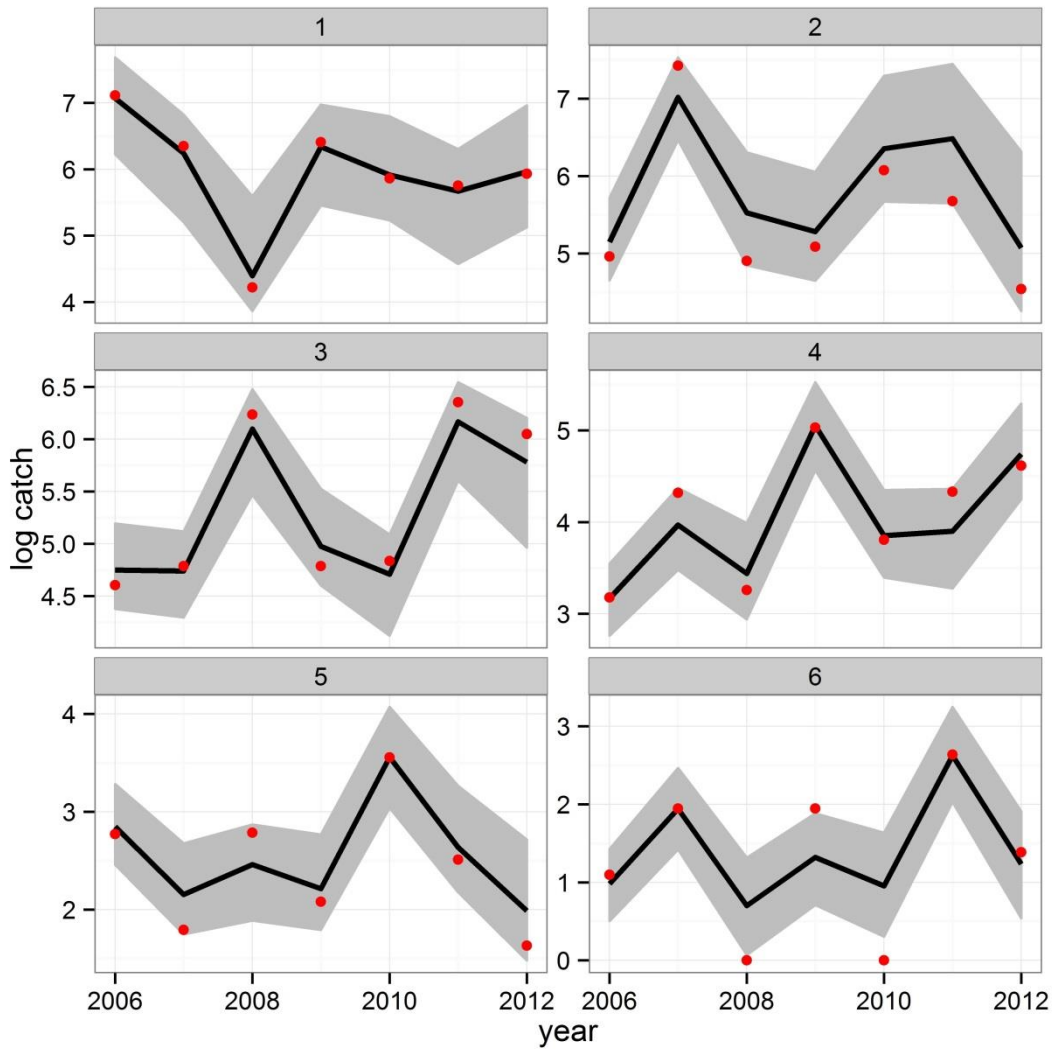


Figure F.5: Time series log catch (in numbers) for the fixed seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

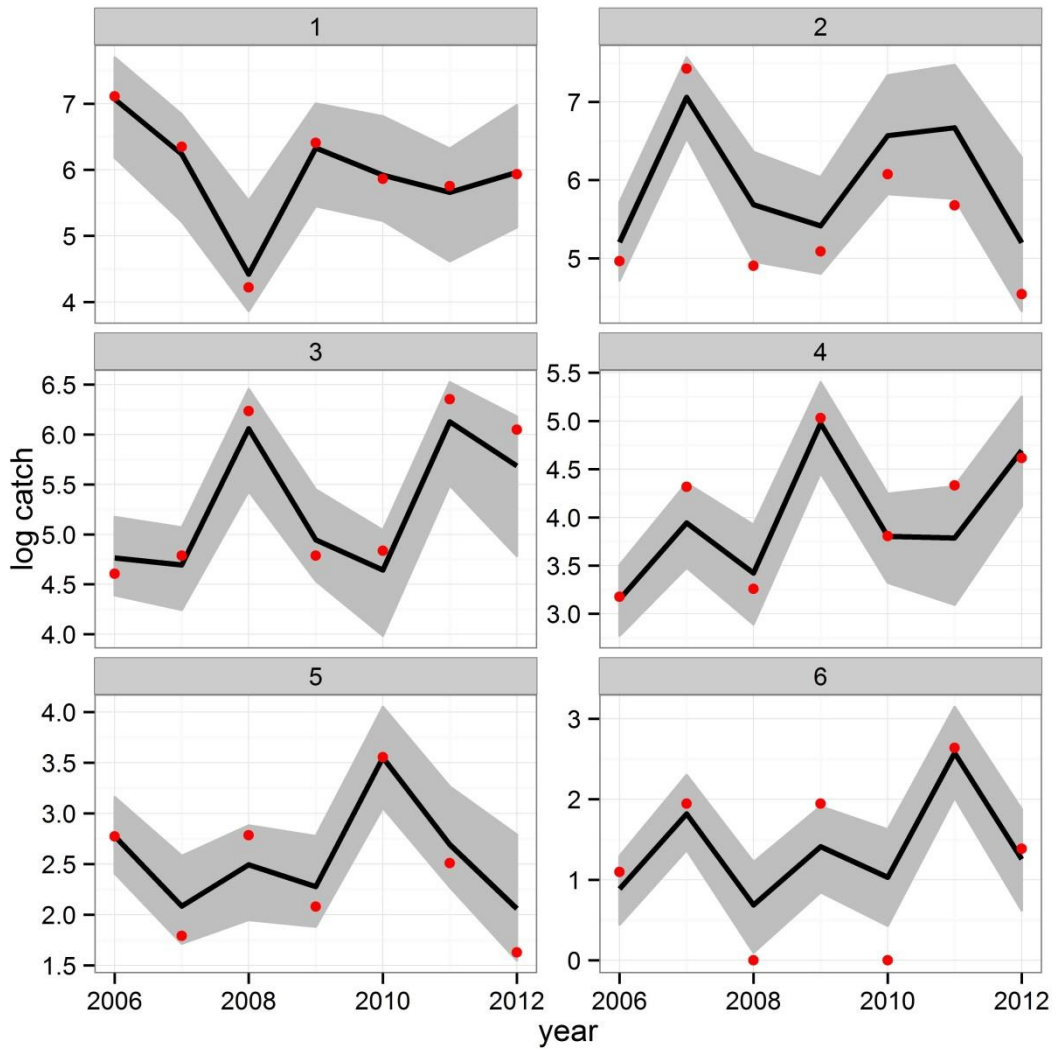


Figure F.6: Time series log catch (in numbers) for the variable seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

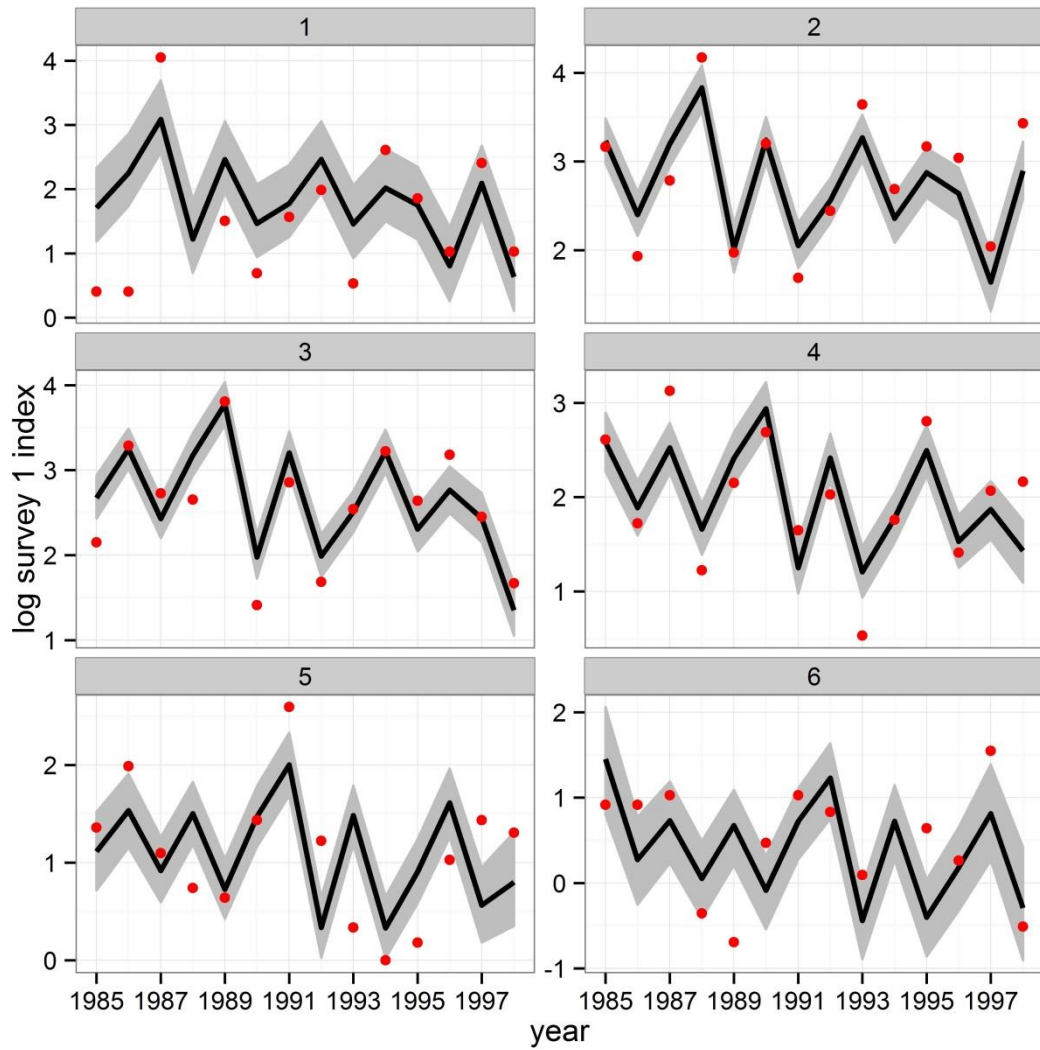


Figure F.7: Time series log abundance indices for the Scottish quarter 1 research survey for the fixed seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

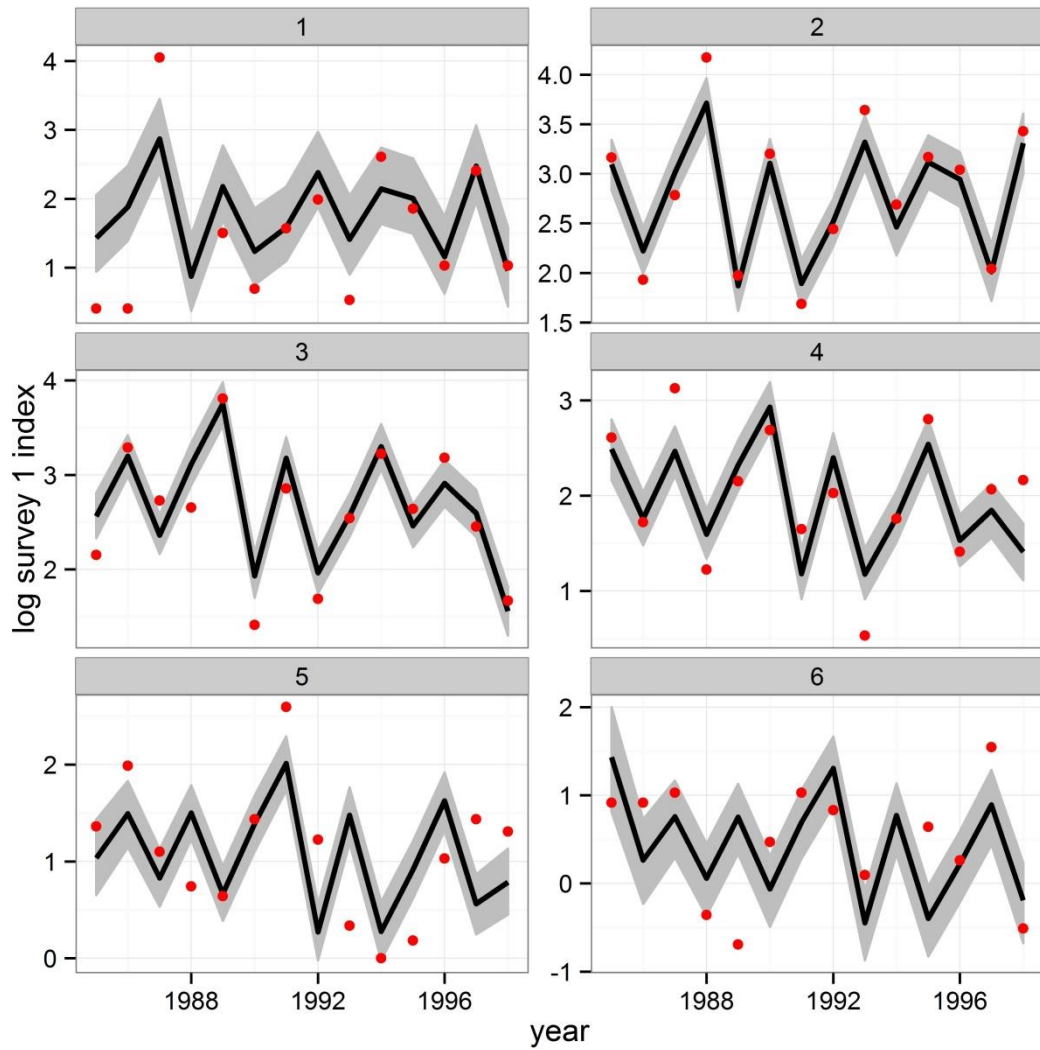


Figure F.8: Time series log abundance indices for the Scottish quarter 1 research survey for the variable seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

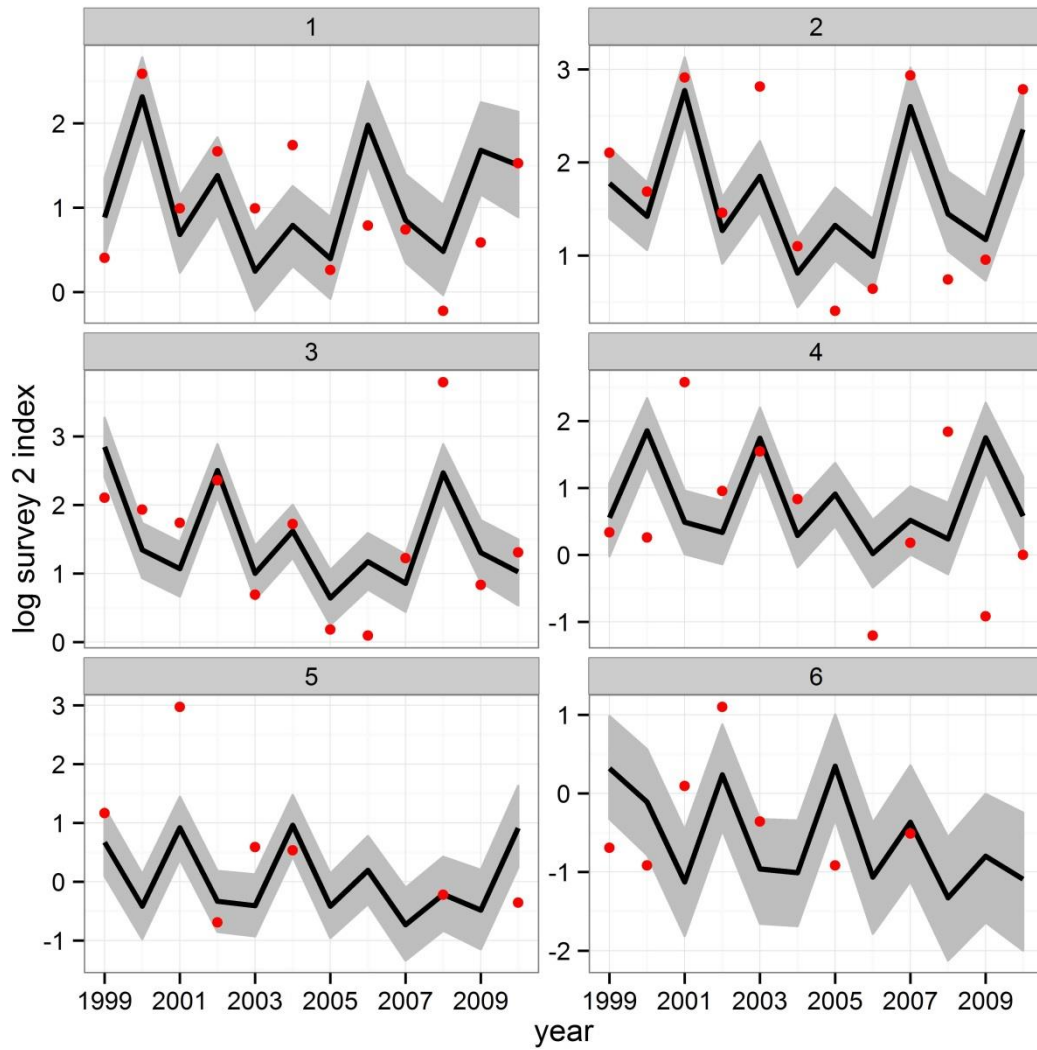


Figure F.9: Time series log abundance indices for the Scottish quarter 1 research survey after change in research vessel and length of the tow for the fixed seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

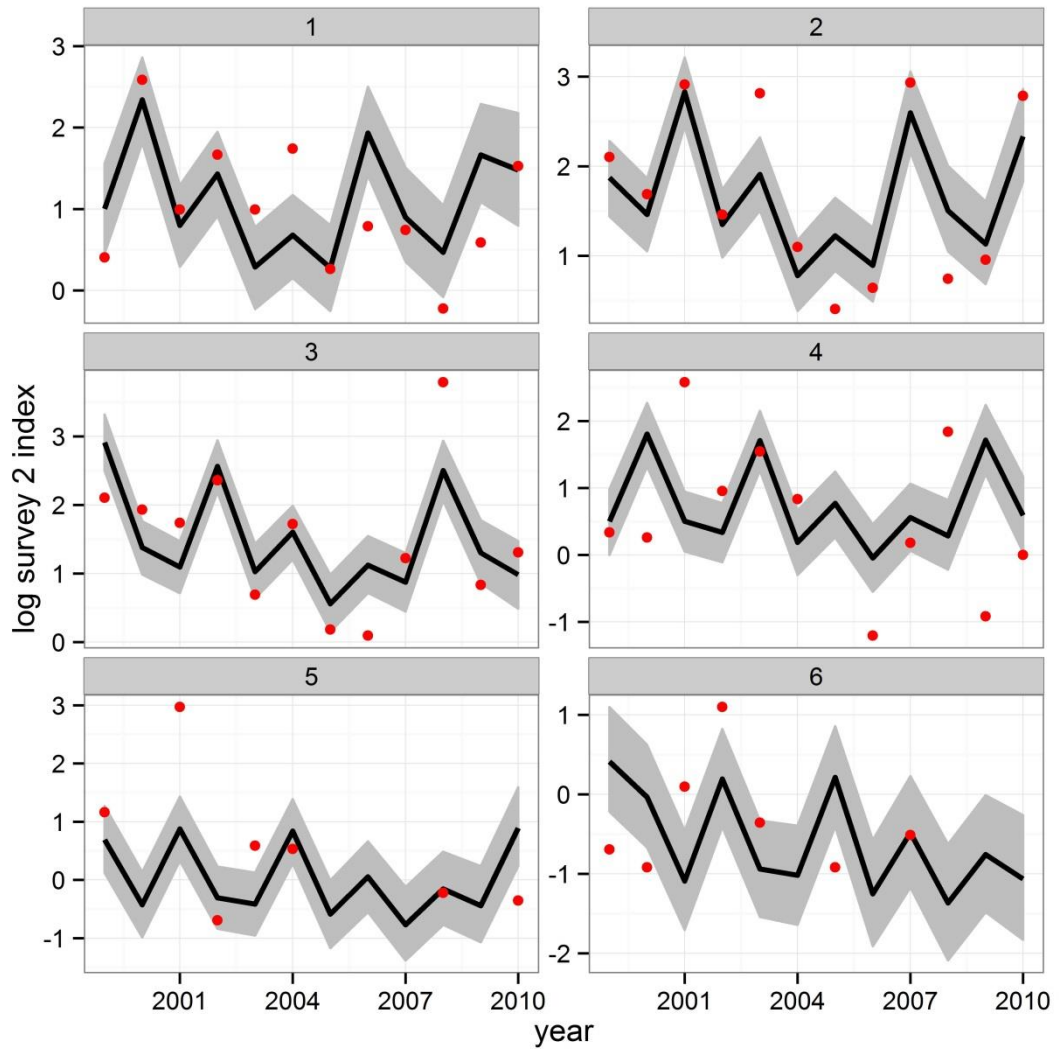


Figure F.10: Time series log abundance indices for the Scottish quarter 1 research survey after change in research vessel and length of the tow for the variable seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

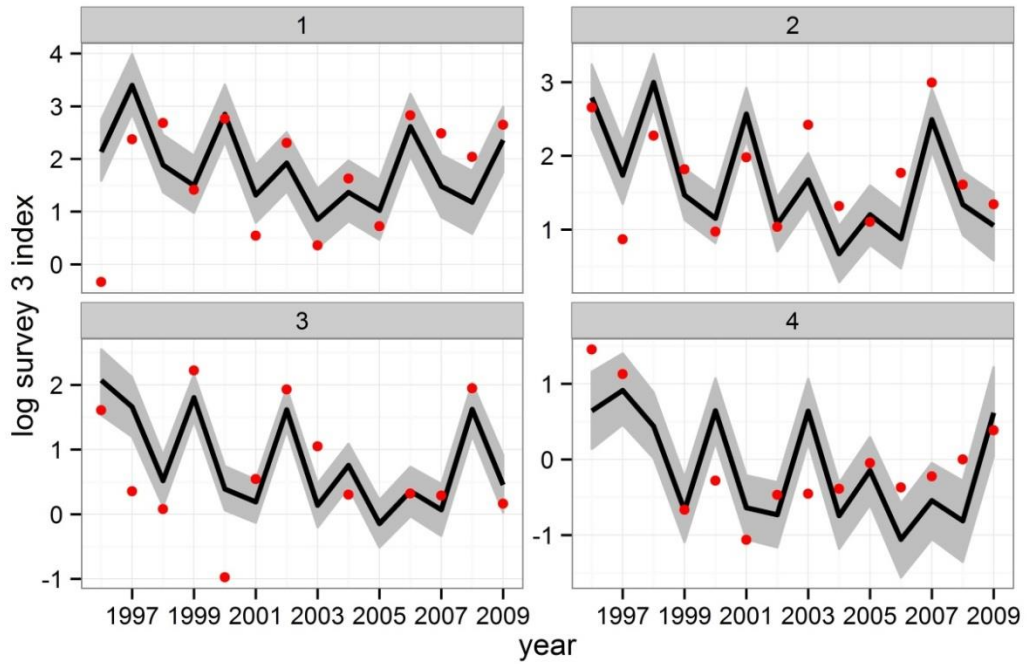


Figure F.11: Time series log abundance indices for the Scottish quarter 4 research survey for the fixed seal predation rate model given by fish age (1 to 4). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

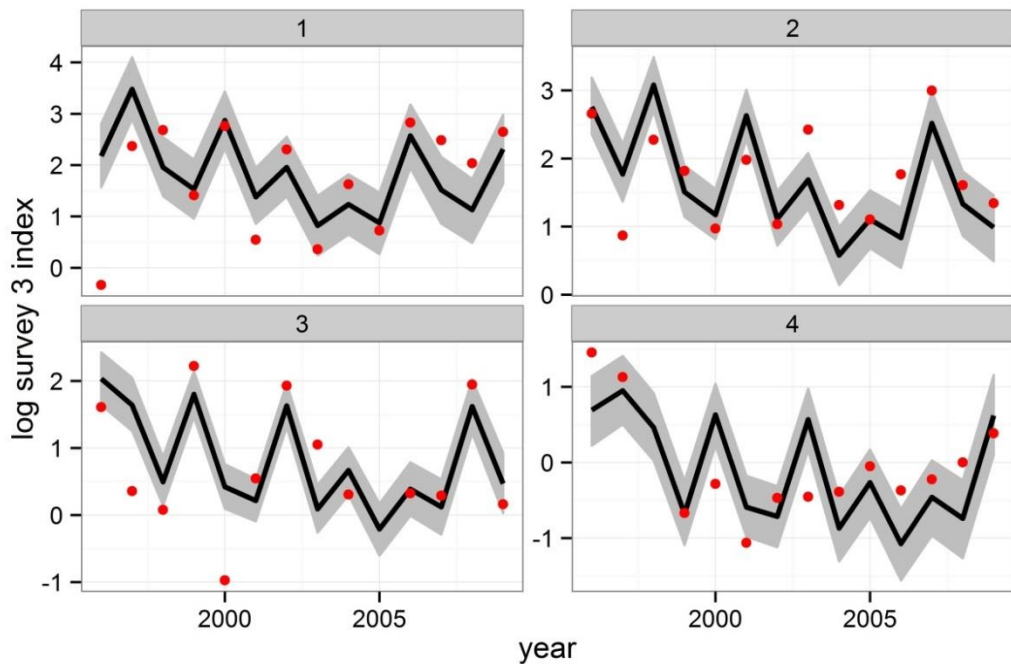


Figure F.12: Time series log abundance indices for the Scottish quarter 4 research survey for the variable seal predation rate model given by fish age (1 to 4). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

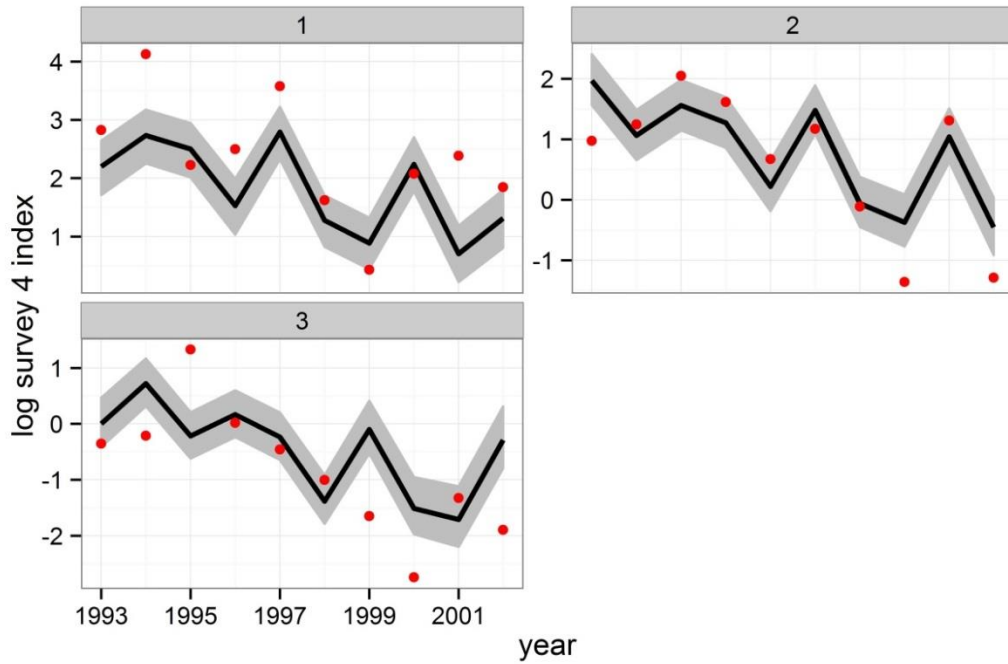


Figure F.13: Time series log abundance indices for the Irish groundfish research survey for the fixed seal predation rate model given by fish age (1 to 3). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

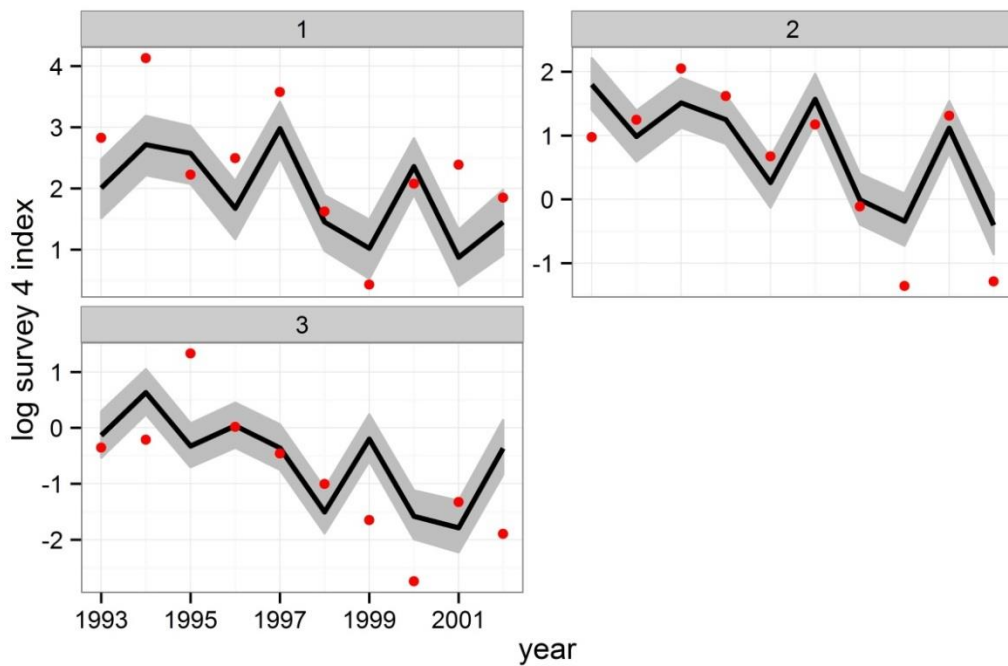


Figure F.14: Time series log abundance indices for the Irish groundfish research survey for the variable seal predation rate model given by fish age (1 to 3). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

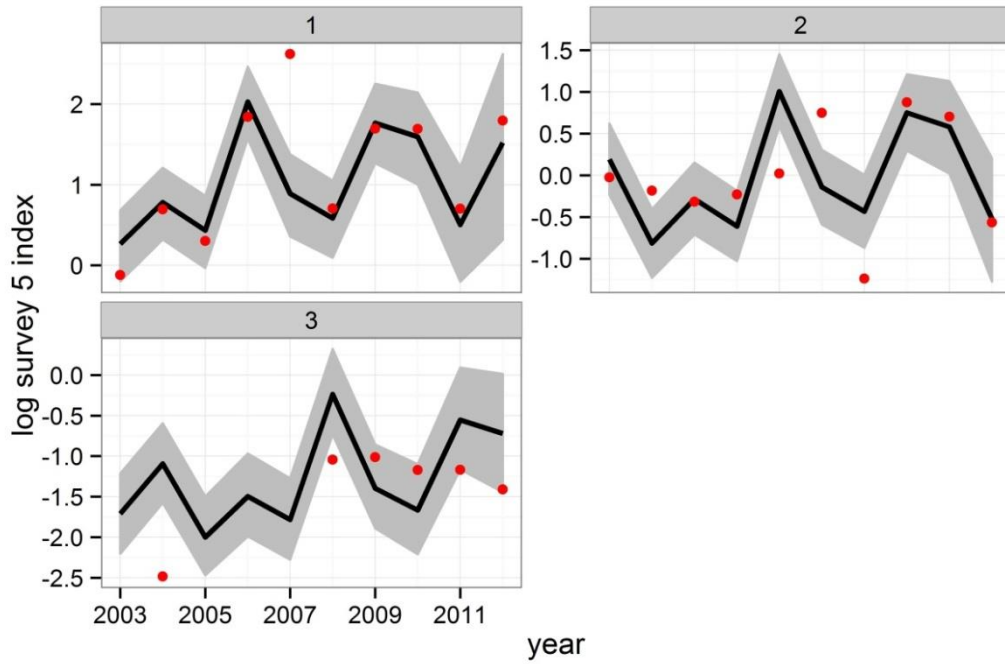


Figure F.15: Time series log abundance indices for the Irish West Coast groundfish research survey for the fixed seal predation rate model given by fish age (1 to 3). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

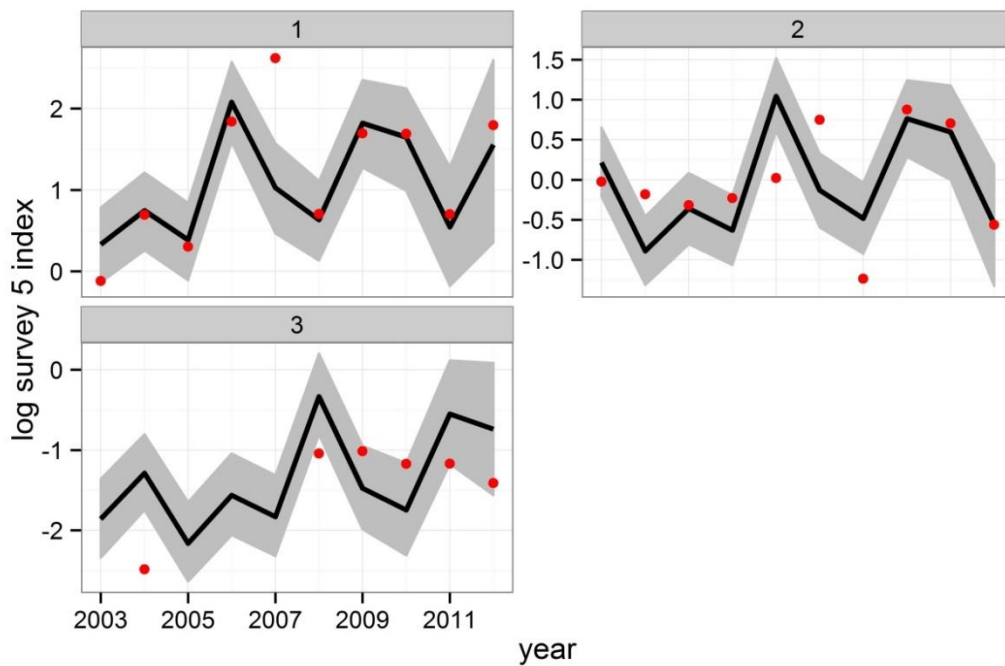


Figure F.16: Time series log abundance indices for the Irish West Coast groundfish research survey for the variable seal predation rate model given by fish age (1 to 3). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

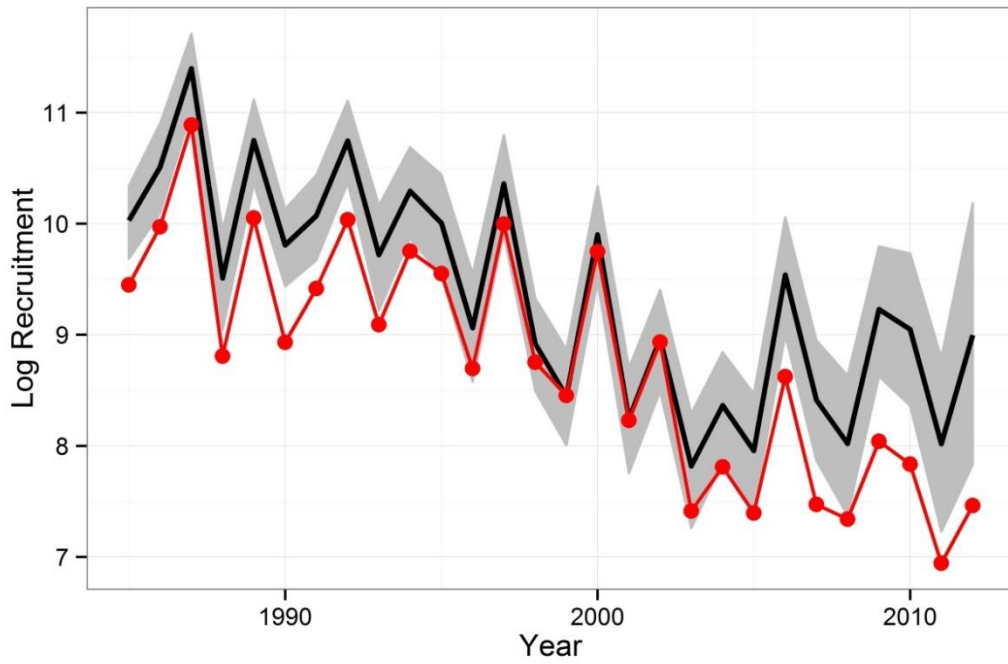


Figure F.17: Time series log recruitment (thousands) for the fixed seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The estimates from ICES are given in red.

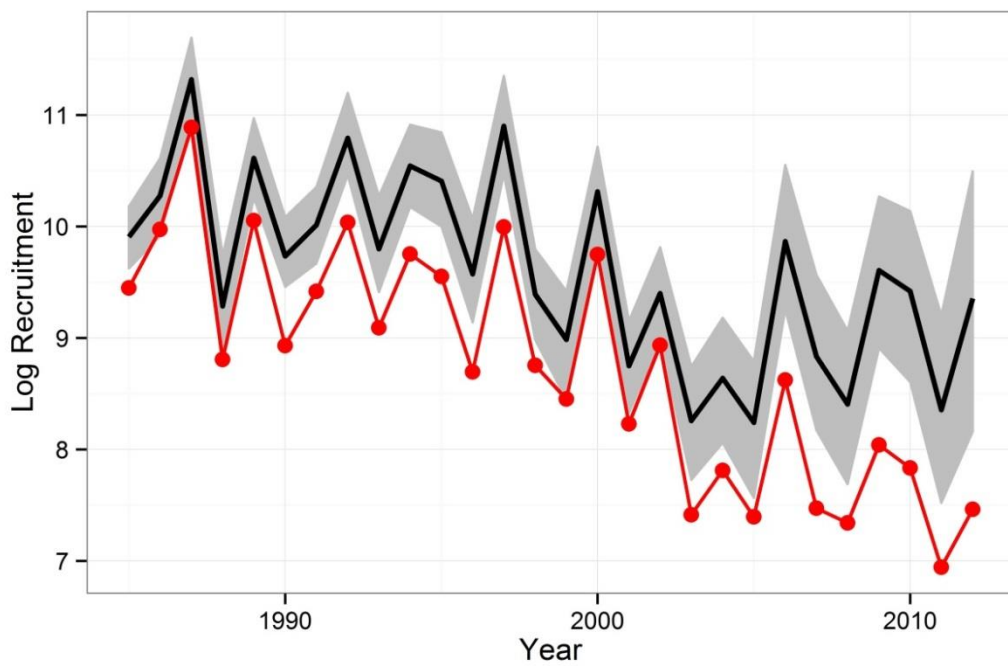


Figure F.18: Time series log recruitment (thousands) for the variable seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The estimates from ICES are given in red.

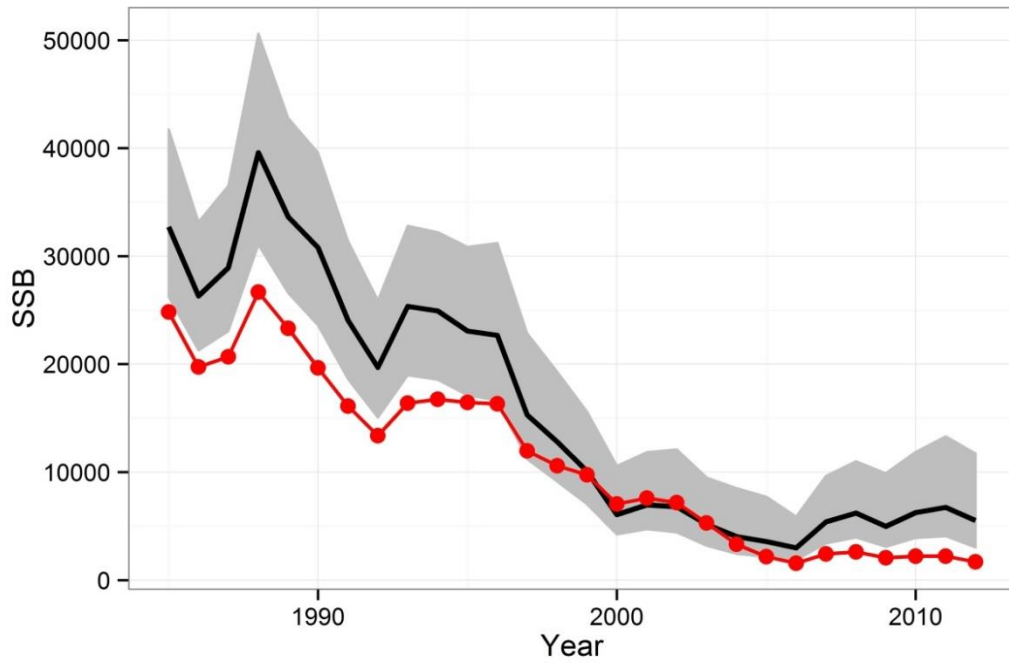


Figure F.19: Time series log SSB (tonnes) for the fixed seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The estimates from ICES are given in red.

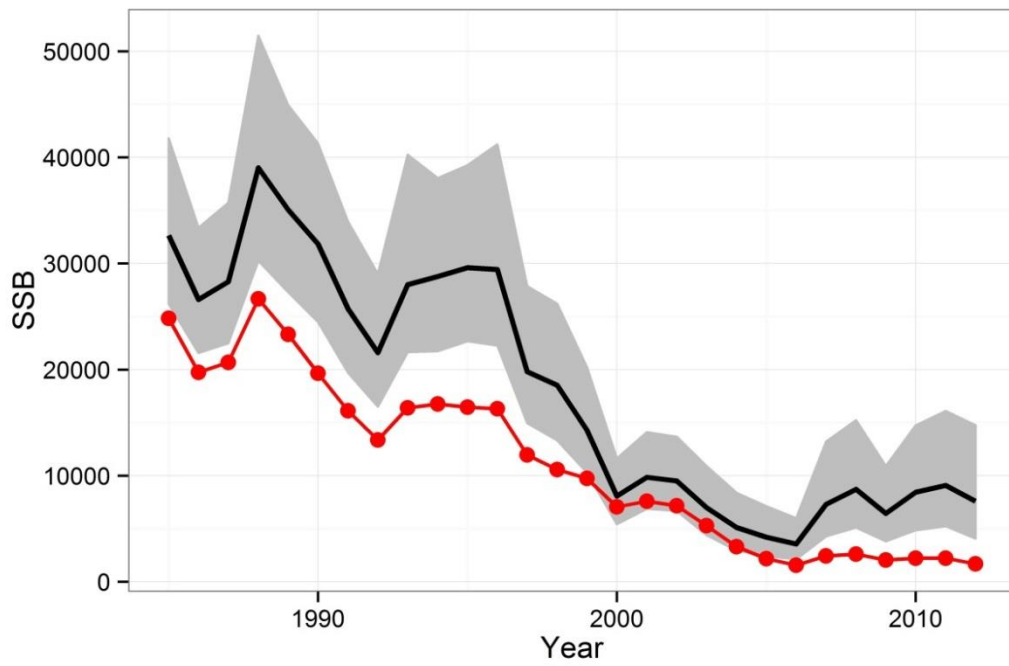


Figure F.20: Time series log SSB (tonnes) for the variable seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The estimates from ICES are given in red.

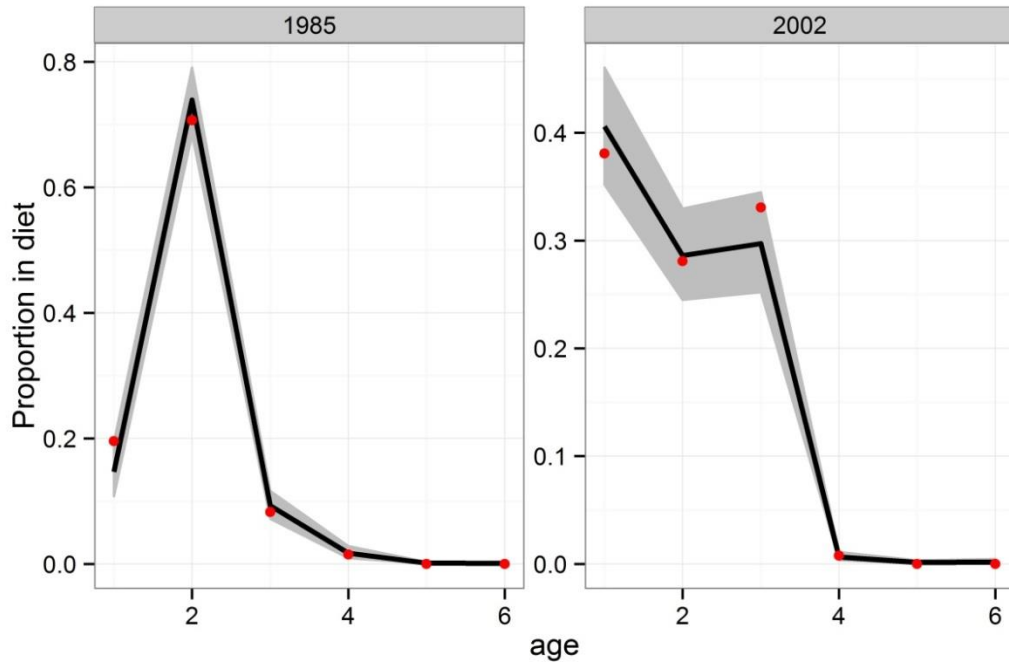


Figure F.21: Proportion at age of cod in grey seal diet for the fixed seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

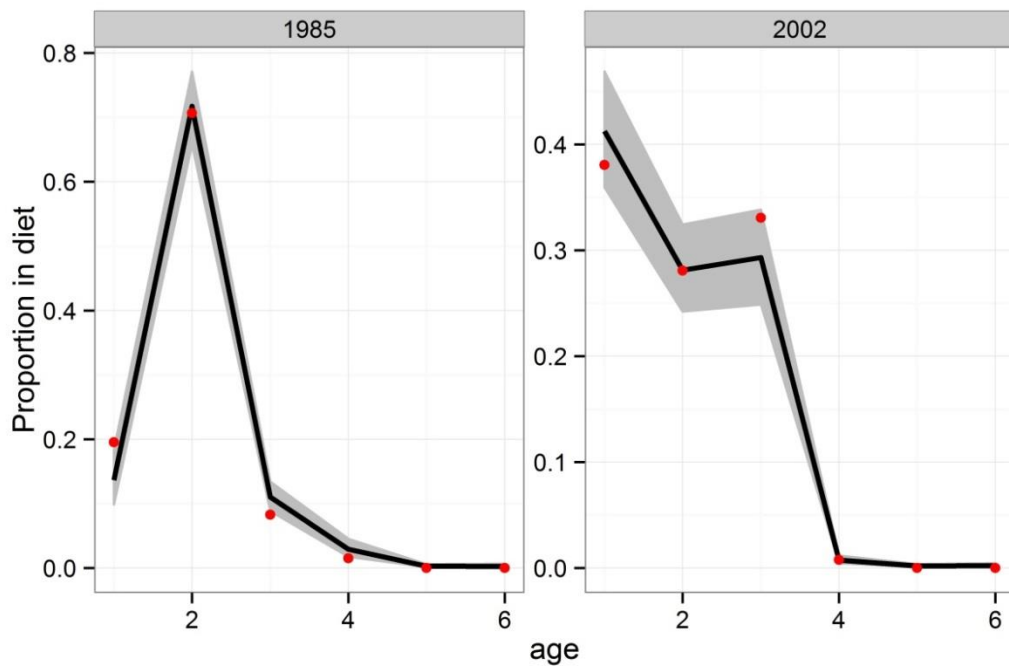


Figure F.22: Proportion at age of cod in grey seal diet for the variable seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

Outputs for haddock

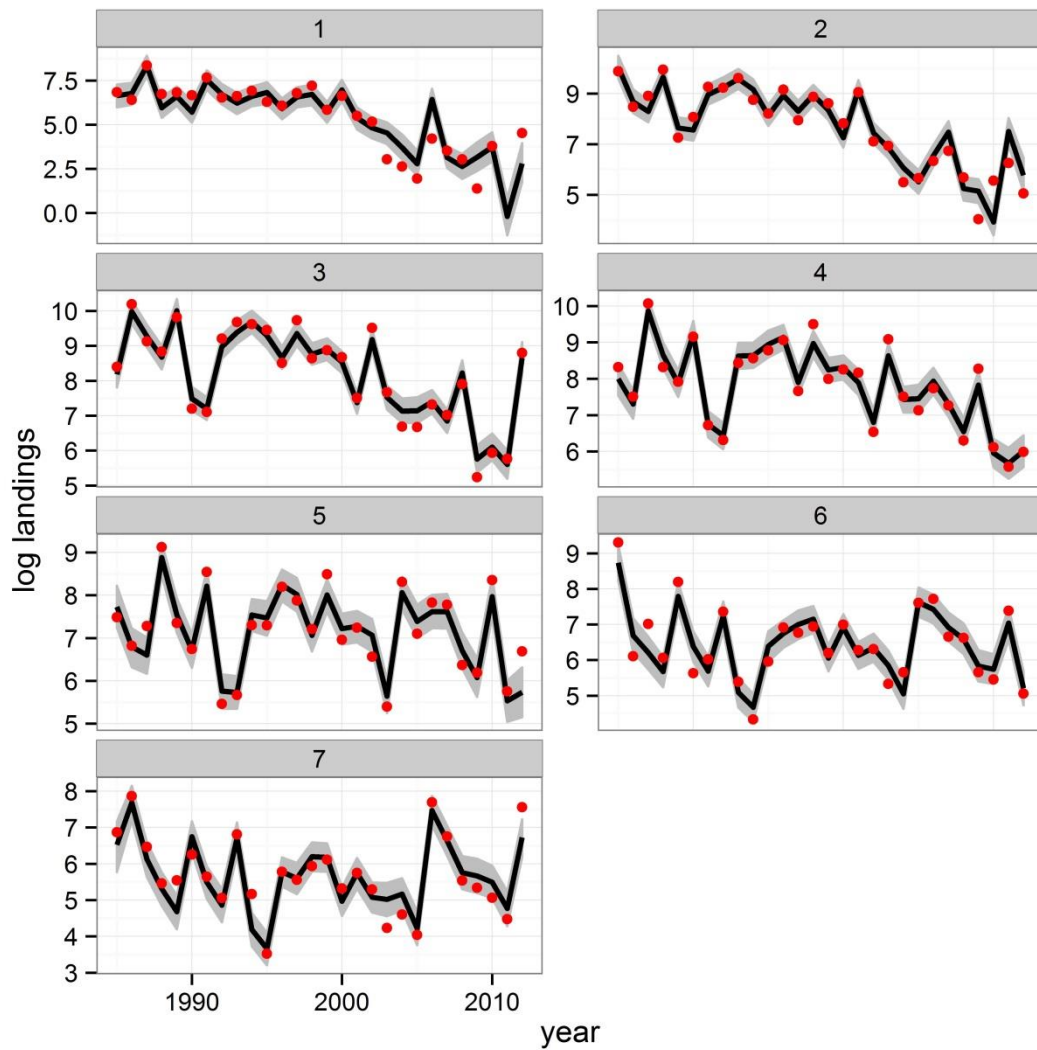


Figure F.23: Time series log landings (in numbers) for the fixed seal predation rate model given by fish age (1 to 7). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

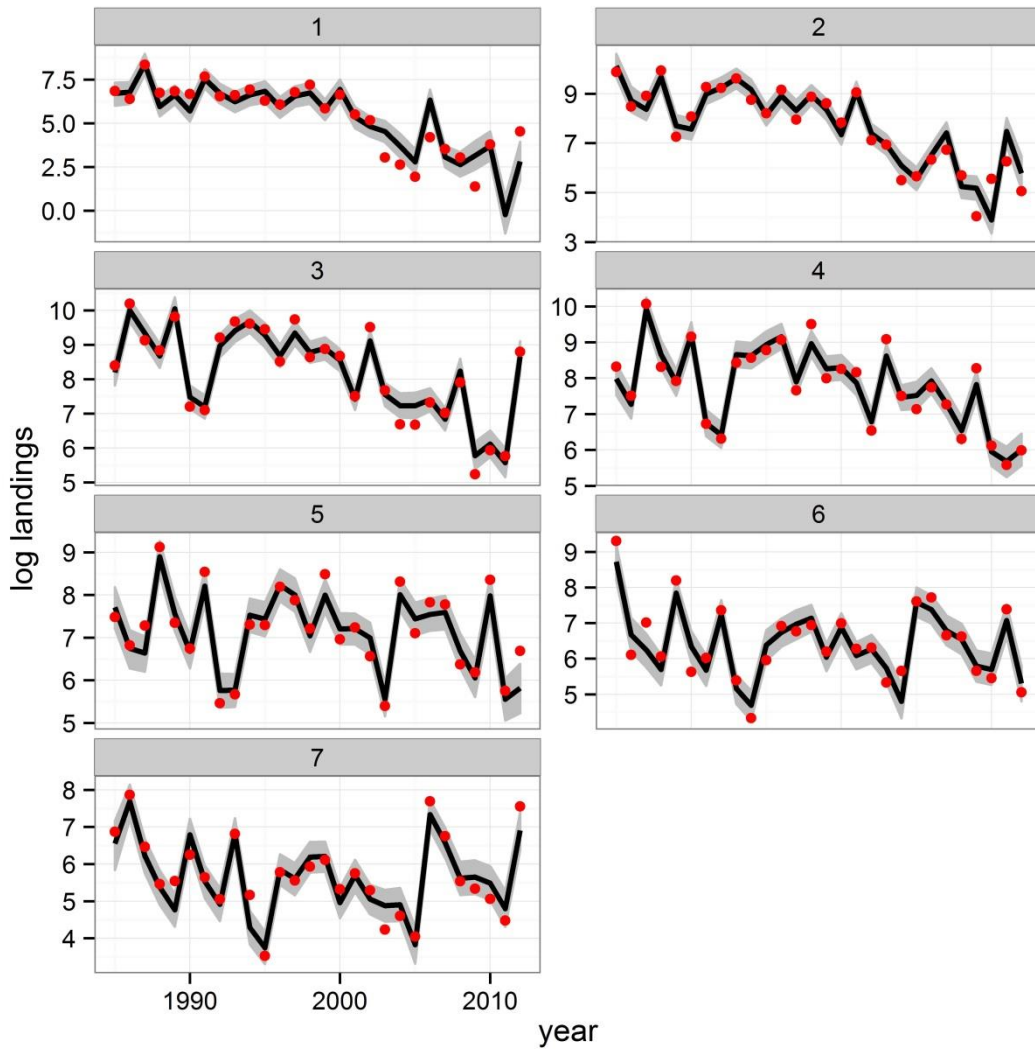


Figure F.24: Time series log landings (in numbers) for the variable seal predation rate model given by fish age (1 to 7). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

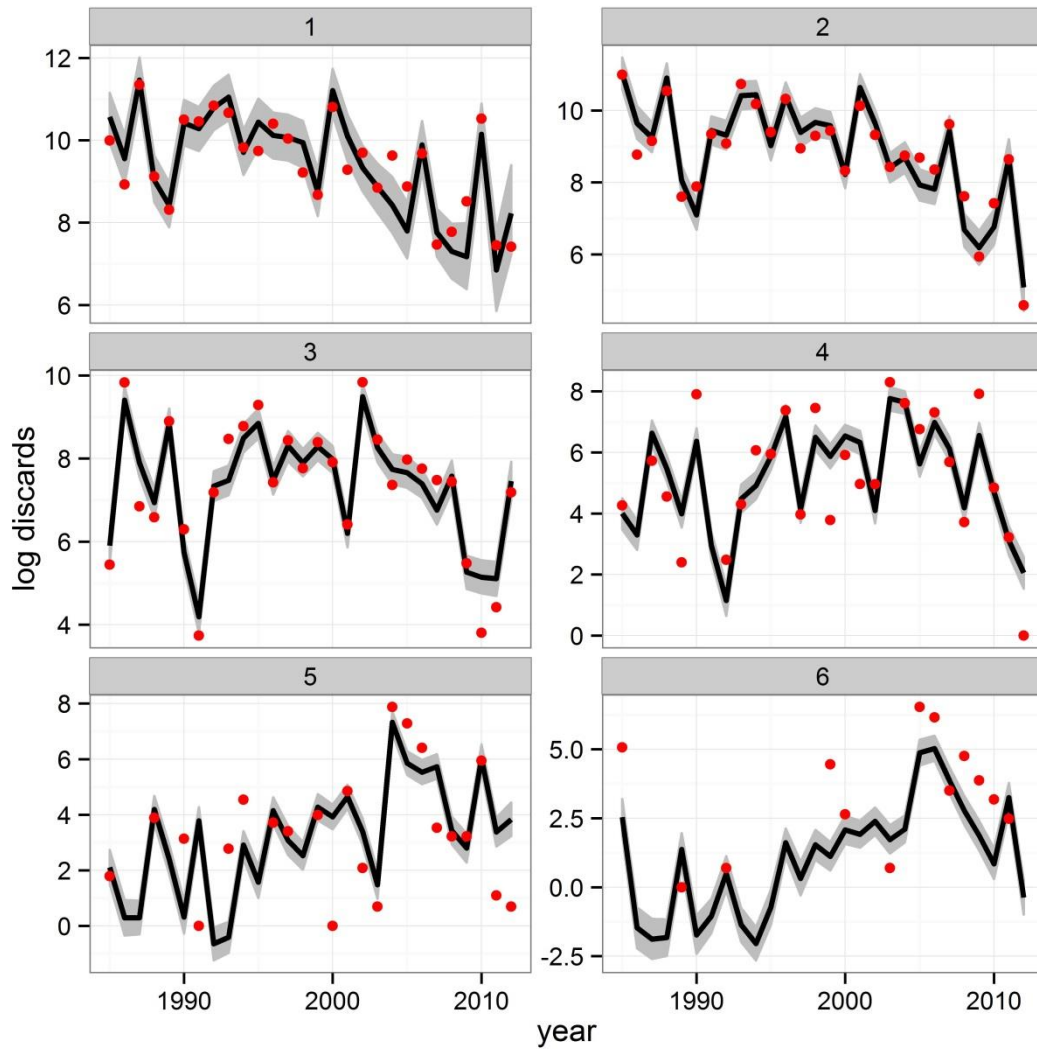


Figure F.25: Time series log discards (in numbers) for the fixed seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

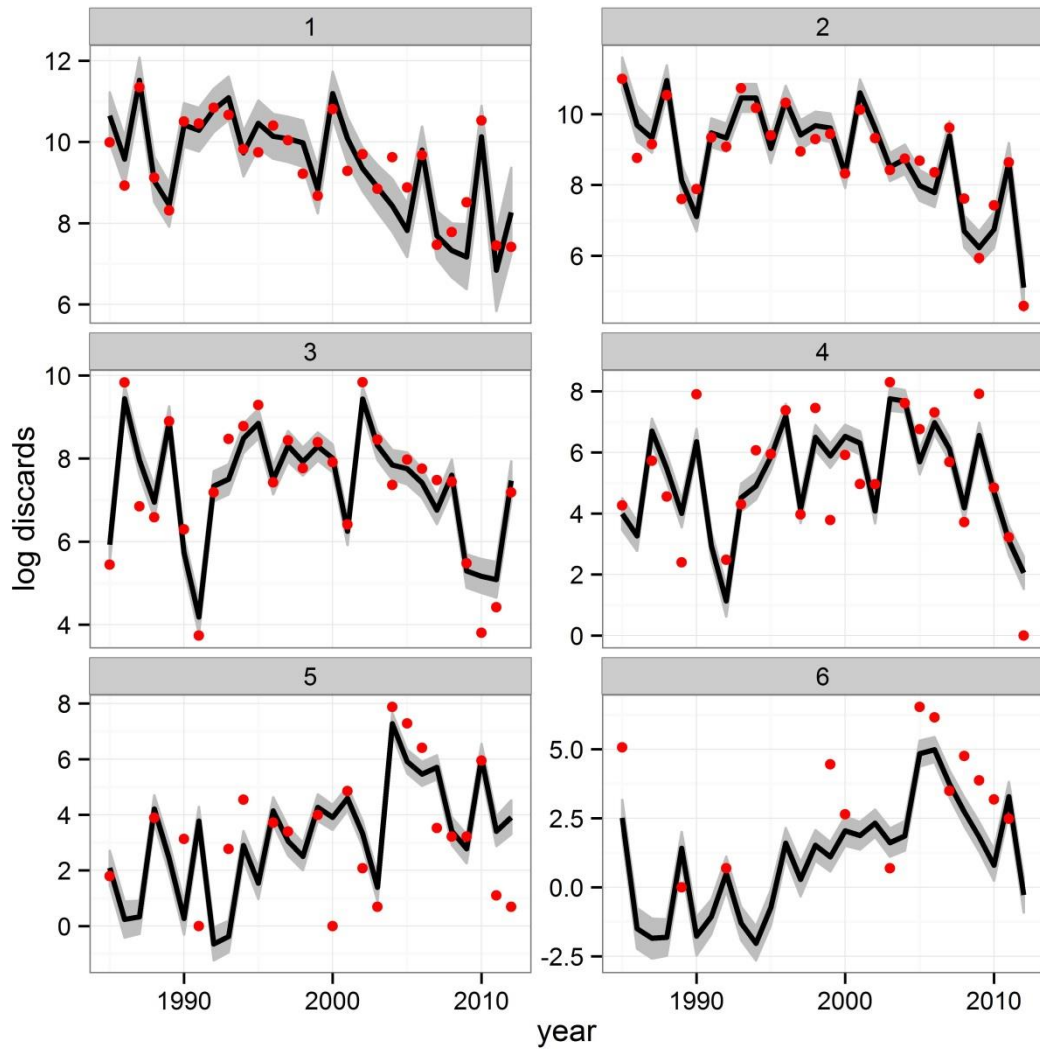


Figure F.26: Time series log discards (in numbers) for the variable seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

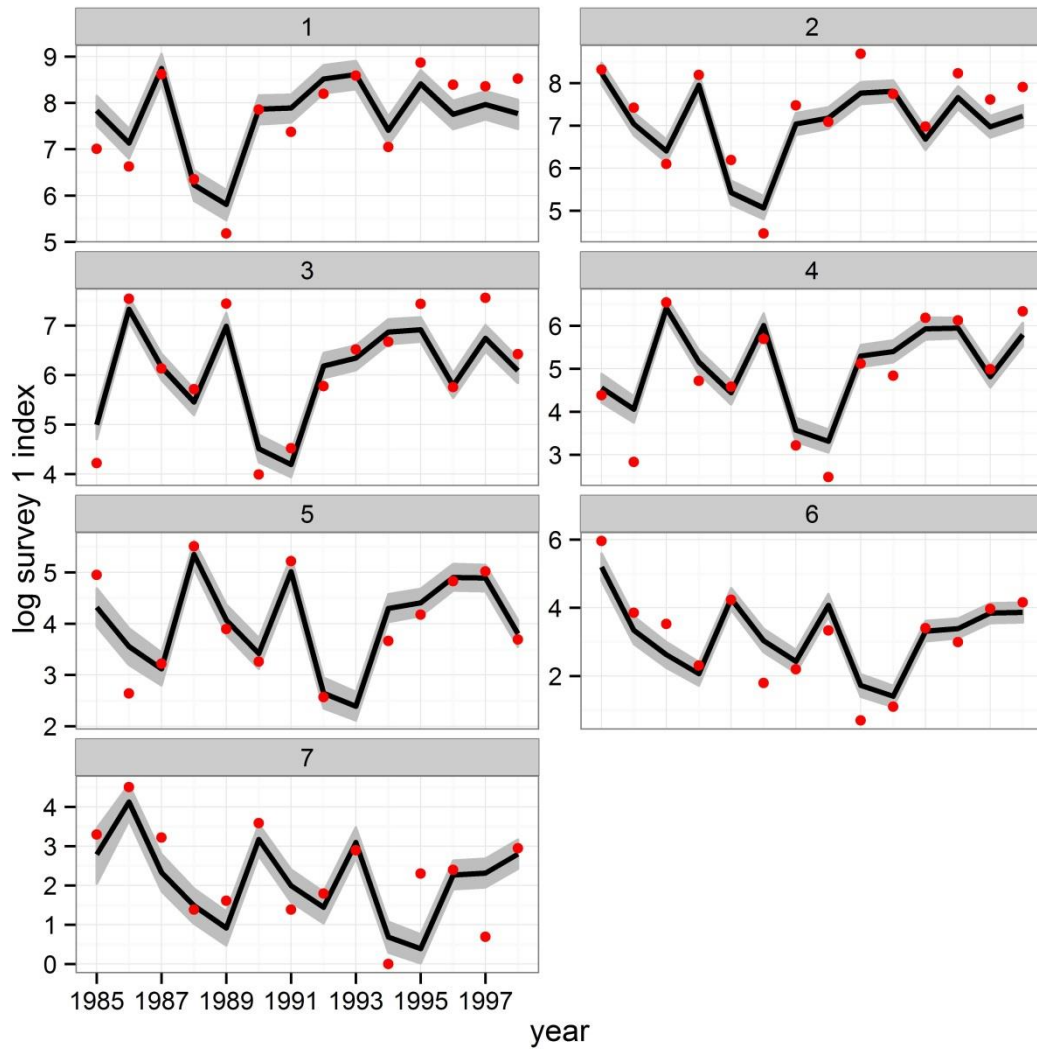


Figure F.27: Time series log abundance indices for the Scottish quarter 1 research survey for the fixed seal predation rate model given by fish age (1 to 7). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

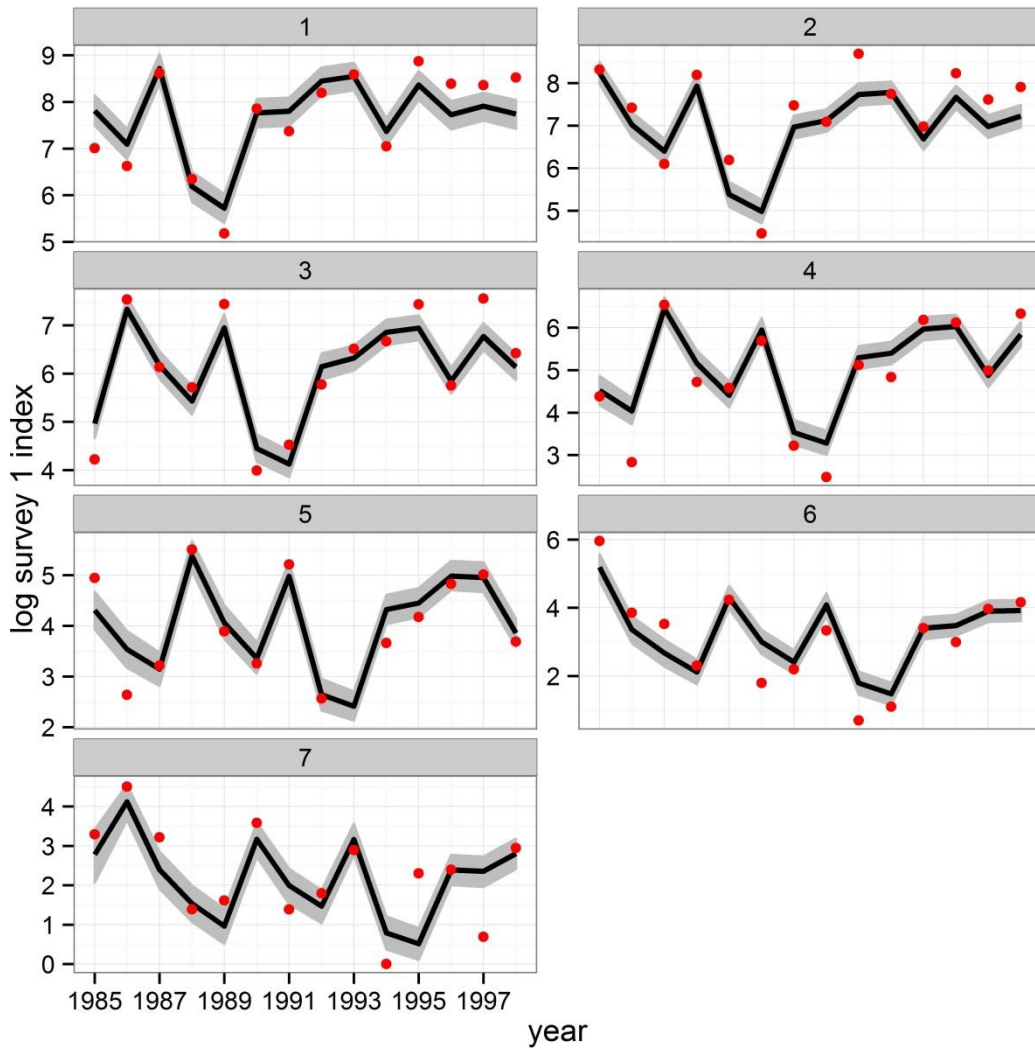


Figure F.28: Time series log abundance indices for the Scottish quarter 1 research survey for the variable seal predation rate model given by fish age (1 to 7). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

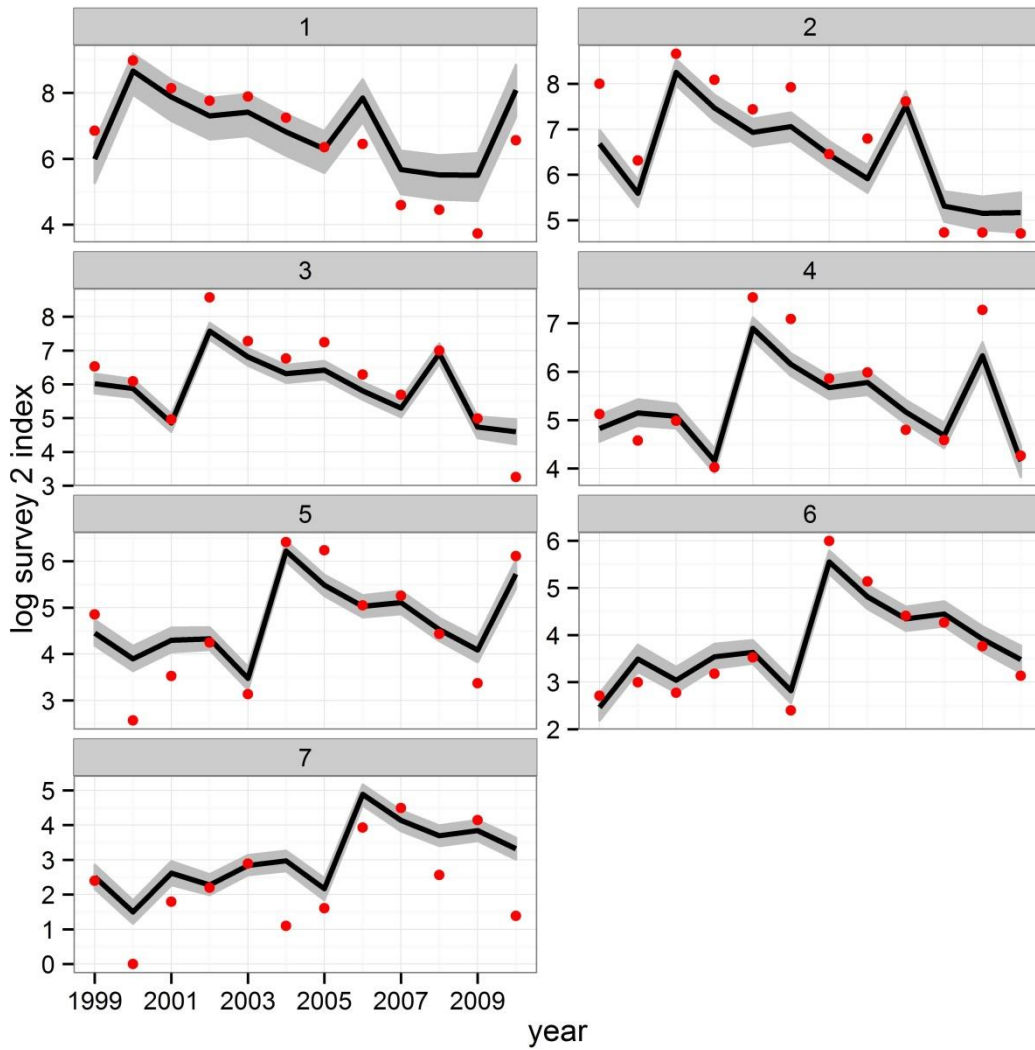


Figure F.29: Time series log abundance indices for the Scottish quarter 1 research survey after change in research vessel and length of the tow for the fixed seal predation rate model given by fish age (1 to 7). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

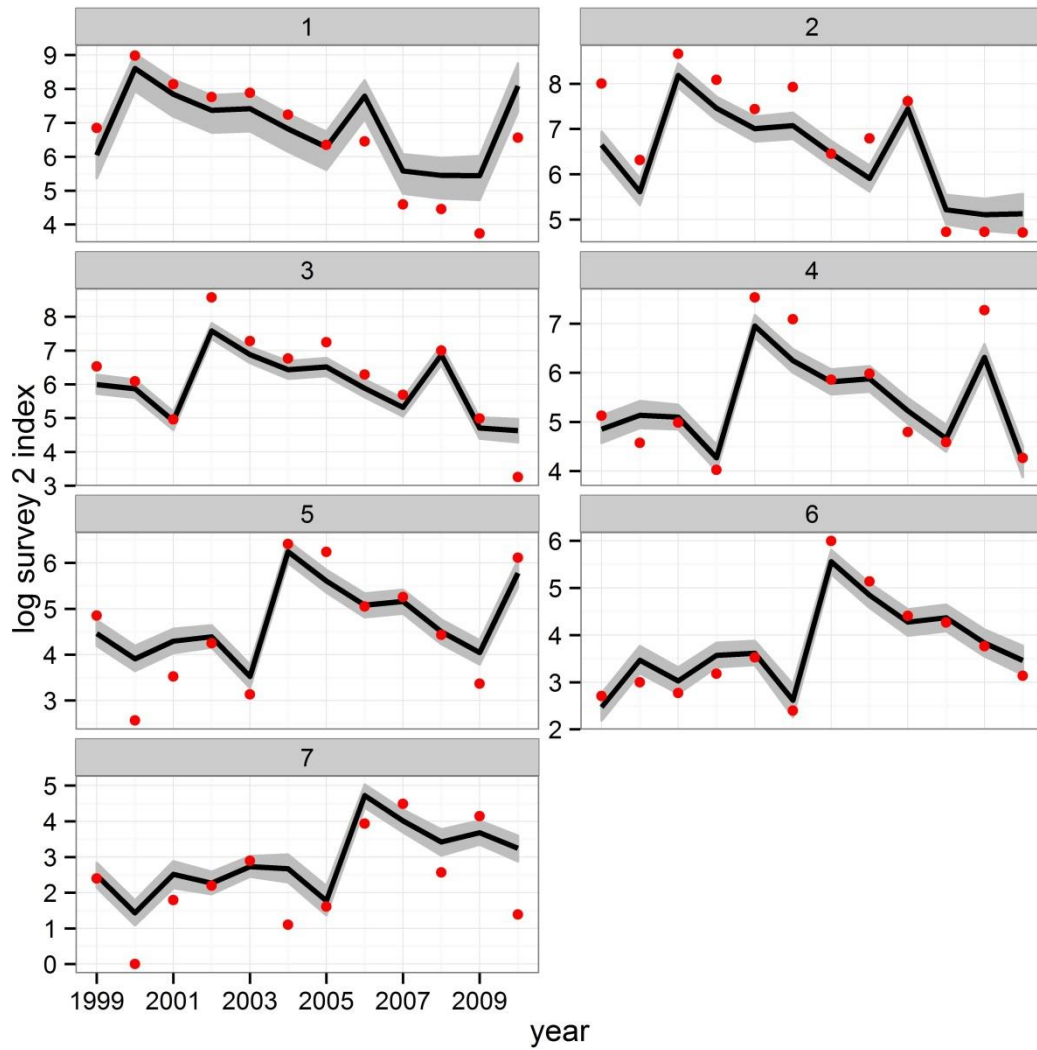


Figure F.30: Time series log abundance indices for the Scottish quarter 1 research survey after change in research vessel and length of the tow for the variable seal predation rate model given by fish age (1 to 7). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

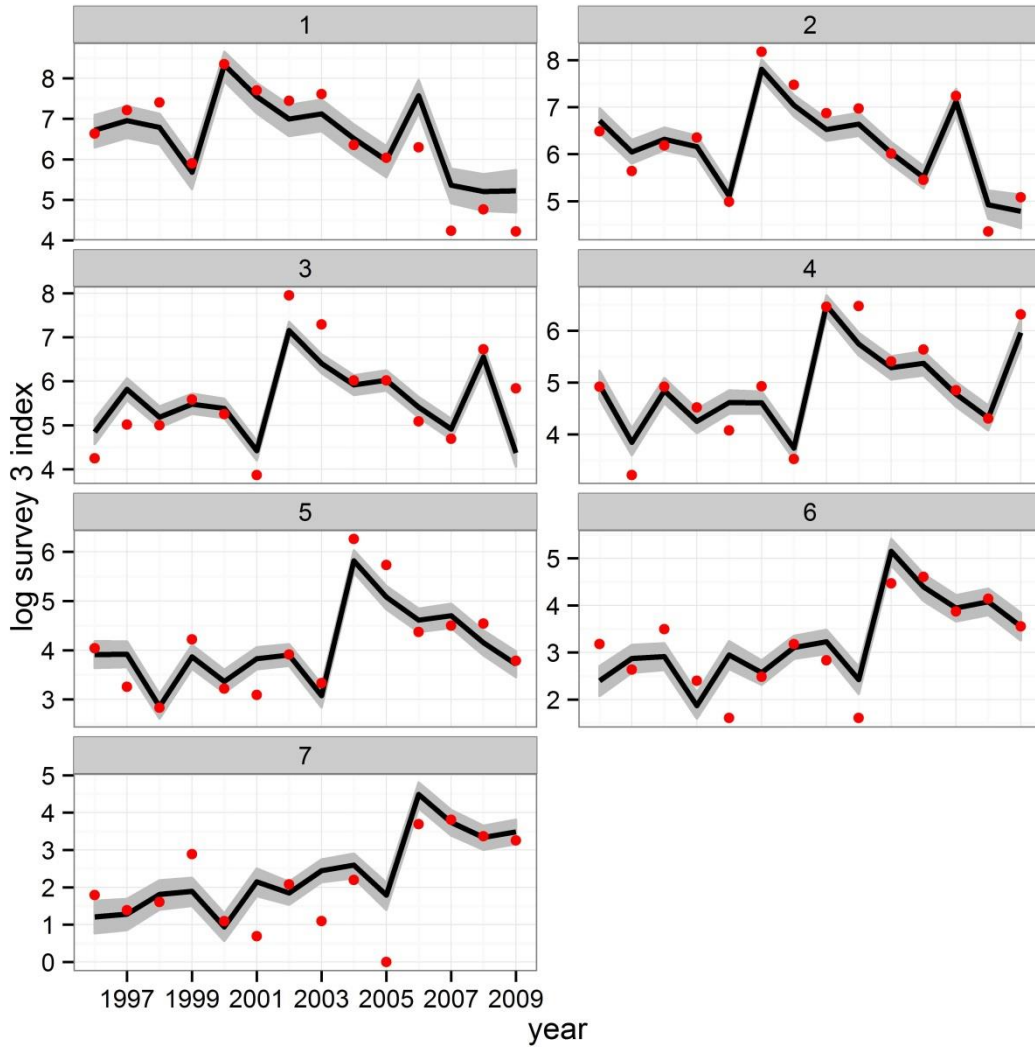


Figure F.31: Time series log abundance indices for the Scottish quarter 4 research survey for the fixed seal predation rate model given by fish age (1 to 7). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

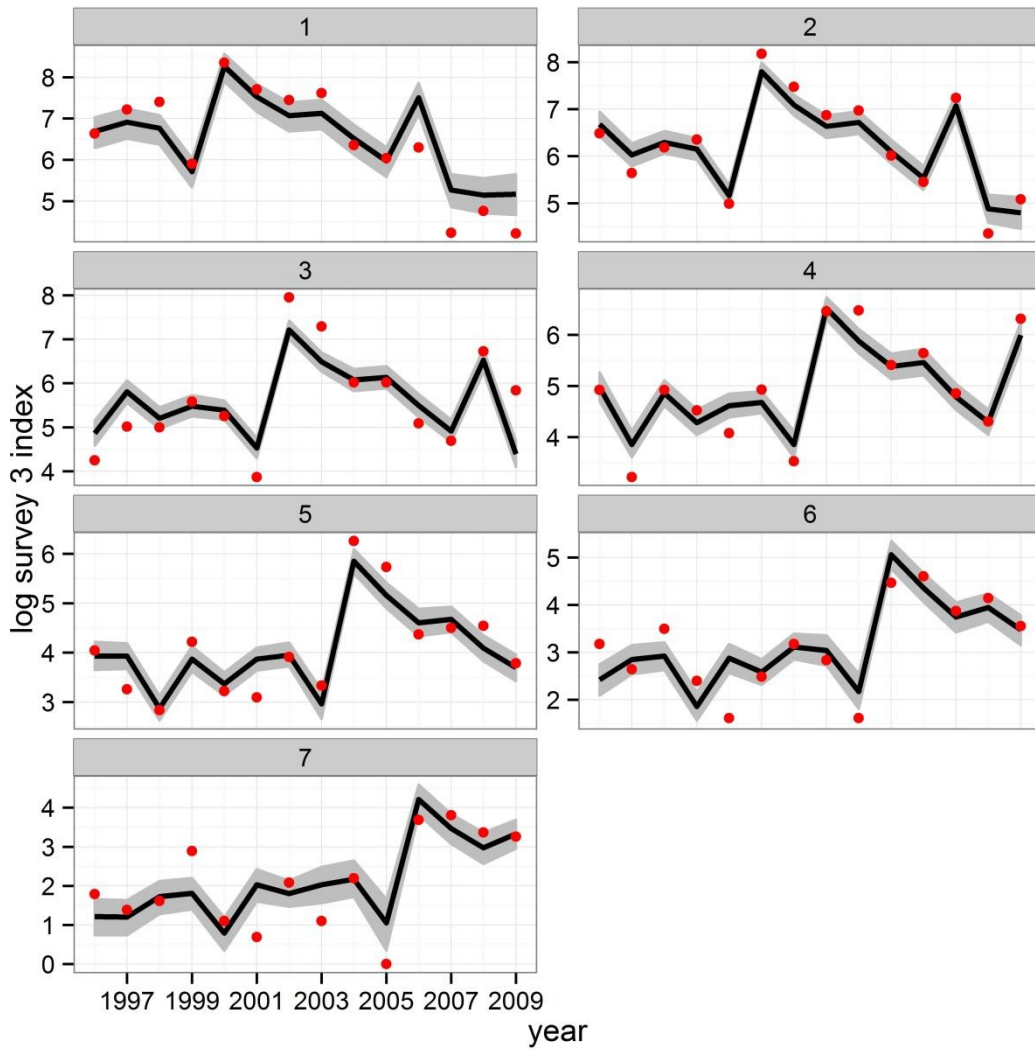


Figure F.32: Time series log abundance indices for the Scottish quarter 4 research survey for the variable seal predation rate model given by fish age (1 to 7). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

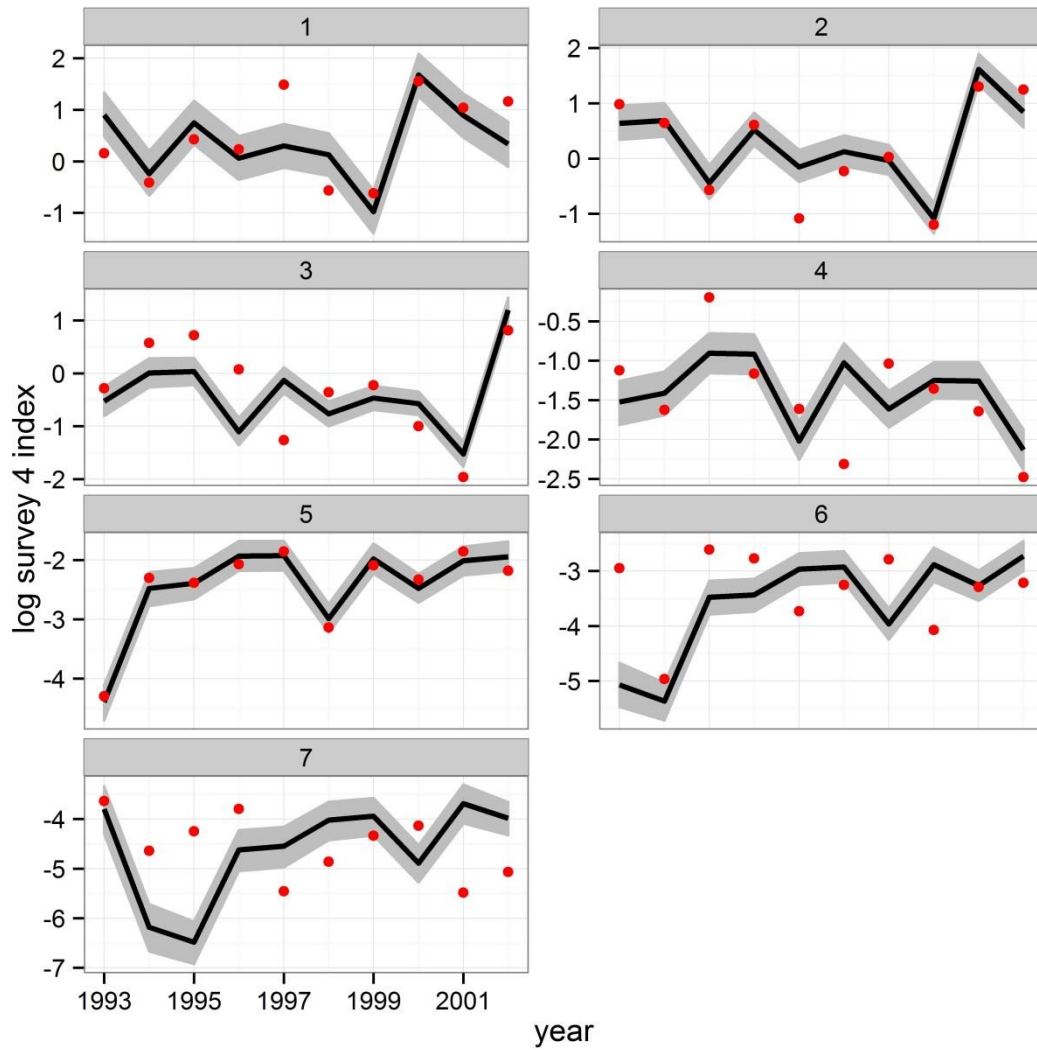


Figure F.33: Time series log abundance indices for the Irish groundfish research survey for the fixed seal predation rate model given by fish age (1 to 7). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

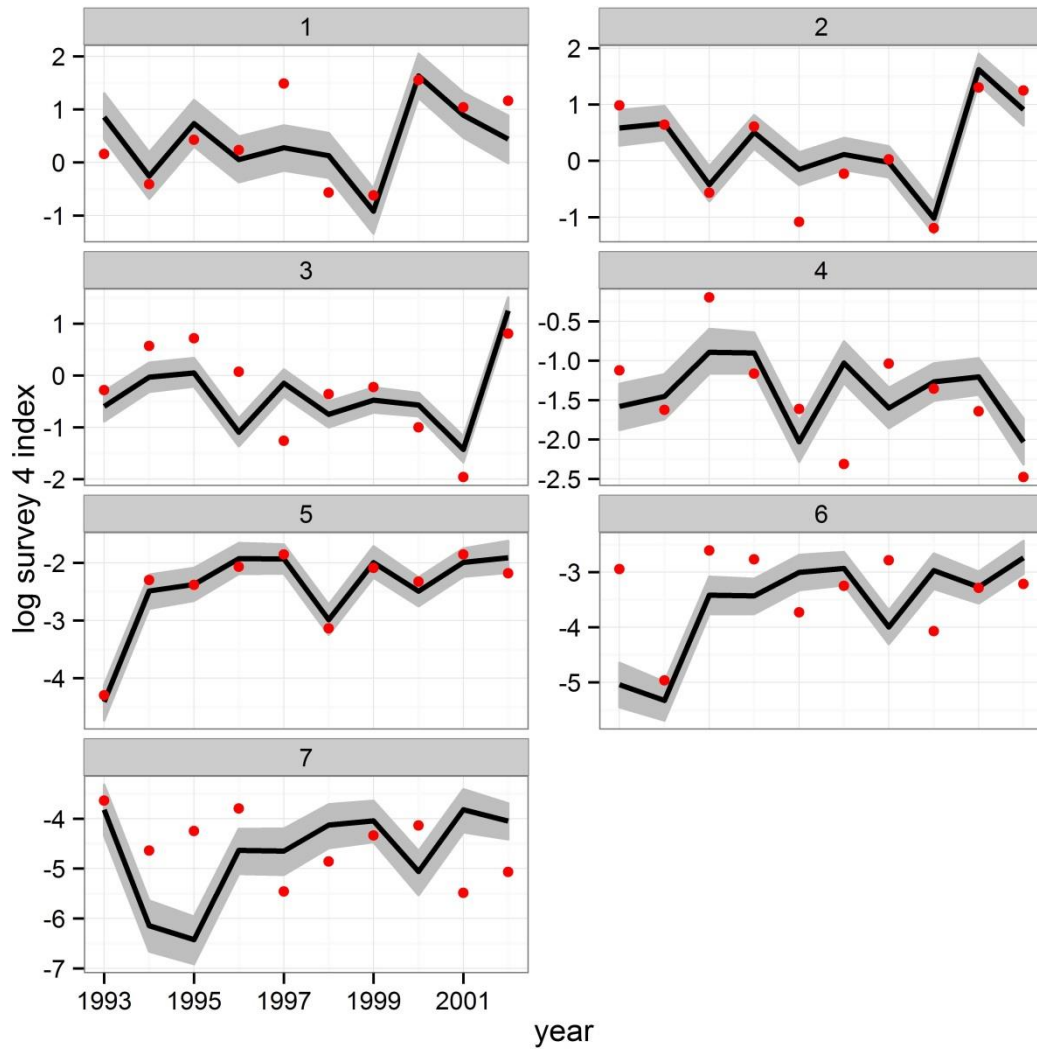


Figure F.34: Time series log abundance indices for the Irish groundfish research survey for the variable seal predation rate model given by fish age (1 to 7). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

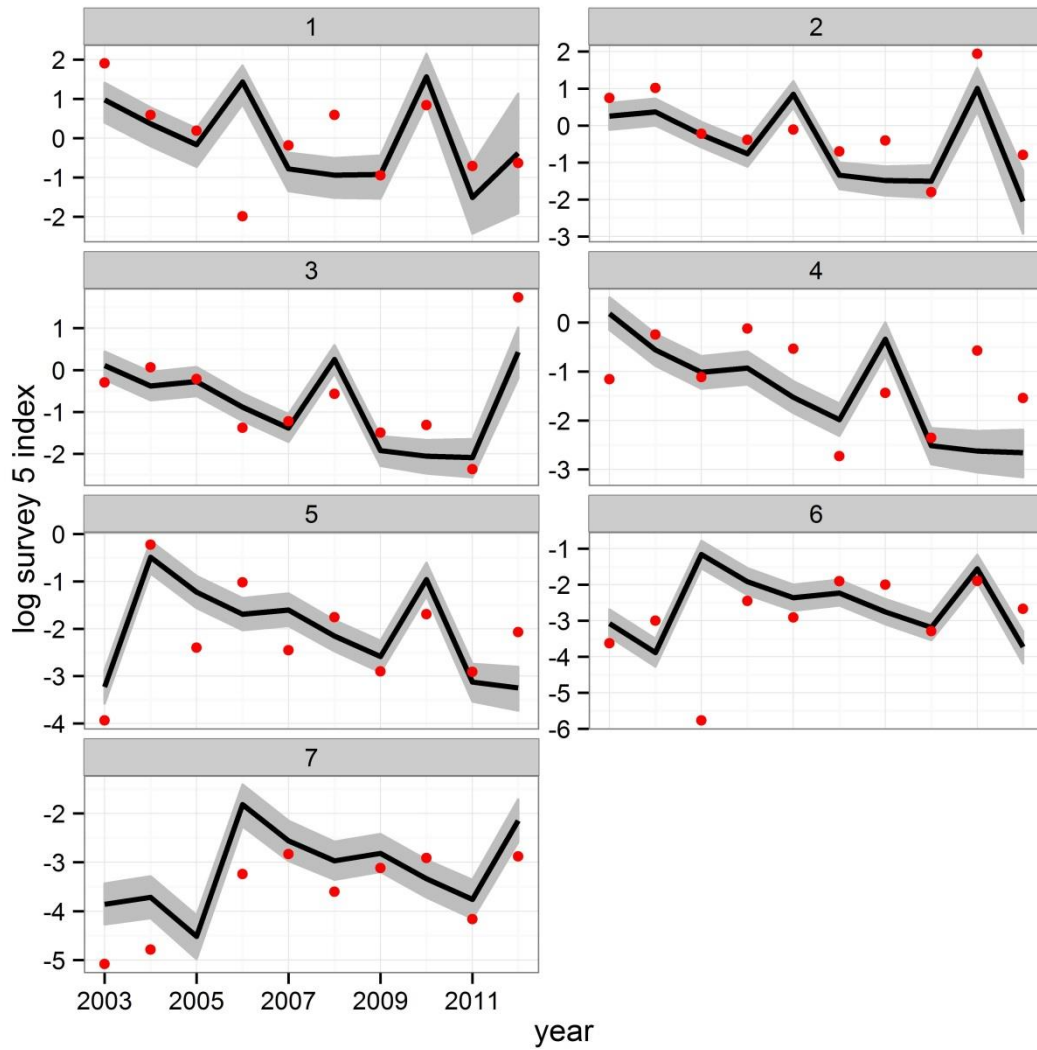


Figure F.35: Time series log abundance indices for the Irish West Coast groundfish research survey for the fixed seal predation rate model given by fish age (1 to 7). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

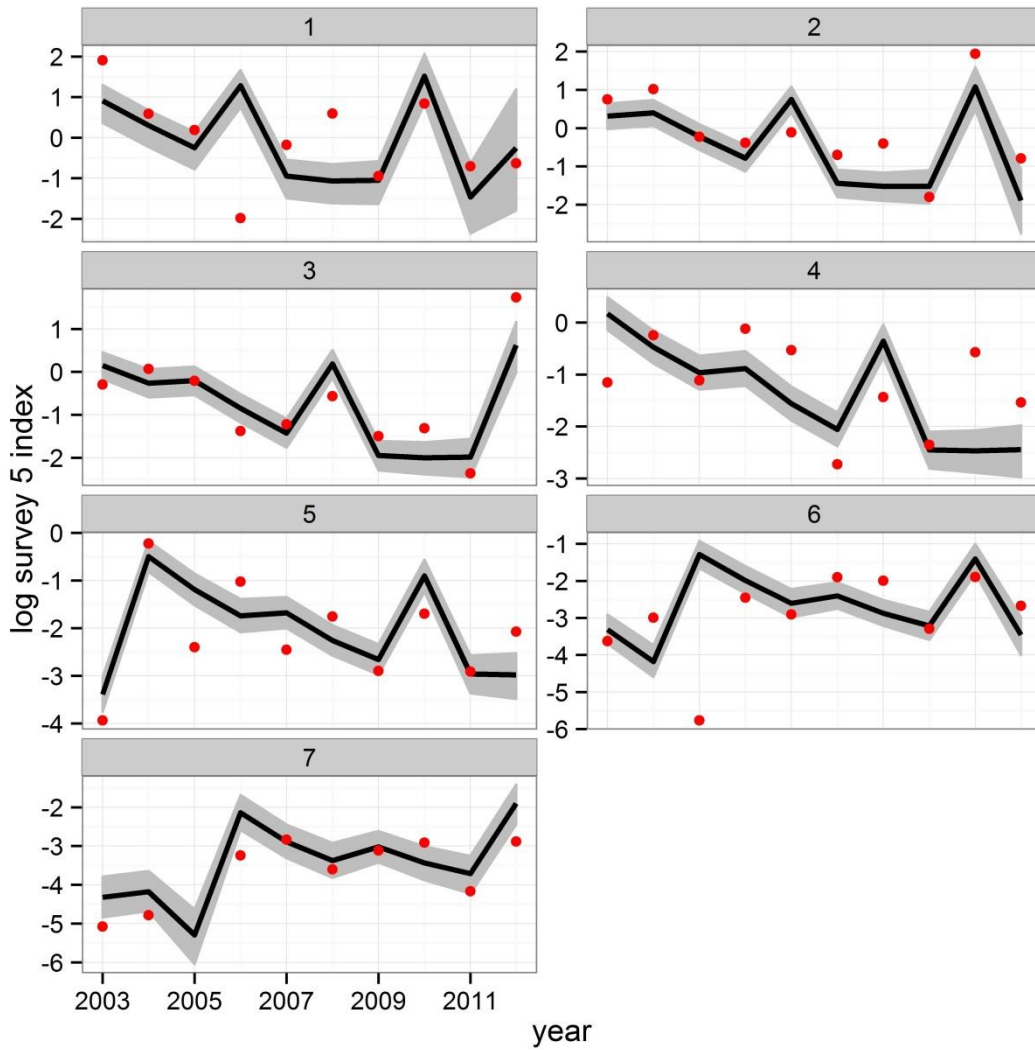


Figure F.36: Time series log abundance indices for the Irish West Coast groundfish research survey for the variable seal predation rate model given by fish age (1 to 7). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

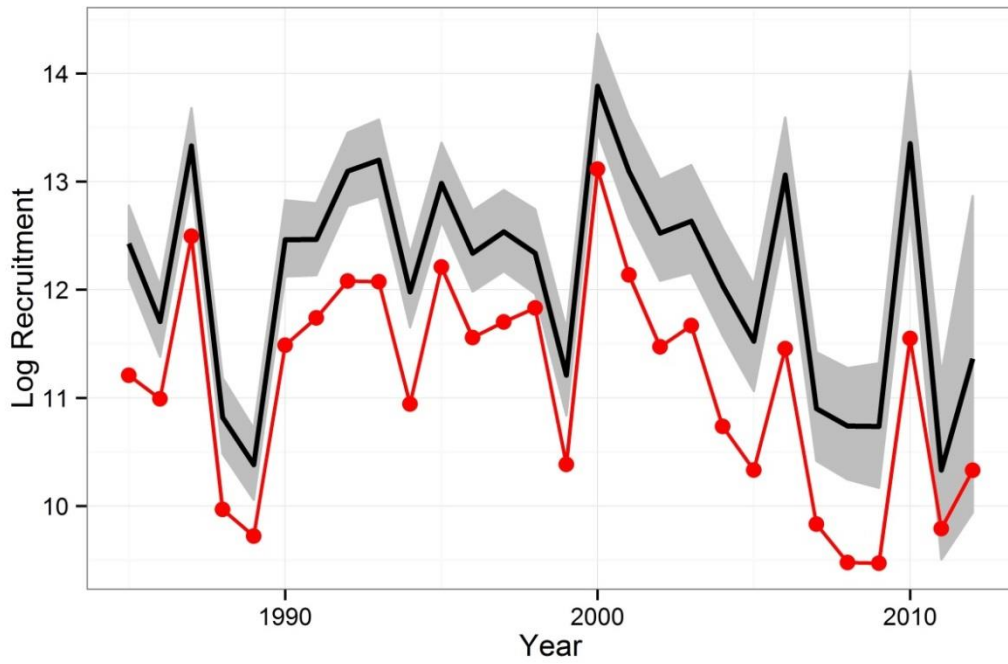


Figure F.37: Time series log recruitment (thousands) for the fixed seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The estimates from ICES are given in red.

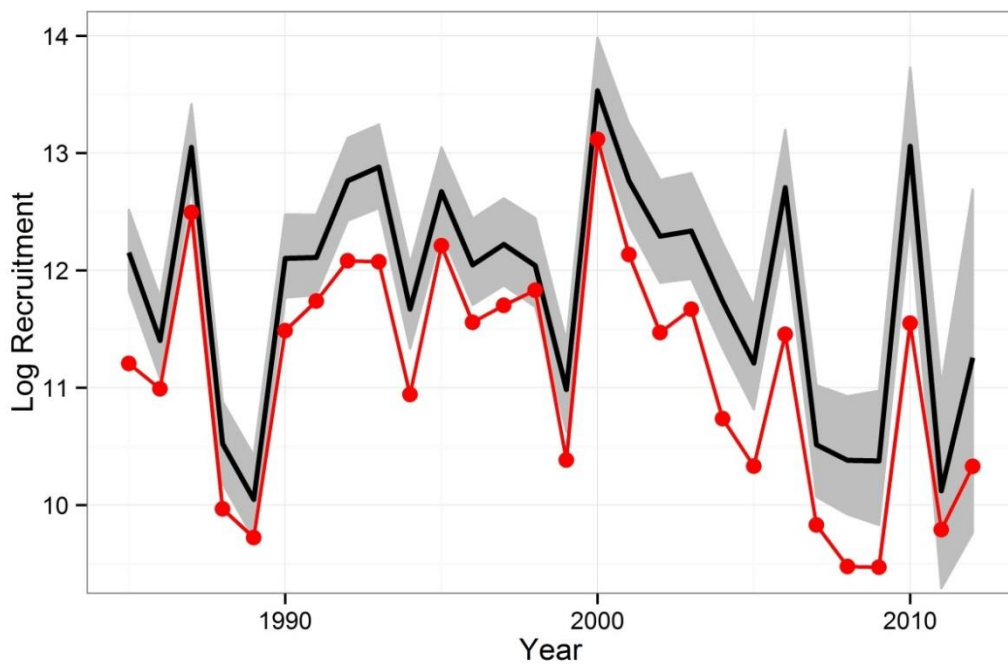


Figure F.38: Time series log recruitment (thousands) for the variable seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The estimates from ICES are given in red.

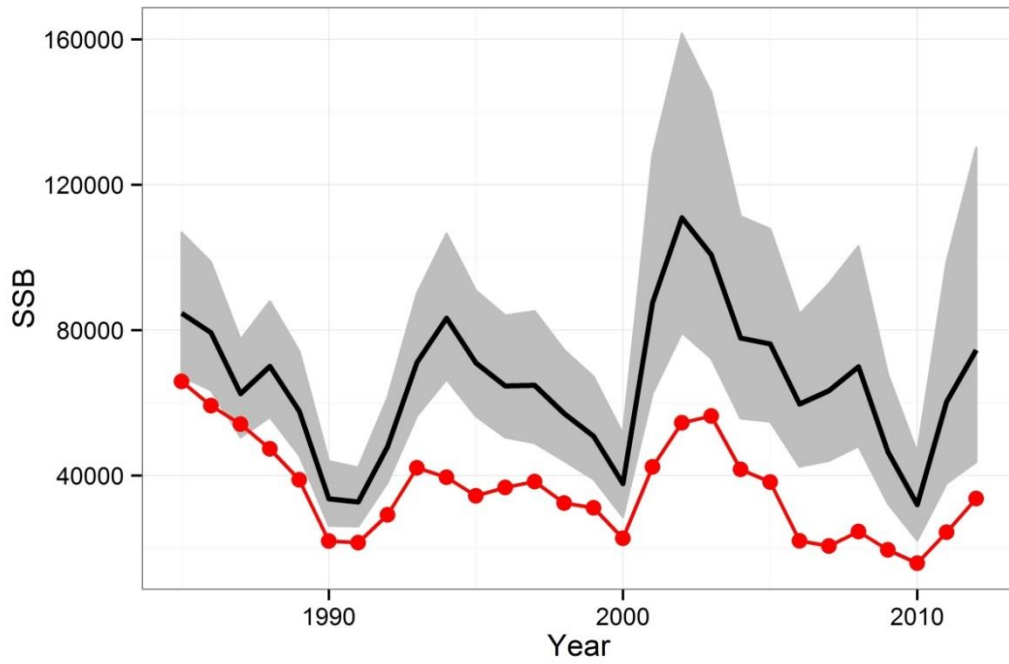


Figure F.39: Time series log SSB (tonnes) for the fixed seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The estimates from ICES are given in red.

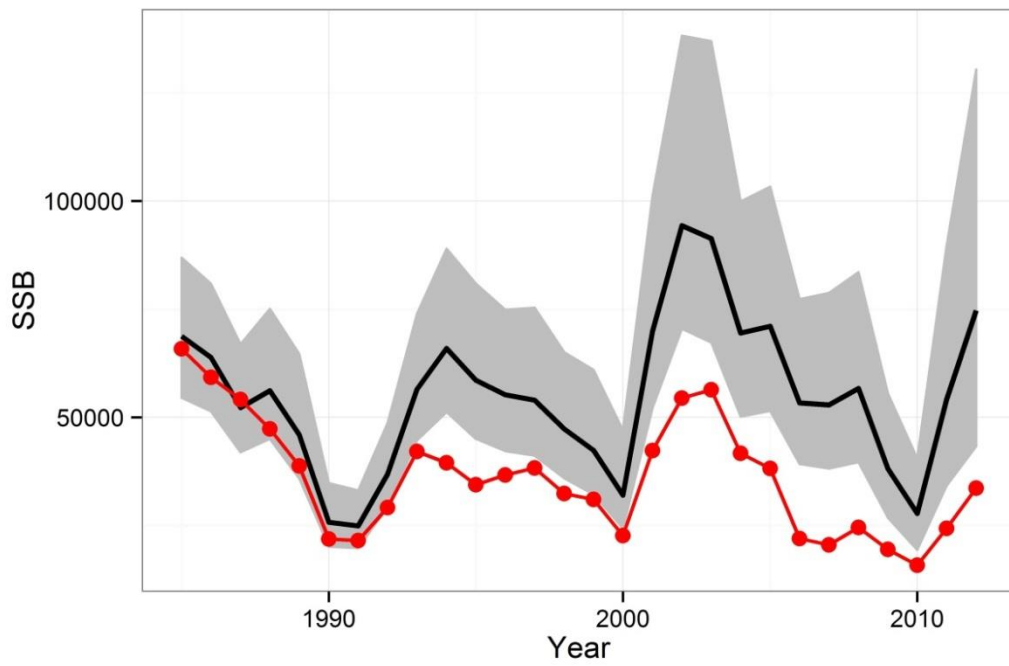


Figure F.40: Time series log SSB (tonnes) for the variable seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The estimates from ICES are given in red.

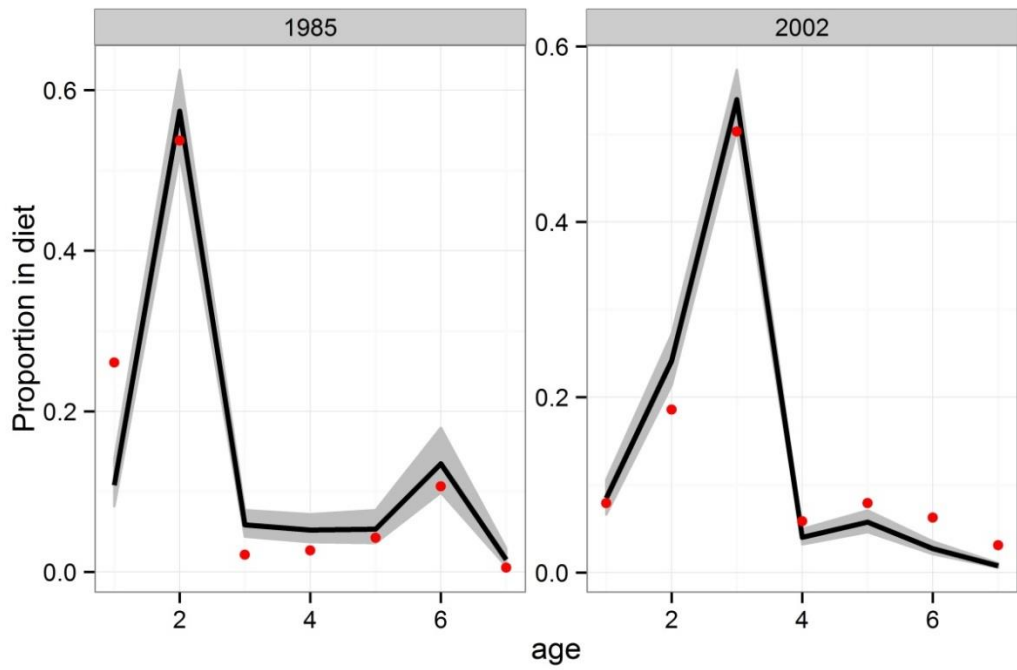


Figure F.41: Proportion at age of cod in grey seal diet for the fixed seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

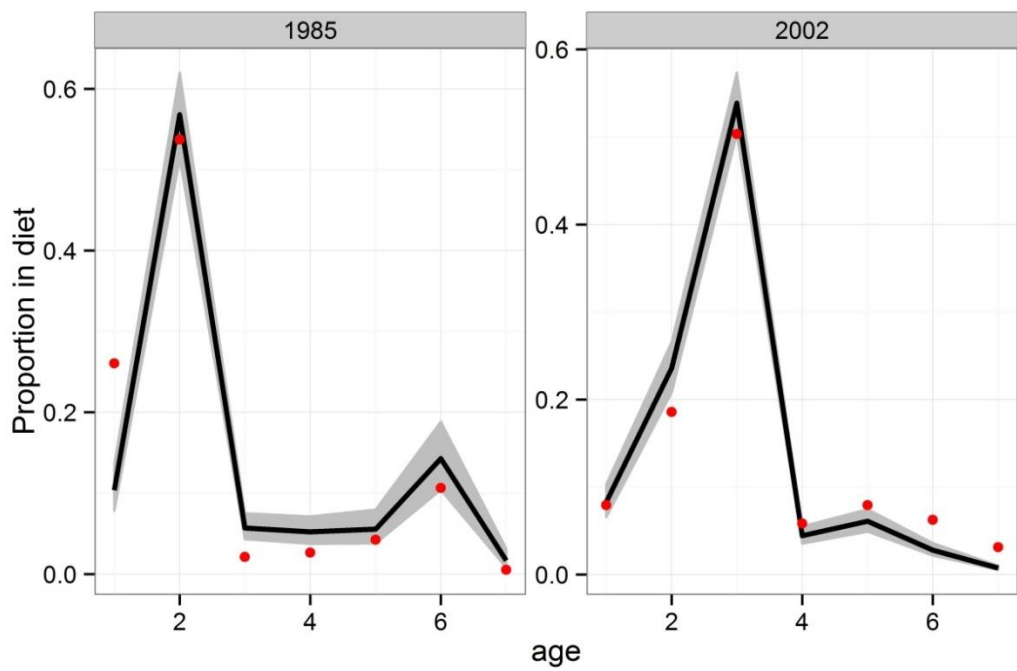


Figure F.42: Proportion at age of cod in grey seal diet for the variable seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

Outputs for whiting (survey data 2001-2005 removed)

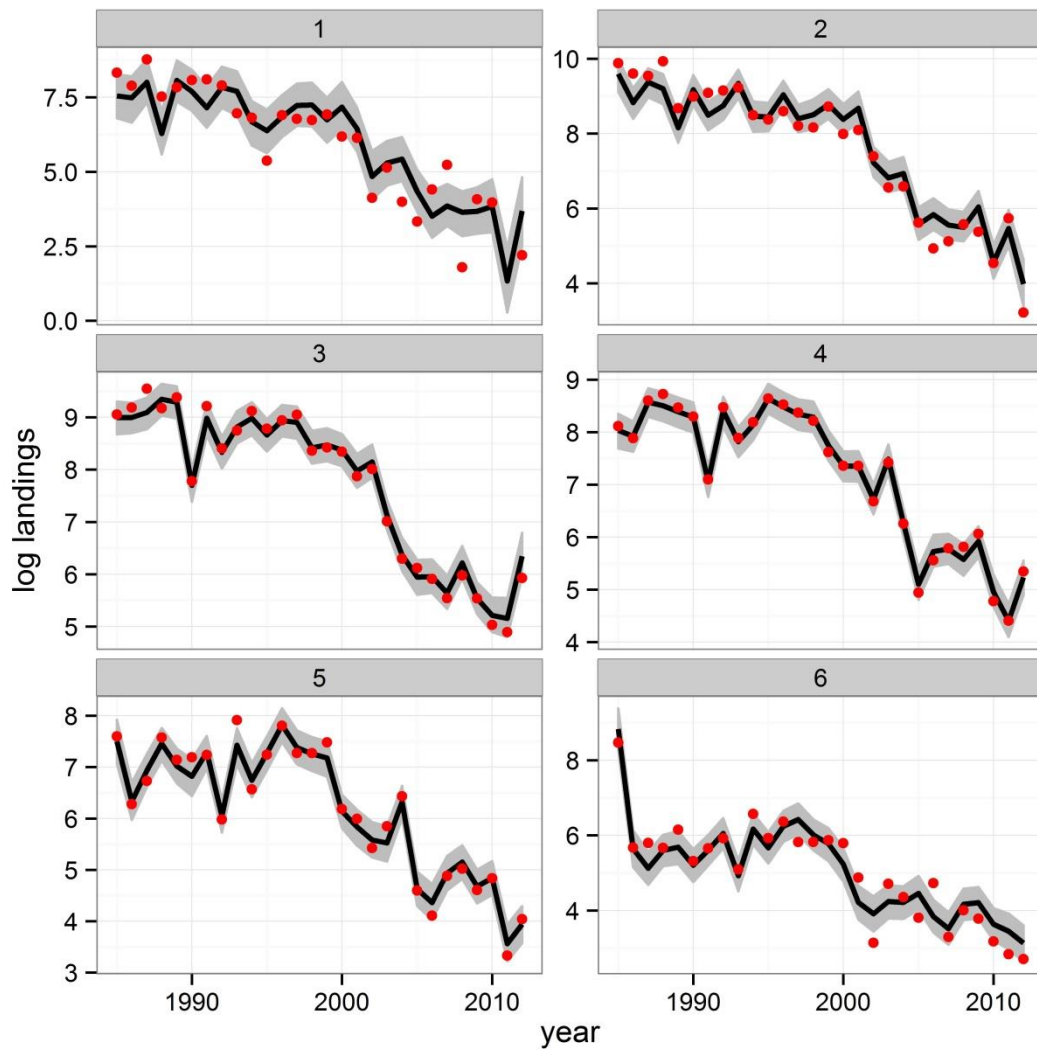


Figure F.43: Time series log landings (in numbers) for the fixed seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

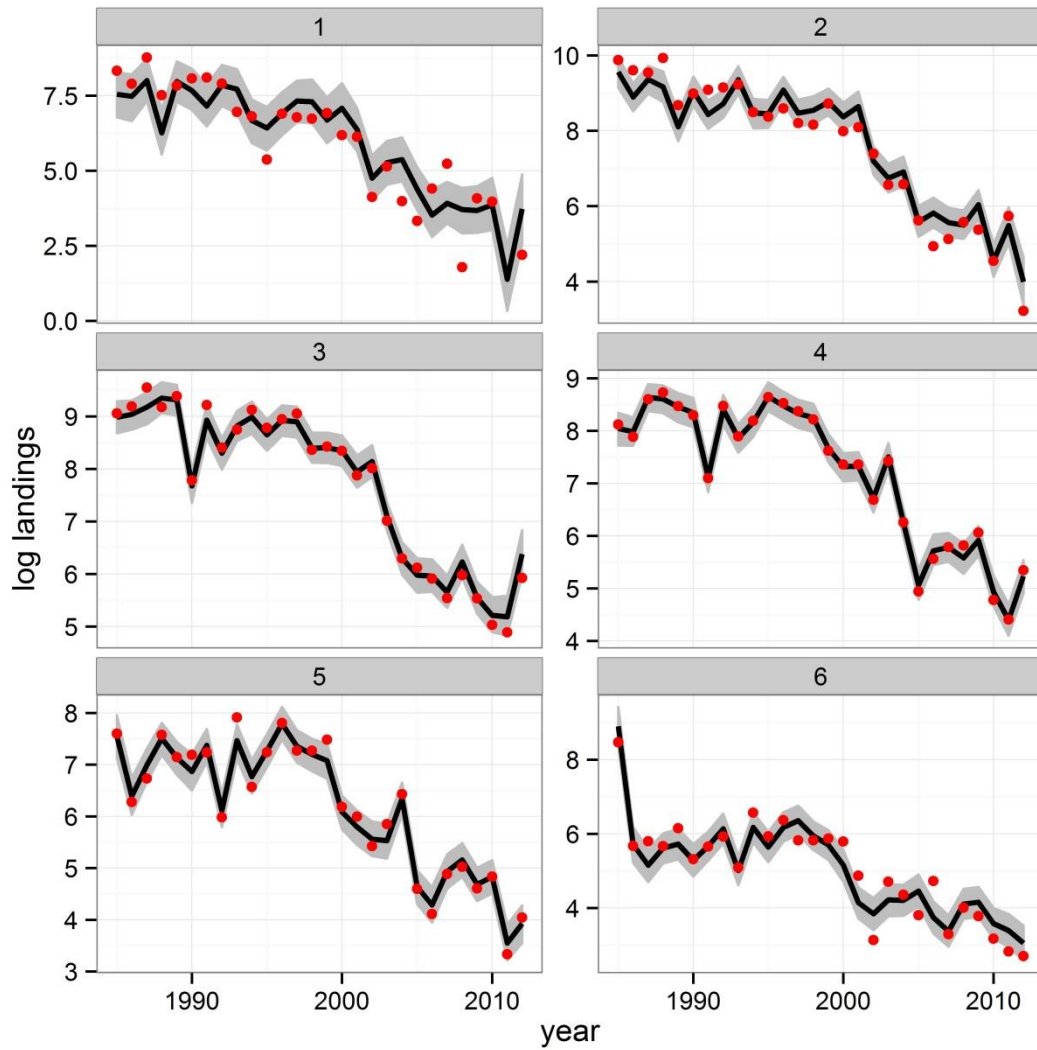


Figure F.44: Time series log landings (in numbers) for the variable seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

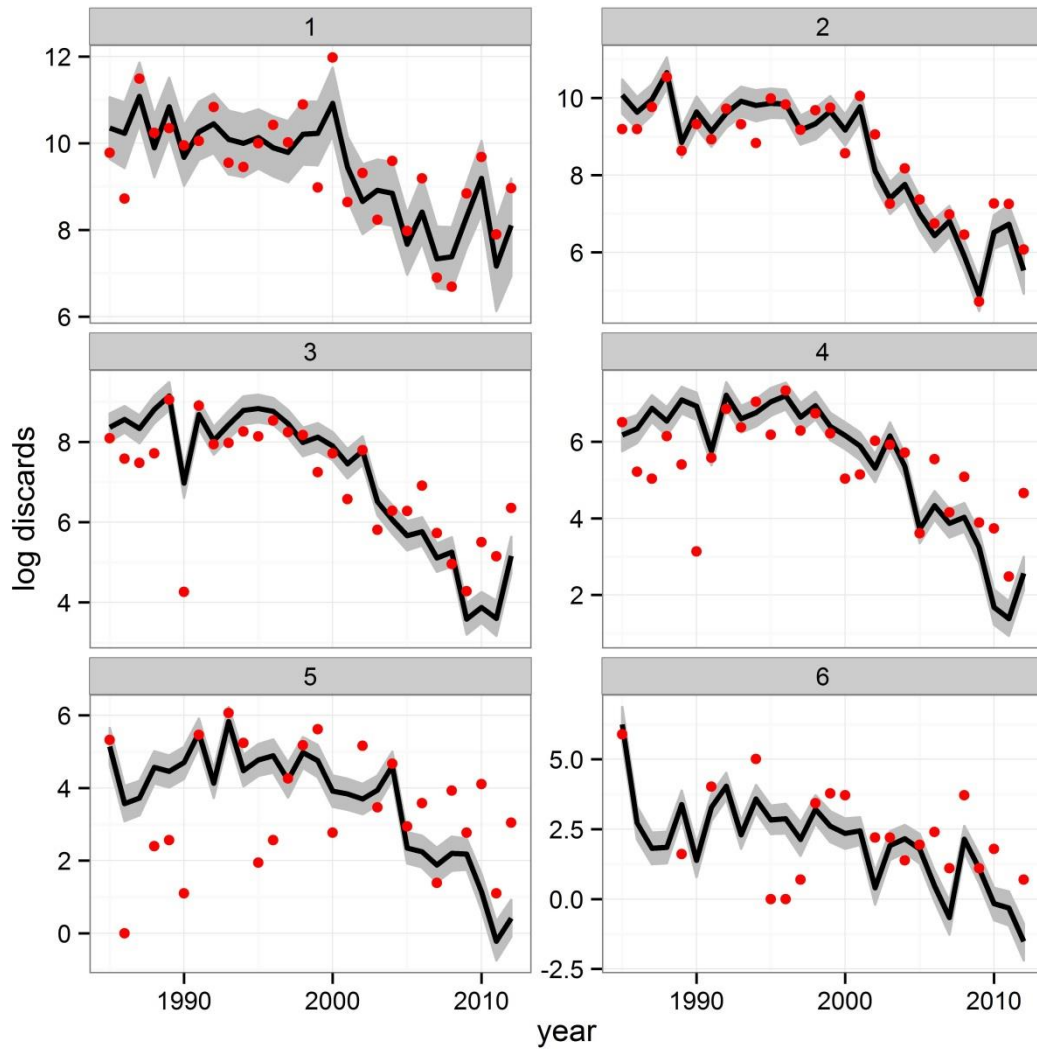


Figure F.45: Time series log discards (in numbers) for the fixed seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

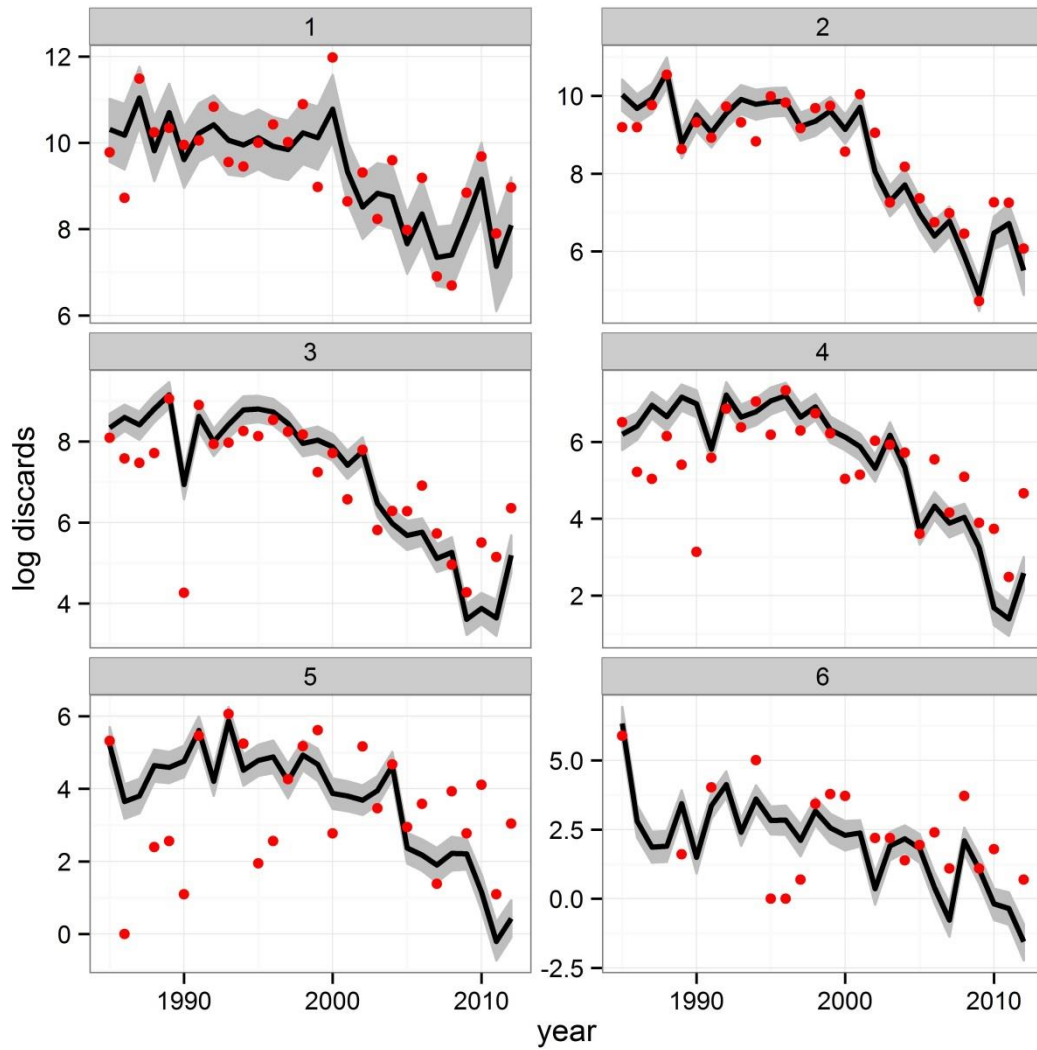


Figure F.46: Time series log discards (in numbers) for the variable seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

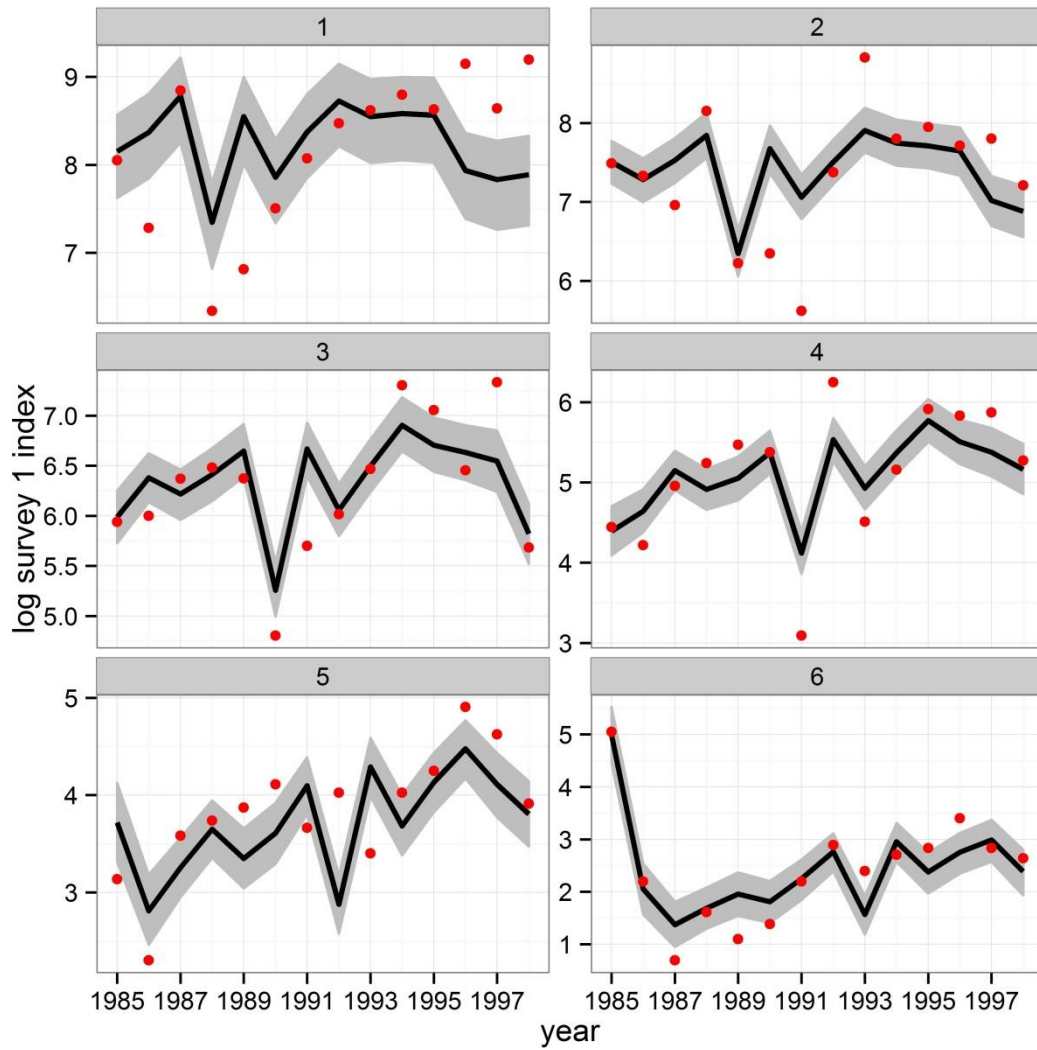


Figure F.47: Time series log abundance indices for the Scottish quarter 1 research survey for the fixed seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

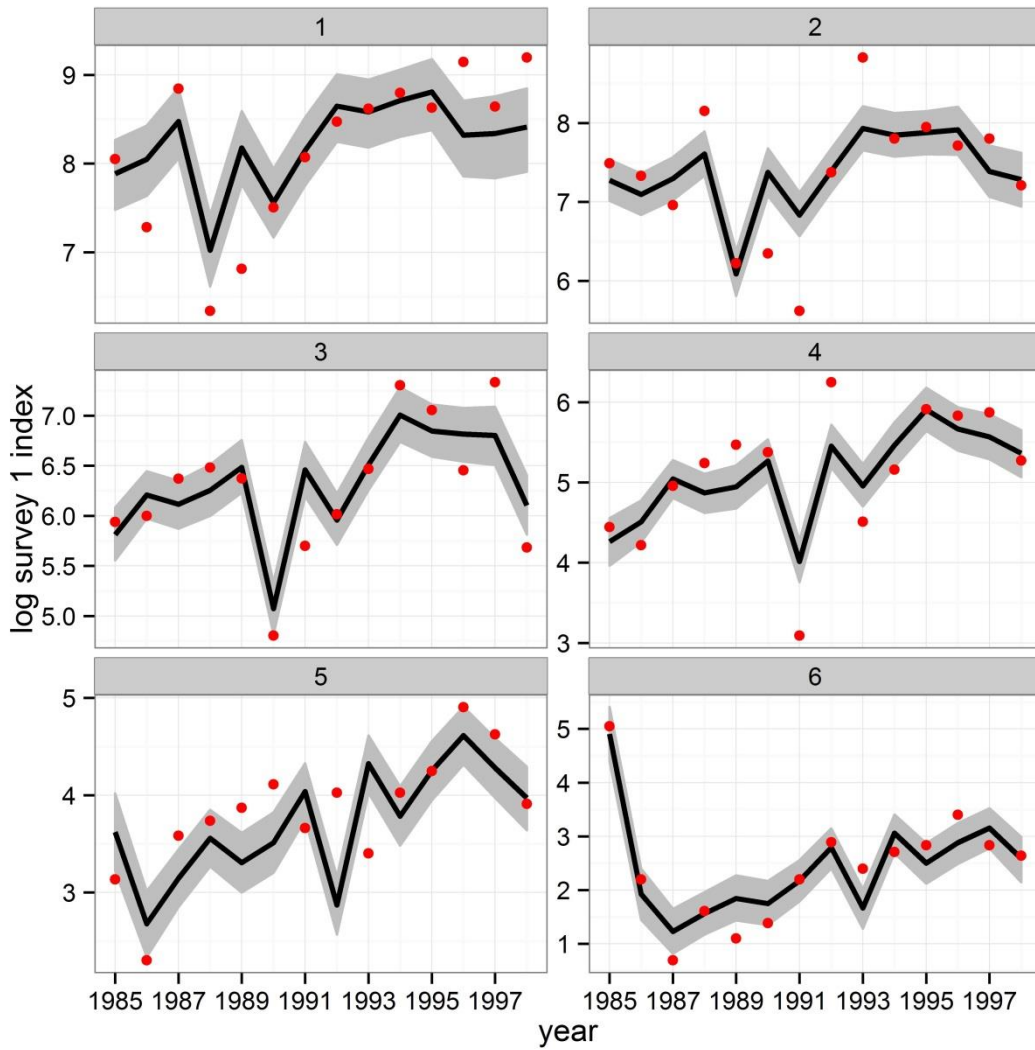


Figure F.48: Time series log abundance indices for the Scottish quarter 1 research survey for the variable seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

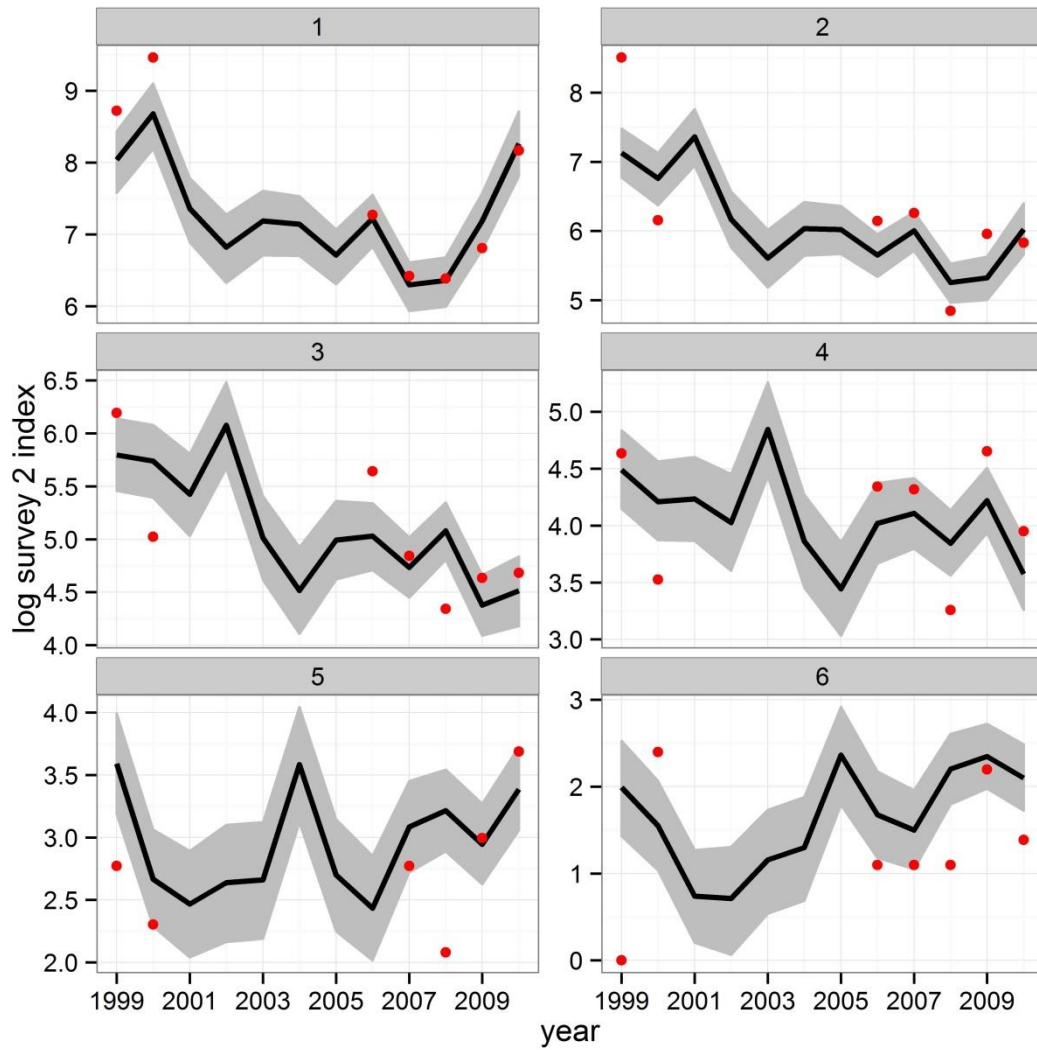


Figure F.49: Time series log abundance indices for the Scottish quarter 1 research survey after change in research vessel and length of the tow for the fixed seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

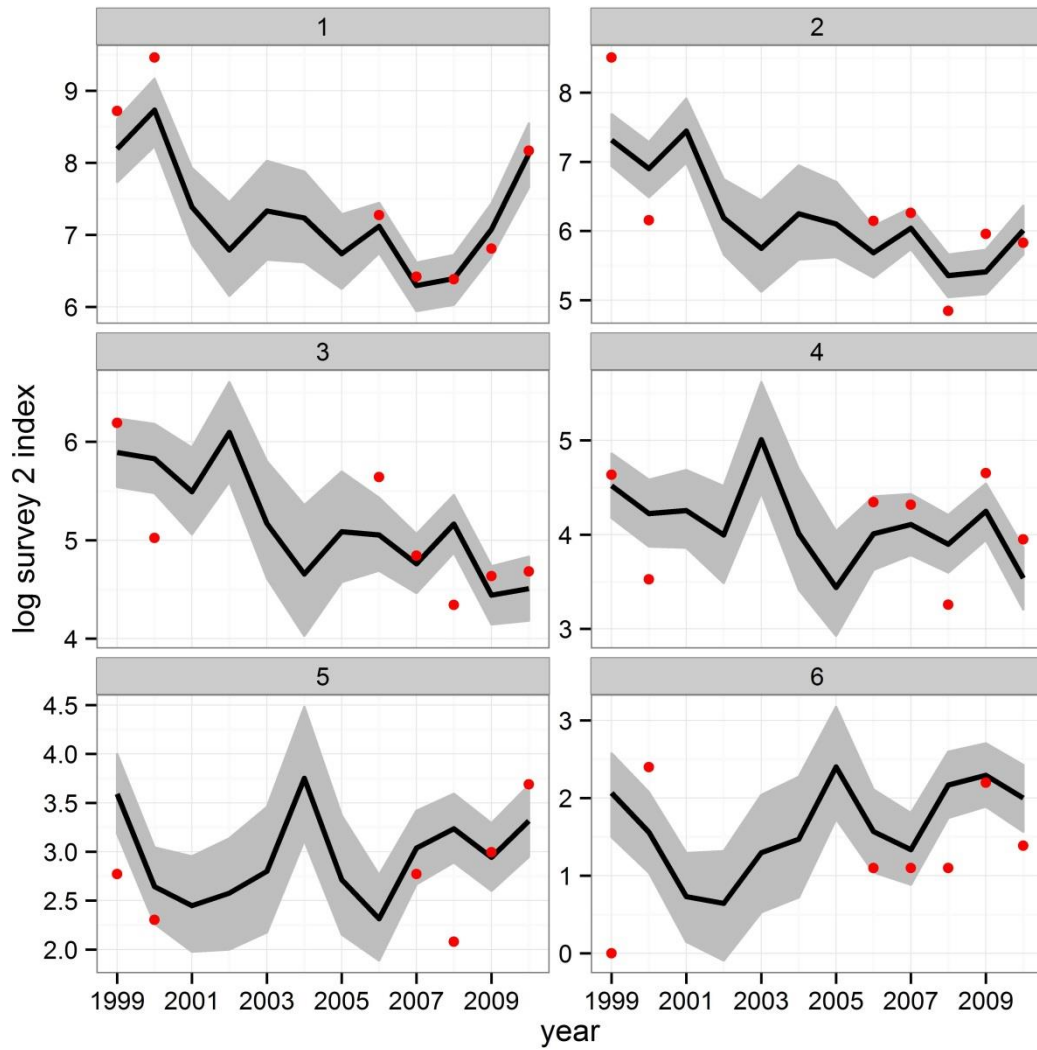


Figure F.50: Time series log abundance indices for the Scottish quarter 1 research survey after change in research vessel and length of the tow for the variable seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

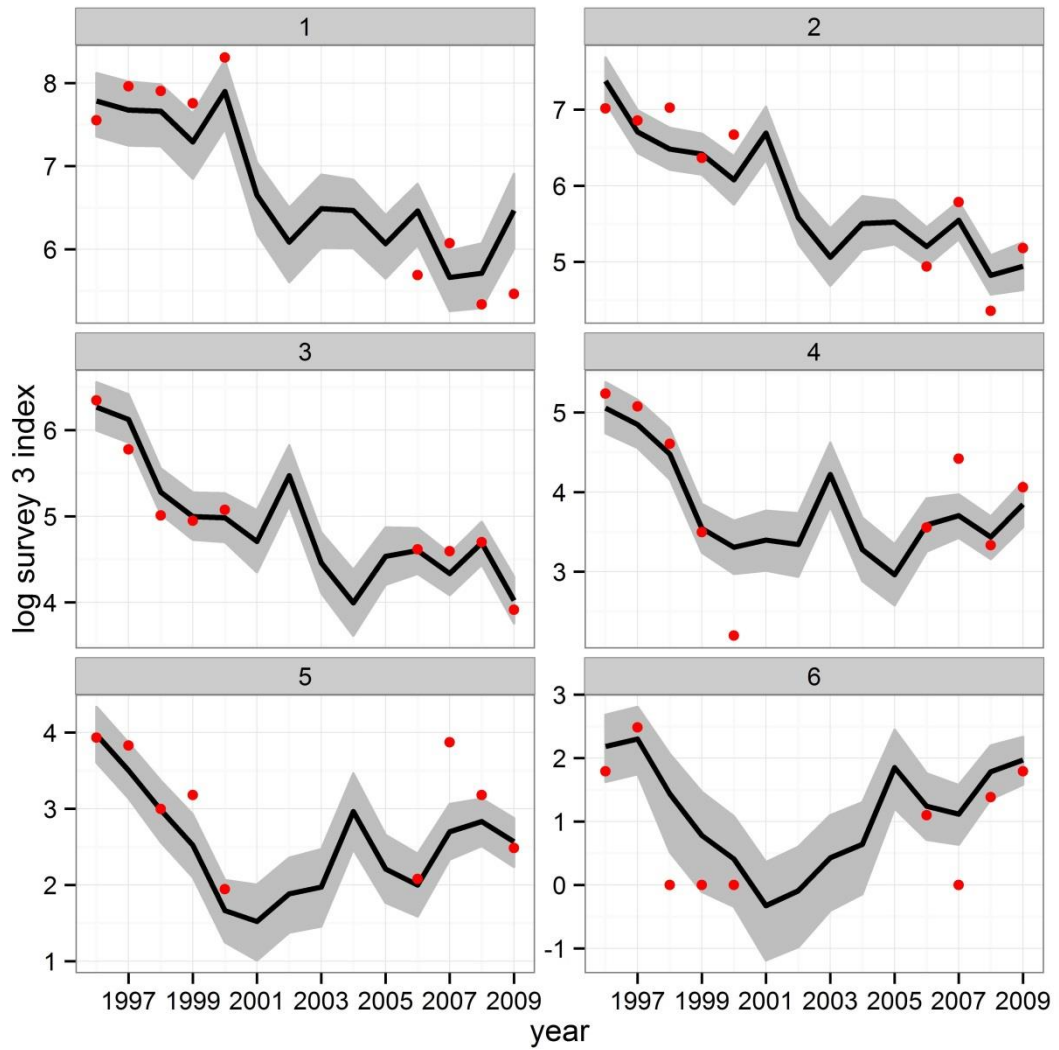


Figure F.51: Time series log abundance indices for the Scottish quarter 4 research survey for the fixed seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

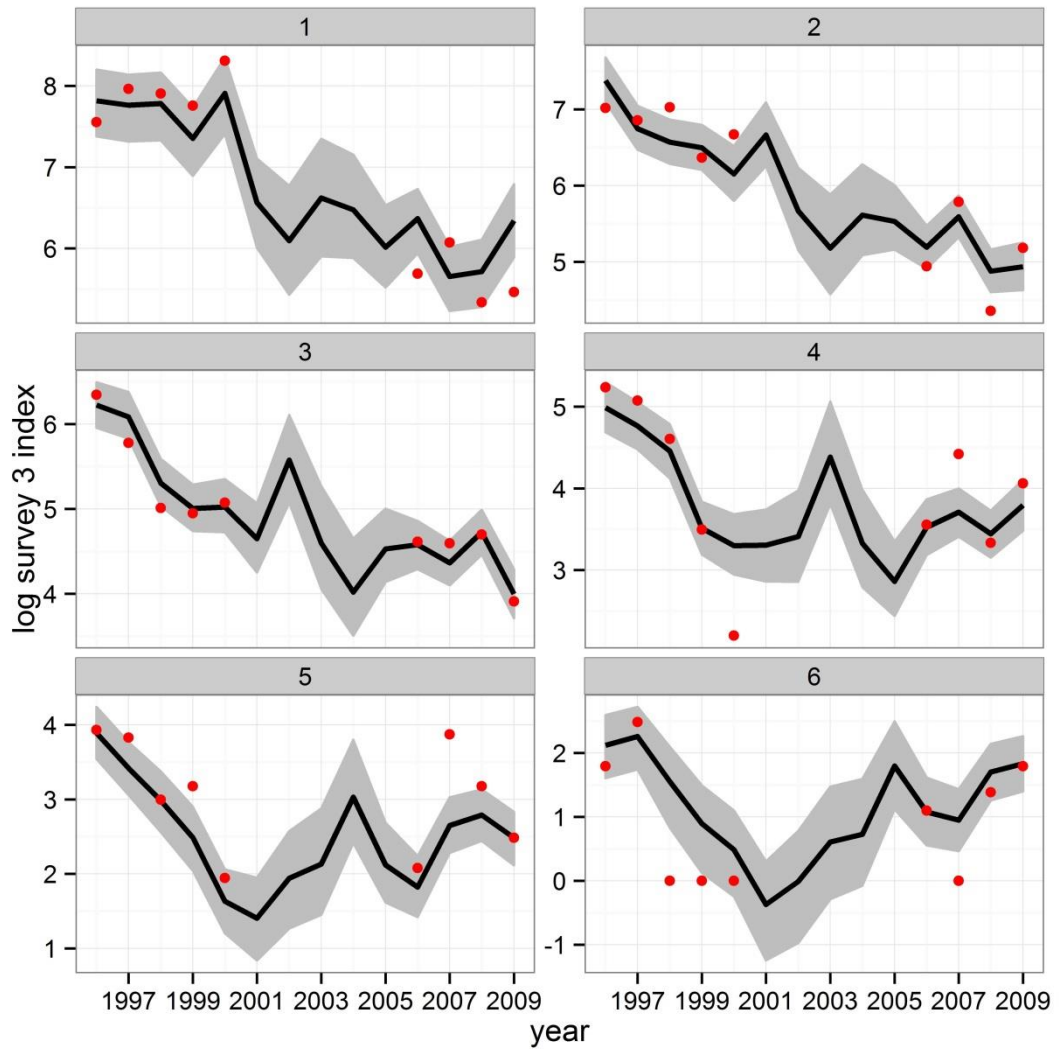


Figure F.52: Time series log abundance indices for the Scottish quarter 4 research survey for the variable seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

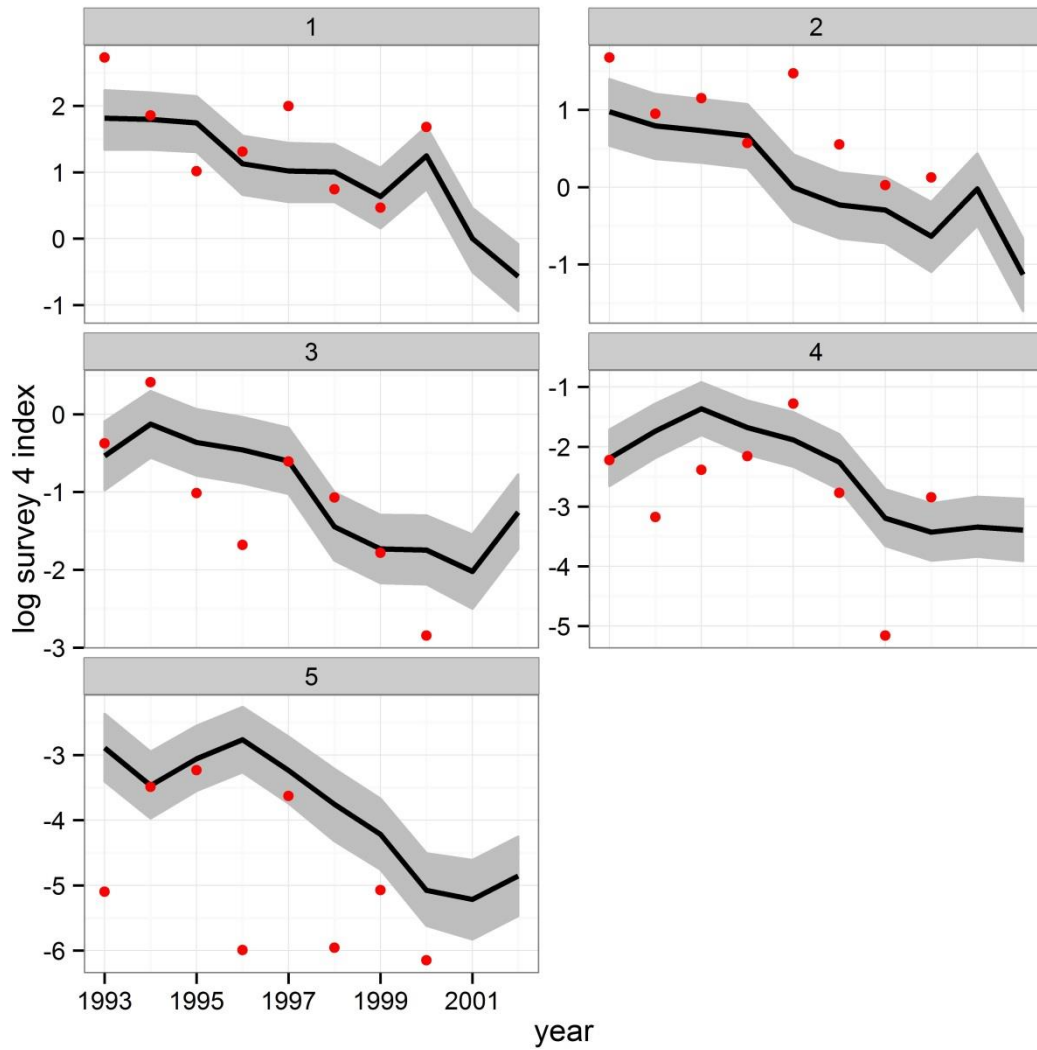


Figure F.53: Time series log abundance indices for the Irish groundfish research survey for the fixed seal predation rate model given by fish age (1 to 5). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

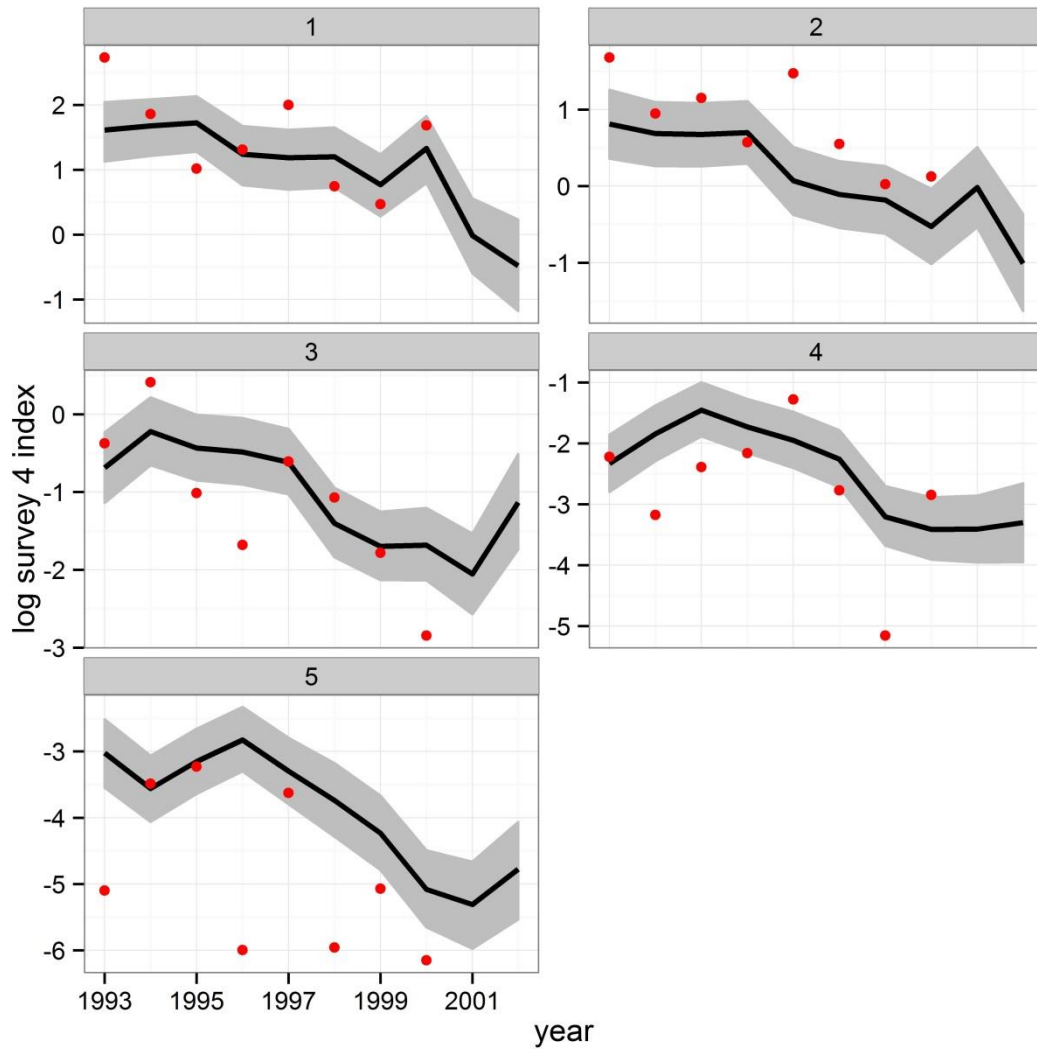


Figure F.54: Time series log abundance indices for the Irish groundfish research survey for the variable seal predation rate model given by fish age (1 to 5). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

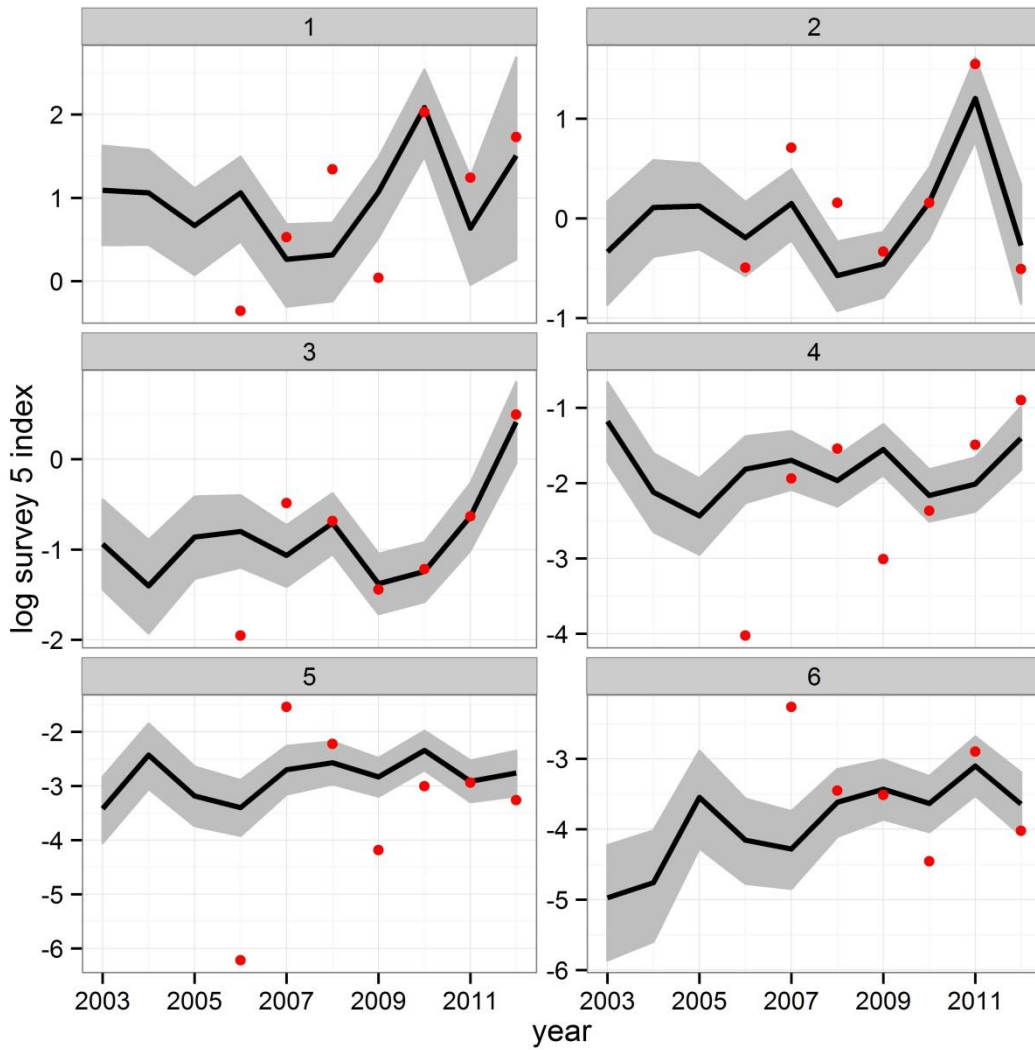


Figure F.55: Time series log abundance indices for the Irish West Coast groundfish research survey for the fixed seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

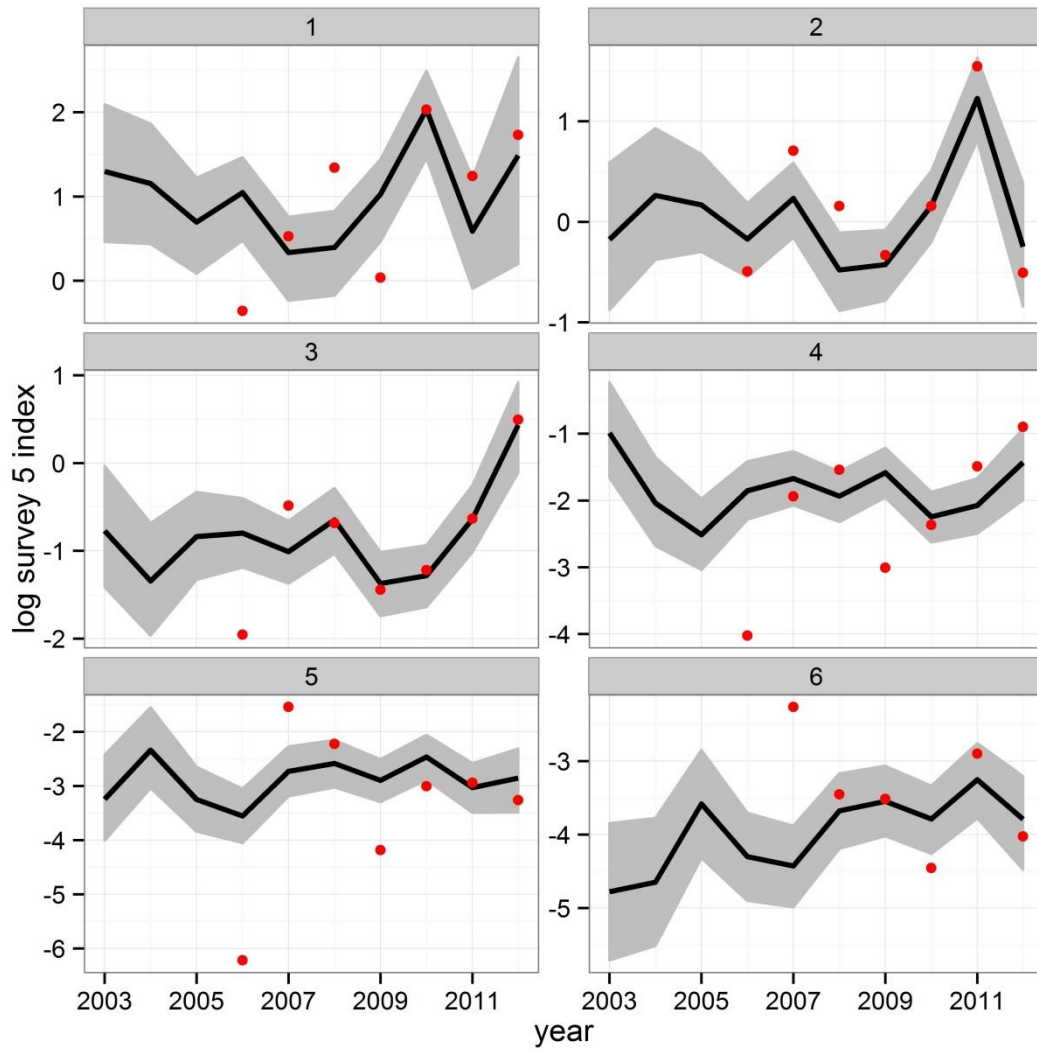


Figure F.56: Time series log abundance indices for the Irish West Coast groundfish research survey for the variable seal predation rate model given by fish age (1 to 6). The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

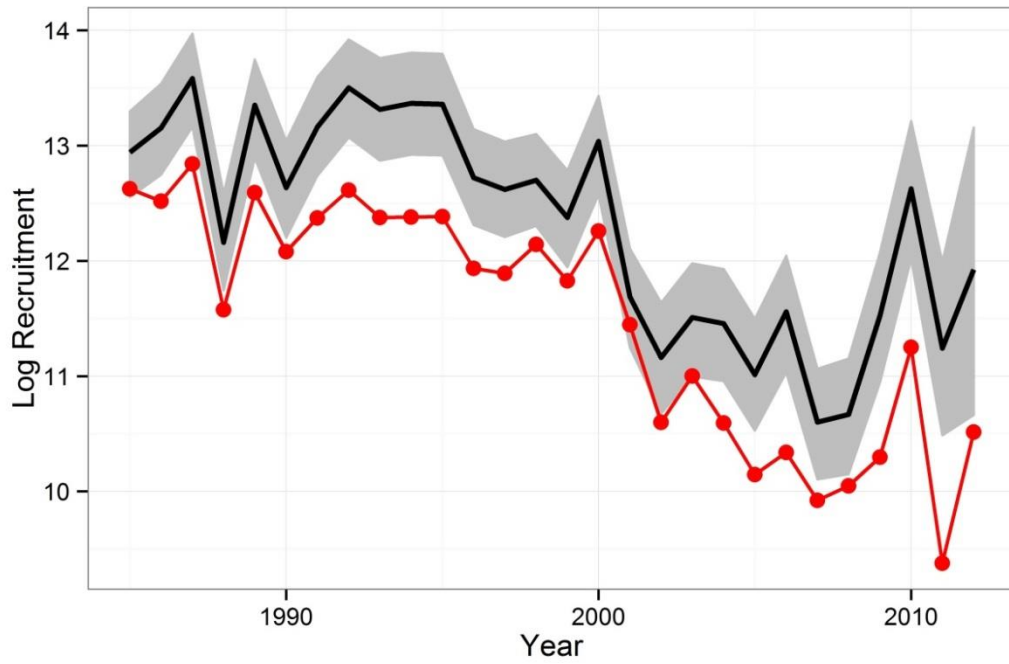


Figure F.57: Time series log recruitment (thousands) for the fixed seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The estimates from ICES are given in red.

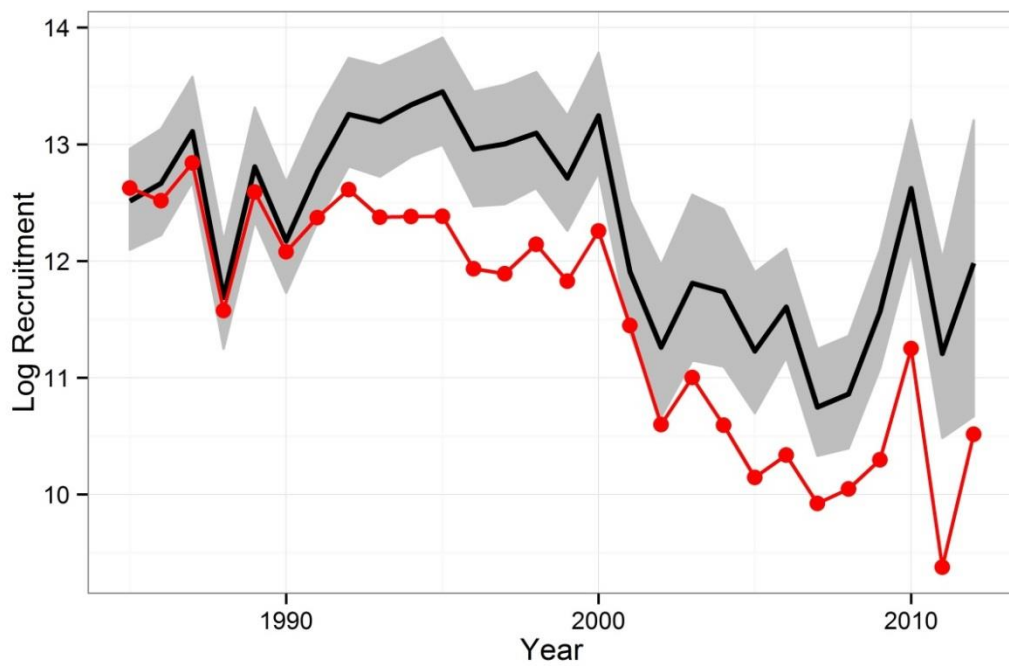


Figure F.58: Time series log recruitment (thousands) for the variable seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The estimates from ICES are given in red.

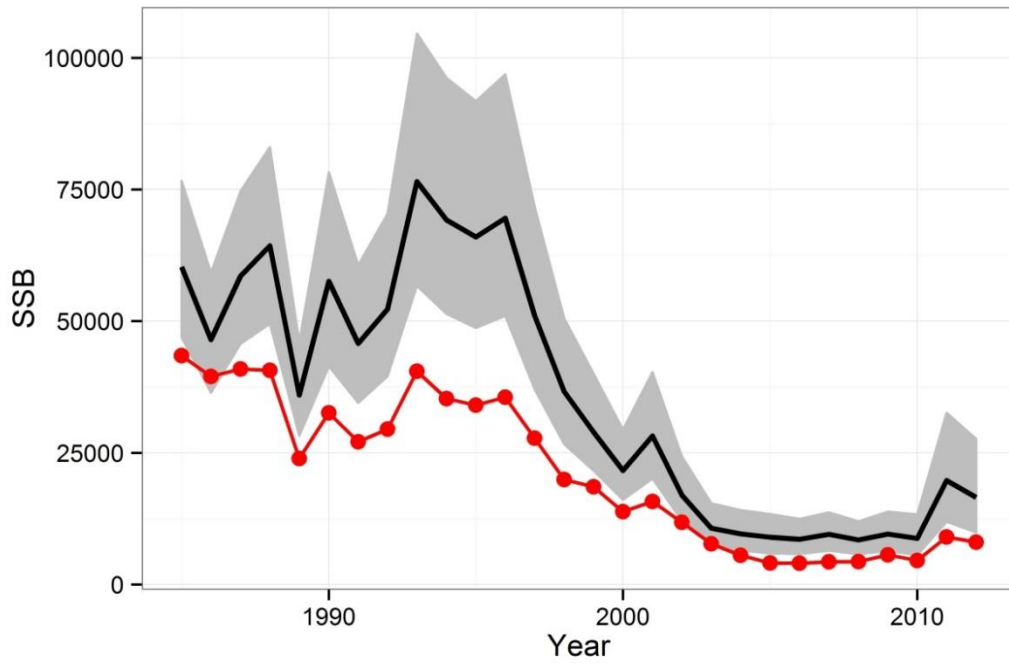


Figure F.59: Time series log SSB (tonnes) for the fixed seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The estimates from ICES are given in red.

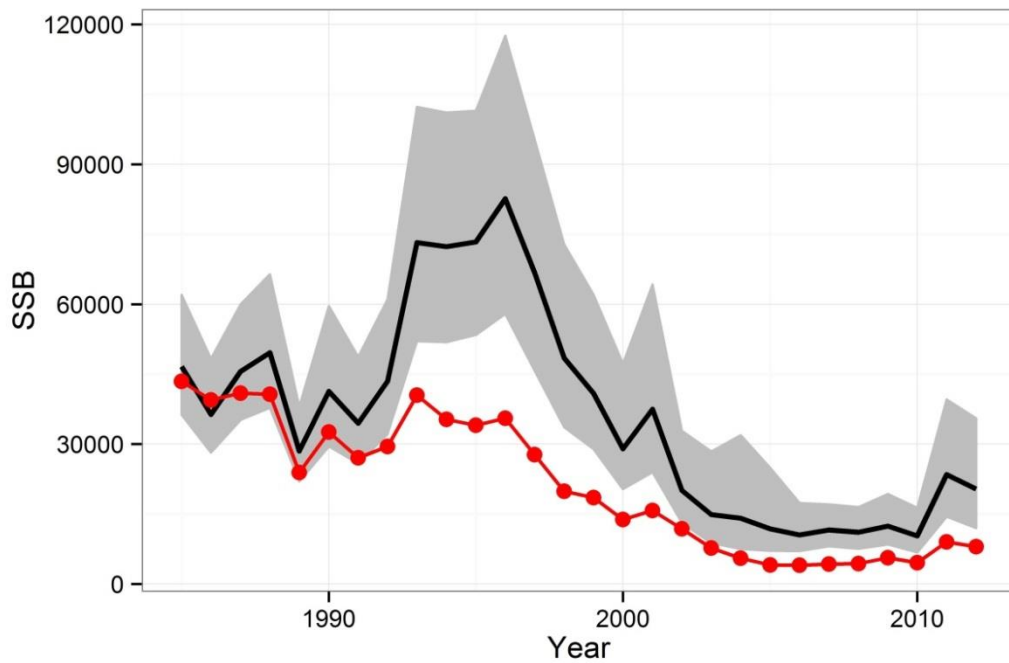


Figure F.60: Time series log SSB (tonnes) for the variable seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The estimates from ICES are given in red.

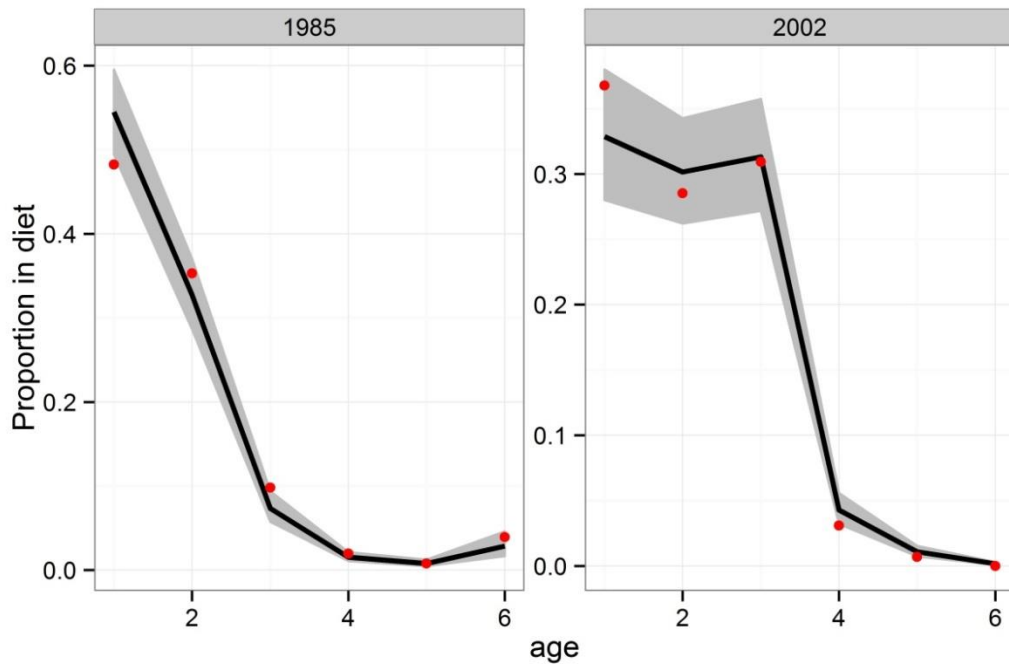


Figure F.61: Proportion at age of cod in grey seal diet for the fixed seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

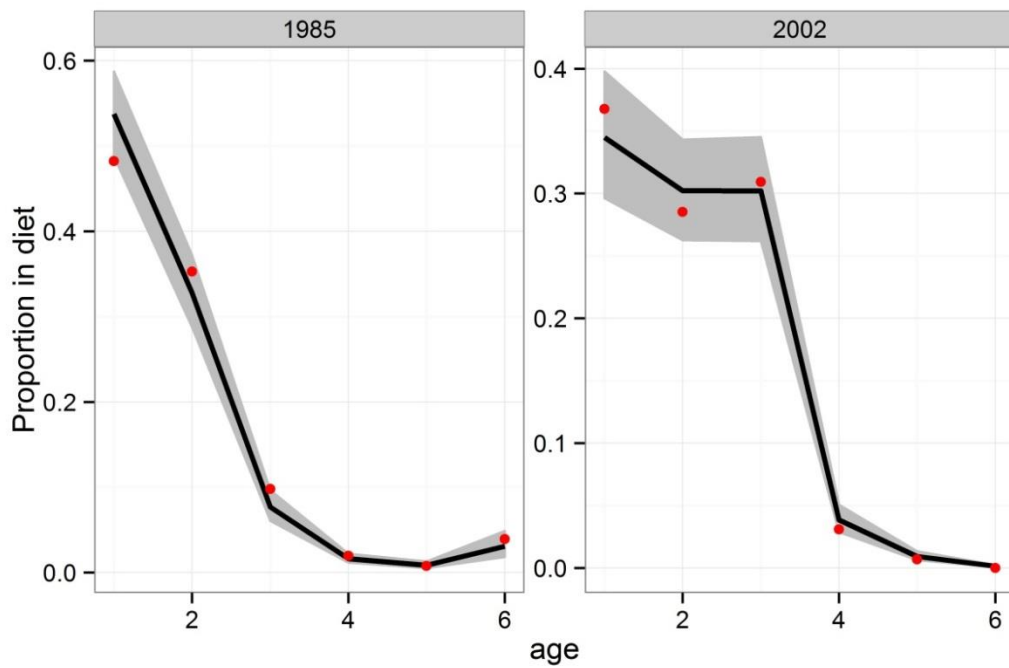


Figure F.62: Proportion at age of cod in grey seal diet for the variable seal predation rate model. The black line is the estimated median and the 95% credible interval is given in grey. The red dots are the empirical data.

Appendix G: Partition of the landings into fleets for the other species

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

The partition inside the UK fleets is more difficult because of the lack of empirical data. Different data source are used by species. Marine Scotland database reports the landings of other species (except *Nephrops*) for the TR2<10 fleet as really small and are then considered insignificant. Consequently, within the model, the TR2<10 fleet does not fish on other species except *Nephrops*.

ICES (2013b) mentions 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 63% of the UK landings are caught by vessels larger than 24 meters and 37% 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 G.1).

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

For *Nephrops*, ICES (2013b) gives the landings in VIa 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 but also the other vessels than the trawlers. 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*. This 2007-2011 data has then been used to partition the landings into TR2<10 and TR1_10-24 for this species.

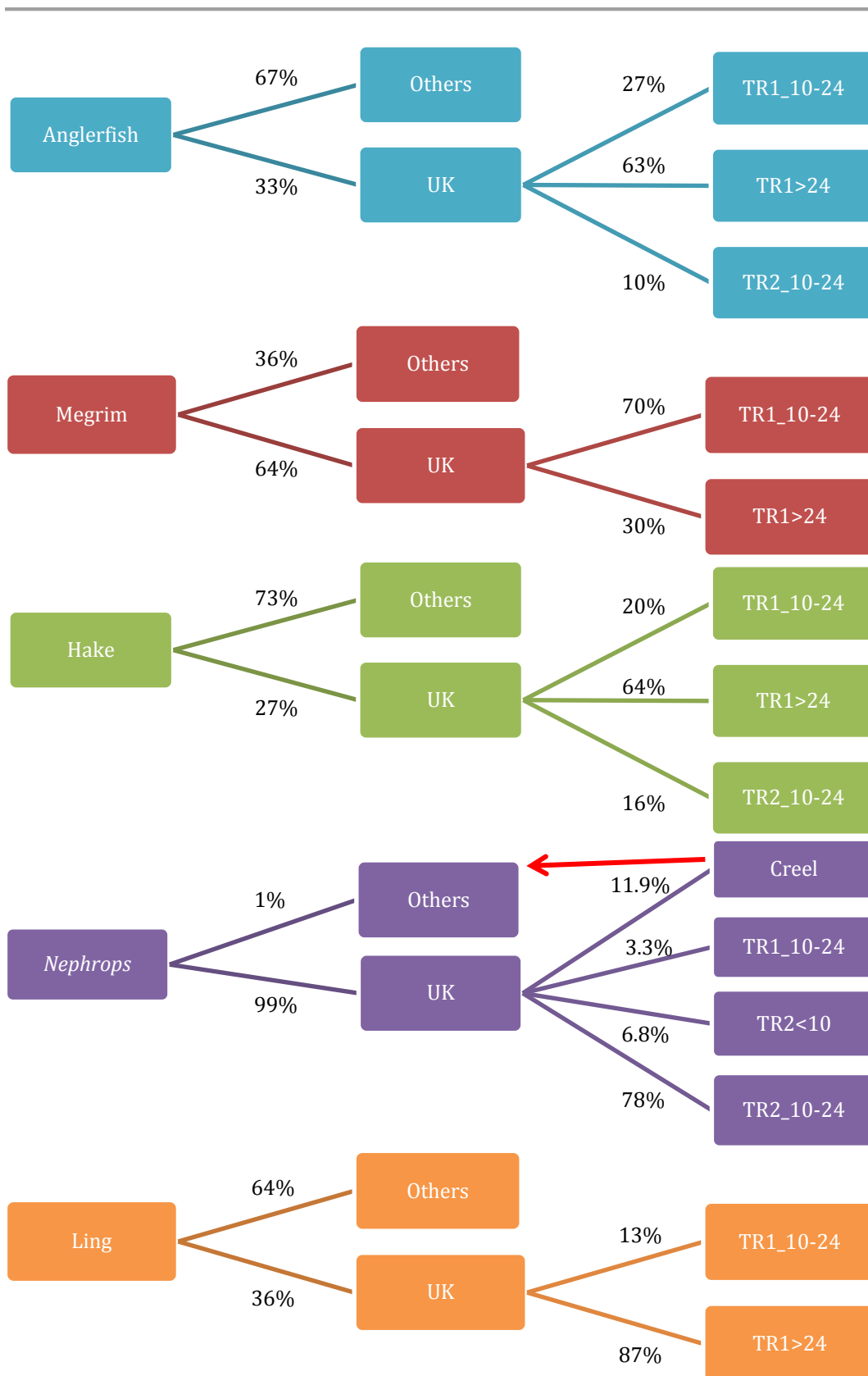


Figure G.1: Partition of landings into fleets for the other species than cod, haddock, whiting and saithe.

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 13% left corresponds to the vessels between 10 and 24 m and there is no information in ICES (2013c) as regards to a possible bycatch by the *Nephrops* trawlers. Consequently these landings have been allocated to the TR1_10-24 fleet.

Finally, 64% of the UK landings for hake 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, 2014d). The 20% and 16% caught by TR1_10-24 and TR2_10-24 respectively has been allocated to correspond to the total landings from other species (except *Nephrops*) recorded in Marine Scotland database when added to the landings of other species estimated above.

This partition is believed to be a good approximation of the current repartition of landings for other species than cod, haddock, whiting and saithe. It is used to calculate the initial landings for ling and the initial fishing mortality for anglerfish, megrim, hake and *Nephrops* used in the bioeconomic models.

Appendix H: Implications of considering grey seal predation in stock assessments

This appendix is a shortened version of the manuscript “Grey seal predation mortality on three depleted stocks in the West of Scotland: What are the implications for stock assessments?” which will be submitted in the Canadian Journal of Fisheries and Aquatic Sciences. This study presents the estimates of grey seal predation mortality on cod, haddock and whiting in VIa and investigates the implication of explicitly considering seal mortality within a stock assessment model.

Introduction

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

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

Methods

Grey seal predation mortality on cod, haddock and whiting was estimated from standard fisheries data and seal diet data collected by the Sea Mammal Research Unit (SMRU, University of St Andrews). These estimates were then used in equilibrium analyses to compare the consequences of considering explicitly seal predation in stock assessments to those which use conventional fixed values of natural mortality.

Estimation of grey seal predation mortality

This part describes the stock assessment model and the Bayesian analysis (see part 4.2.1.1 for more detail). The different models are described again here to provide the model codes (A, B and C) for this study.

The models were:

- A. Seal predation rate (q) was allowed to vary annually according to a simple time series model (Table H.1, Equation (8)). This parameter determines the ability of seals to find and consume fish. It incorporates “attack rate” and “handling time” from the Holling type II functional response equation (Holling, 1959) and is expected to vary over time in response to fish biomass.
- B. The seal predation rate was fixed over time (i.e. the process error standard deviation in the Equation (8) in Table H.1 was set equal to 0). Given the paucity of seal diet data, estimating annual values of q in Model A may over-fit the data.
- C. Seal predation was considered as subsumed within natural mortality M and was not explicitly estimated in the model (i.e. $Z = F + M$). This most closely resembles the standard ICES assessments and was used as baseline to determine the implication of considering seal predation in stock assessments.

Equilibrium analyses

In order to investigate how inclusion of seal predation changes perceptions of stock productivity and therefore the estimation of management reference points, two equilibrium analyses were performed.

A simple per recruit analysis was used to calculate the fishing mortality at which the slope of the yield per recruit curve is 10% the slope of the curve at its origin ($F_{0.1}$) following the method of Thompson and Bell (1934). This is a simple way of quantifying productivity in response to changes in biological parameters without being affected by the uncertainties associated with estimating the stock-recruitment function.

A second equilibrium yield analysis was also performed where the stock-recruitment relationship was modelled. The fish populations were projected to the steady state for different scenarios of fishing and seal predation mortality. Maximum sustainable yield (MSY), fishing mortality at MSY (F_{MSY}) and SSB at MSY (SSB_{MSY}) were then calculated. The projection model was similar to the stock assessment model except that it considers a structural stock-recruitment function. Annually, to account for measurement errors, the projection model bootstraps 30 000 replicates of the following parameters from the stock assessment models: fishing mortality F , Lorenzen parameters for natural mortality, seal selectivity parameters (γ and δ), seal predation rate (q), fish partial biomass (PB), SSB and recruitment. The replicates of the SSB and recruitment were used to fit a Ricker stock-recruitment relationship. Given the lack of data at high SSB, some runs may induce unrealistic large SSB values. The recruitment was therefore assumed constant and equal to the fitted recruitment at maximum SSB estimated by the stock assessment model when the SSB values were larger than the maximum estimated SSB. Stochasticity was added to the stock-recruitment curve by bootstrapping the residuals to account for process errors. The model is robust to the choice of stock-recruitment curve and using another common relationship such as Beverton-Holt gives similar management reference points estimates. By default, for the three species the replicates of the seal predation rate (q) and seal selectivity were kept constant in the analysis. In addition, for cod, the replicates of q and the partial biomass (PB) were also used to fit a type II functional response (Holling, 1959) of seals to cod biomass, similarly to Cook and Trijoulet (2016), where θ and ρ are constants.

$$q_y = \frac{\theta}{1 + \theta \rho PB_y}$$

When the type II functional response is considered, the model bootstraps the q and PB replicates and also the residuals from the fitted relationship to account for process

errors. The poor fit of the functional response for haddock and whiting prevents its use in the present study so the functional response scenario is run only for cod.

Both equilibrium analyses used the outputs of the three stock assessment models described earlier (Models A, B and C). Averages over 2008 to 2012 were used to supply age specific fishing mortality, the fish weight and, after use of a length-weight relationship (Coull et al., 1989), the length of fish to estimate seal selectivity. Because only two years of seal diet data are available and the variations in grey seal diet for the recent years are not known, an average seal predation rate (q) of the two years 1985 and 2002 was used as the estimates in these years are informed by real observations. A test on the sensitivity of the results to the omission of survey data for whiting showed that this did not affect the estimates for the years 1985 and 2002. The average number of seals taken from 2008 to 2012 was used to scale the seal predation rate to seal predation mortality representative of recent years. Because grey seal predation is the product of three components including seal numbers (Table H.1, Equation (6)), a change in seal predation mortality can be interpreted as a linear change in seal population.

Results

Estimated total natural mortality

The estimates of non-fishing mortality at age (in effect the total natural mortality) obtained from the Model A are larger than those obtained from the Model B for cod but slightly smaller for haddock and whiting (Figure H.1). Models B and C give similar values for haddock and whiting. However models that consider grey seal predation explicitly estimate larger non-fishing mortalities for cod no matter the seal predation rate assumption. For the West of Scotland, generally the estimated non-fishing mortality was larger across all ages than those from ICES. Mortality estimates at young age classes are higher for the North Sea than the West of Scotland.

Equilibrium analyses

The estimated management reference points for the three species assuming the current number of grey seals in the West of Scotland are shown in Table H.2. As expected, the values of $F_{0.1}$ for the three species differ from the values of F_{MSY} since no account is taken of the effect of SSB on recruitment.

For cod, considering grey seal predation in the stock assessment model (A, B and type II) leads to larger values of $F_{0.1}$ but results in a decrease in F_{MSY} . The current fishing mortality is above F_{MSY} no matter the model considered.

For haddock, the current fishing mortality is below F_{MSY} . The assumption on the seal predation rate is important in giving the direction of the change in both $F_{0.1}$ and F_{MSY} due to the explicit consideration of the seal predation in the models. The value of F_{MSY} increases in the Model A and decreases in the Model B but the difference in values is small and inversely for $F_{0.1}$. The estimated values of MSY and SSB_{MSY} are relatively close for the three models.

For whiting, the MSY results differ substantially between Models A and B. The Model B gives results close to Model C, but Model A estimates much larger values of MSY and SSB_{MSY} . In this case, the current fishing mortality is below F_{MSY} while it is the contrary for Models B and C.

Despite, a clear change in the median F_{MSY} values when grey seal predation is considered in the stock assessment for the three species, the large 90% confidence intervals show however that this difference may not be significant.

MSY and F_{MSY} are also studied as a function of relative seal predation mortality for the three models (Figure H.2). As expected an increase in seal predation mortality results in a decrease in MSY and F_{MSY} for the three species. However, for haddock, the change in F_{MSY} is small. The value is almost constant no matter the change in predation mortality or the choice of model. For cod, the results are similar to those observed in Table H.2 with the Model A showing the smallest values of MSY. The type II Model shows a steeper decrease in F_{MSY} and the collapse of cod occurs when the current seal predation is multiplied by a factor of 2. The results for whiting are similar to those for cod with a clear decrease in MSY and F_{MSY} when the grey seal population is increased.

Discussion

The West of Scotland stocks are adjacent to those of the same species in the North Sea and it might be expected that similar non-fishing mortality rates would prevail in both areas. In the North Sea, separate estimates of non-fishing mortality that include seal and other predation, have been made from multispecies models and provide a comparison to our estimates (ICES, 2015c). They are very similar for whiting but show marked differences for cod and haddock mostly in the shape of the mortality rate by age rather than the overall scale. This is likely to be due to the fact that the North Sea estimates do not make use of age composition data for the seal catch and hence do not have the same size resolution as the data used in our analysis. Clearly in the case of haddock, however, the conventional VIa value of 0.2 appears too low both in relation to our estimates and those derived for the North Sea. The recent amalgamation of the West of Scotland and the North Sea stock assessments by ICES should overcome this problem (ICES, 2015c).

A surprising result is that explicitly including seal predation in the model estimates larger non-fishing mortality for cod but lower for haddock and whiting. This arises partly from the selectivity pattern for seal predation which differs between cod and the two other species but is also due to changes in the estimates of the natural mortality. For haddock and whiting, the Lorenzen parameters estimated when grey seal predation is subsumed into natural mortality (Model C) result in larger values of non-fishing mortality to be consistent with empirical data on catch and abundance indices.

The estimated total non-fishing mortality at young ages in the North Sea is larger than that in the West of Scotland for all species. Moreover, it is important to note that in the current ICES cod assessment for VIa, the average natural mortality (age 1-6) used is 0.308 and implicitly includes the mortality due to seal predation. The average non-fishing mortality on cod estimated from Models A and B in this study is larger than this value suggesting that the current cod natural mortality values considered in ICES assessments for the Division VIa may be too low. Unlike recent studies in the North Atlantic where seal predation was considered as insignificant compared to the total mortality on fish stocks (Boyd and Hammond, 2010; MacKenzie et al., 2011; Alexander

et al., 2014) these values seem of sufficient magnitude to matter in evaluating stock status for fishery management.

The MSY analysis implies an unlikely recovery of cod and whiting (in the Models B and C) at the current level of fishing mortality. Indeed the current F is larger than F_{MSY} and the current SSB is smaller than SSB_{MSY} . This may be evidence of the necessity of reducing the current fishing mortality on both stocks in the area like it is already highly recommended by ICES (2016b). However, even if the fishing mortality is reduced to F_{MSY} for both stocks, the catches are expected to be larger than the current yield but the fishery will never reach the historical levels of yield that were observed in the 1980s (Table H.3). Nevertheless, if the Model A for whiting is more realistic, the stock may recover given that the current F and SSB are smaller than F_{MSY} and SSB_{MSY} . However, in this scenario also, the MSY will never reach high historical yield levels.

For haddock, the current fishing mortality is well below F_{MSY} so the stock may recover in the future, but the current SSB is larger than SSB_{MSY} , so reaching the equilibrium may necessitate a decrease in the current SSB. Similarly to the two other stocks, despite the fact that the yield can be increased compared to the current catch by reaching F_{MSY} , the yield will still be below the large historical level. Even a reduction in seal predation in VIa cannot increase the MSY to historical levels, except maybe for cod. However, it necessitates a decrease in seal predation of more than 50% which is obviously unrealistic.

The assumption on grey seal predation rate is important for whiting because it can lead to different conclusions as regards to the estimation of F_{MSY} with larger estimates when the seal predation rate is assumed to vary annually. The comparable seal consumption fit for both models, the fact that the Model B outputs are closer to that of the Model C, and the large increase in seal consumption estimates for the Model A in the late 1990s possibly suggest the Model B is a better model choice for this species.

Despite a weight of haddock consumed in 2002 larger than the weight of cod consumed (Harris, 2007) and a seal predation mortality of the same order of magnitude for haddock and whiting, the haddock F_{MSY} and MSY are little affected by a change in grey seal predation mortality suggesting a low impact on the stock. This highlights the limits

of assessing the impact of seals on a stock by only comparing seal consumption (Harris, 2007) with fishing landings (ICES, 2013b). Also, despite some differences in median measurements, the F_{MSY} values are only slightly impacted by the consideration of grey seal predation in the stock assessment for haddock compared to the other species.

This study demonstrates that considering grey seal predation mortality can change the perception of the state of the stocks, even if the seal mortality is low, and this can affect the estimates of management reference points such as $F_{0.1}$ and F_{MSY} (Mohn and Bowen, 1996). The large estimates of seal predation mortality compared to the other species make cod the stock the most affected by a change in seal population and for which the impacts on fisheries management may be the largest. However, the large confidence intervals observed for F_{MSY} may be evidence that despite the apparent impact of considering grey seal predation in the stock assessment on the estimated values of F_{MSY} , the difference observed may not be significant due to the large uncertainty around the stock-recruitment and the variability around the mortality estimates. It is therefore difficult to estimate precise values of F_{MSY} .

As is usual in per recruit analysis, all the mortality values are assumed to be fixed which could be an over-simplification if seals respond dynamically to the abundance of prey as suggested by previous studies (Matthiopoulos et al., 2003; Middlemas et al., 2006; Smout et al., 2014; Cook et al., 2015; Cook and Trijoulet, 2016). Our results should therefore be seen more as an indication of sensitivity to seal predation rather than robust estimates of $F_{0.1}$. Similar assumptions are taken for Models A and B in the MSY analysis. The consideration of a seal functional response to cod biomass increases the sensitivity of cod to an increase in fishing and seal predation mortality. However, the type II response was fitted on the seal predation and partial biomass estimates for which only two years of data over the time series of 28 years were available. The paucity of seal diet data brings uncertainty to the seal response. In this study, a type III functional response is not considered despite the well-known seal switching behaviour (Smout et al., 2014). This comes from the fact that two years of seal diet data do not allow a significant estimation of the third parameter necessary to fit the type III response.

In our equilibrium analysis for whiting we used the stock assessment outputs where abundance indices for some years were removed due to an apparent anomaly in the estimated values of seal predation. It is debatable whether this is fully justified because censoring the data is based purely on a perception of how seal predation should change. Large values of total mortality in the survey data over the period 2001-2005 may explain the increase in seal consumption in the Model A, where seal predation can vary annually. When the seal predation rate is fixed (Model B), the increase in total mortality is attributed to unreported fishing mortality. A similar spike in fishing mortality is observed for some runs in the ICES assessment (ICES, 2014c). As the ICES assessment uses a different model it suggests this anomaly is related to the input data rather than the modelling assumptions. Omitting the data affected the estimated biomass and mortality rates in 2004-2005 but for other years the omission had little effect. As we used estimated values for seal predation from 1985 and 2002 in subsequent analyses our results are fairly insensitive to this problem, though it does mean that estimated stock trends during this period are subject to particularly large uncertainty.

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

This study only considers the direct effect of seal predation on the mortality rates of the three species and the potential implications for routine stock assessments. In the case of cod the implications appear important, for whiting the impact on stock perception is slightly smaller and for haddock even less so. However, there is a more general question of the economic impact of seal predation on the fishery. Even if the

implications seem less important for haddock and whiting, as mentioned earlier the seal catches are relatively large in weight for haddock and in numbers for whiting (Harris, 2007), so it is premature to conclude that seal predation on haddock and whiting is unimportant simply because predation mortalities are fairly low. An economic analysis of the fishery would be needed to address this issue.

Tables

Table H.1: Main equations of the population model.

Equation number	Equation	Description
(1)	$N_{a+1,y+1} = N_{a,y}e^{-Z_{a,y}}$	The population of fish N at age a and year y decays exponentially as a result of the total mortality Z
(2)	$Z_{a,y} = M_{a,y} + P_{a,y} + F_{a,y}$	The total mortality Z is partitioned between natural mortality M , fishing mortality F and seal predation mortality P
(3)	$F_{a,y} = sel_{a,y}E_y$	F is the product of an age component or selectivity sel and a year effect or fishing effort E
(4)	$E_y = E_{y-1}e^{\varepsilon_y}$	E can vary every year following a random effect $\varepsilon \sim Normal(0, \sigma^2_\varepsilon)$, $y \neq 1$
(5)	$M_{a,y} = \alpha(w_{a,y})^\beta$	M is estimated following Lorenzen (1996) and depends of the fish weight w . The constants α and β are estimated within the model
(6)	$P_{a,y} = s_{a,y}q_yG_y$	P is function of seal selectivity s for a certain age class, the ability to catch fish or seal predation rate q and the number of seals G
(7)	$s_{a,y} = \left(\frac{l_{a,y}}{(\gamma - 1)\delta}\right)^{\gamma-1} e^{\left(\gamma-1-\frac{l_{a,y}}{\delta}\right)}$	s follows a gamma curve assuming a preference for certain fish length l . The constants γ and δ are estimated within the model
(8)	$q_{y+1} = q_y e^{\varepsilon_{q,y}}$	q is allowed to vary every year following a time series with a random effect $\varepsilon_{q,y} \sim Normal(0, \sigma^2_{q,y})$
(9)	$PB_y = \sum_a (s_{a,y}w_{a,y}N_{a,y})$	Fish partial biomass (PB) corresponds to the biomass available to seal predation

Table H.2: Estimated reference management points when the current seal predation mortality is assumed. F_{08-12} and SSB_{08-12} correspond respectively to the average current (2008-2012) fishing mortality and spawning stock biomass estimated by the stock assessment models. F_{MSY} , MSY and SSB_{MSY} correspond to median measurements and the 90% confidence interval is given in parenthesis.

Species	Model	F_{08-12}	$F_{0.1}$	F_{MSY}	MSY (tonnes)	SSB_{08-12} (tonnes)	SSB_{MSY} (tonnes)
Cod	A	0.38	0.33	0.309 (0.219–0.421)	9,553 (5,666–15,504)	8 435	43,930 (27,989–63,861)
	B	0.50	0.25	0.321 (0.246–0.398)	11,650 (9 529–14,071)	6 362	53,620 (46,634–72,856)
	C	0.71	0.21	0.365 (0.289–0.430)	15,490 (11 347–20,270)	4 140	59,970 (46,076–86,611)
	Type II	0.38	NA	0.244 (0.165–0.325)	13,510 (9437–19,052)	NA	76,040 (54,119–118,928)
Haddock	A	0.10	0.35	0.435 (0.267–0.663)	16,310 (11 655–20,548)	51 884	41,120 (31,808–58,482)
	B	0.10	0.45	0.402 (0.228–0.666)	15,800 (8 980–22,502)	58 352	43,460 (32,355–64,675)
	C	0.14	0.38	0.414 (0.197–0.623)	14,580 (9 707–18,387)	46 790	46,170 (37,820–70,979)
Whiting	A	0.07	0.43	0.161 (0.084–0.250)	8,831 (4754–20,733)	16 056	80,370 (52,671–112,508)
	B	0.08	0.58	0.072 (0–0.138)	2,709 (825–6,378)	12 926	50,810 (32,443–95,772)
	C	0.09	0.48	0.065 (0–0.136)	2,496 (548–95,925)	12 336	49,700 (29,379–95,925)

Table H.3: Current yield (average 2008-2012) and historical yield (average 1981-1990) recorded by ICES (2013b).

Species	Current yield (tonnes)	Historical yield (tonnes)
Cod	1 556	19 514
Haddock	4 661	33 315
Whiting	895	17 178

Figures

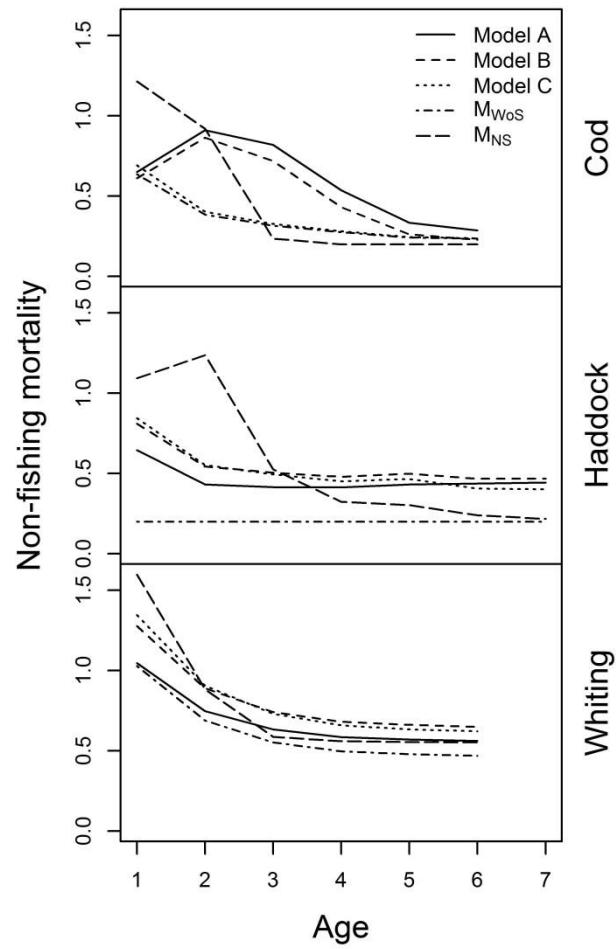


Figure H.1: Comparison of estimated total non-fishing mortality at age (Models A and C) with the ICES values in West of Scotland (M_{WoS}) (ICES, 2013) and the natural mortality estimated in the North Sea (ICES, 2015) which includes seal predation (M_{NS}). When seal predation is considered the outputs come from the model with the lowest DIC (variable seal predation rate, Model A).

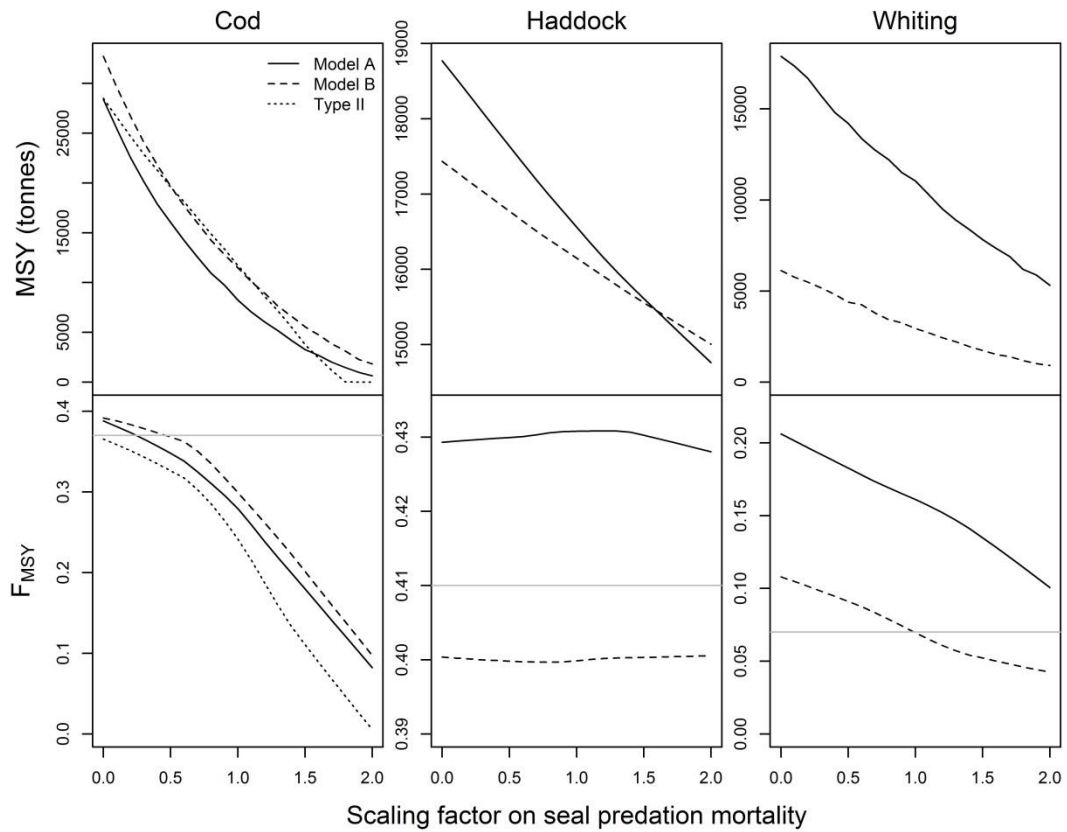


Figure H.2: Estimated median maximum sustainable yield (MSY) in tonnes and fishing mortality at MSY (F_{MSY}) as a function of relative seal predation mortality. The x-axis represents the scaling factor on seal predation mortality. A scaling factor of 1 corresponds to the current predation mortality (average for the two years 1985 and 2002 scaled to the current number of seals in the West of Scotland). The grey horizontal line represents F_{MSY} when seal predation is not explicitly considered (Model C).

References

The Registration of Fish Sellers and Buyers and Designation of Auction Sites (Scotland) Regulations 2005. *In* Scottish Statutory Instruments 2005 No.286. The Stationery Office Limited.

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

Andersen, B. S., Vermard, Y., Ulrich, C., Hutton, T., and Poos, J. J. 2010. Challenges in integrating short-term behaviour in a mixed-fishery Management Strategies Evaluation frame: a case study of the North Sea flatfish fishery. *Fisheries Research*, 102: 26-40.

Andersen, S. M., Teilmann, J., Harders, P. B., Hansen, E. H., and Hjøllund, D. 2007. Diet of harbour seals and great cormorants in Limfjord, Denmark: interspecific competition and interaction with fishery. *ICES Journal of Marine Science: Journal du Conseil*, 64: 1235-1245.

Anderson, J., Stewart, A.-M., Curtis, H., and Dawe, R. 2013. 2011 Economic Survey of the UK Fishing Fleet, Key Features. *Seafish Economics*.

Anderson, L. G., and Seijo, J. C. 2011. *Bioeconomics of fisheries management*, Wiley-Blackwell.

Ardito, A., Ricciardi, P., and Schiaffino, A. 1993. The effects of seasonal fluctuations on an open access fishery problem. *Journal of Mathematical Biology*, 31: 879-890.

Armstrong, C. W. 2007. A note on the ecological-economic modelling of marine reserves in fisheries. *Ecological Economics*, 62: 242-250. doi: 10.1016/j.ecolecon.2006.03.027.

Armstrong, C. W., and Skonhøft, A. 2006. Marine reserves: A bio-economic model with asymmetric density dependent migration. *Ecological Economics*, 57: 466-476. doi: 10.1016/j.ecolecon.2005.05.010.

Arnett, R. T. P., and Whelan, J. 2001. Comparing the diet of cod (*Gadus morhua*) and grey seals (*Halichoerus grypus*): an investigation of secondary ingestion. *Journal of the Marine Biological Association of the United Kingdom*, 81: 365-366.

Babyak, M. A. 2004. What you see may not be what you get: a brief, nontechnical introduction to overfitting in regression-type models. *Psychosomatic medicine*, 66: 411-421.

Baranov, F. I. i. 1945. *On the Question of the Biological Basis of Fisheries: On the Question of the Dynamics of the Fishing Industry*, Indiana University.

Barten, A. P., and Bettendorf, L. J. 1989. Price formation of fish: An application of an inverse demand system. *European Economic Review*, 33: 1509-1525.

Baxter, J. M., Boyd, I. L., Cox, M., Cunningham, L., Holmes, P., and Moffat, C. F. 2008. *Scotland's seas: towards understanding their state*. Aberdeen 174 pp.

Beattie, A., Sumaila, U. R., Christensen, V., and Pauly, D. 2002. A model for the bioeconomic evaluation of marine protected area size and placement in the North Sea. *Natural Resource Modeling*, 15: 413-437.

Beck, C. A., Iverson, S. J., Bowen, W. D., and Blanchard, W. 2007. Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative fatty acid signature analysis. *J Anim Ecol*, 76: 490-502. doi: 10.1111/j.1365-2656.2007.01215.x.

Benoît, H. P., Hammill, M. O., and Swain, D. 2011a. Estimated consumption of southern Gulf of St. Lawrence cod by grey seals: bias, uncertainty and two proposed approaches. *ICES Document 2011/041*, iv + 29 pp.

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

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

Bjørge, A., Bekkby, T., Bakkestuen, V., and Framstad, E. 2002. Interactions between harbour seals, *Phoca vitulina*, and fisheries in complex coastal waters explored by combined Geographic Information System (GIS) and energetics modelling. *ICES Journal of Marine Science*, 59: 29-42. doi: 10.1006/jmsc.2001.1137.

Bjørge, A., Christensen, I., and Øritsland, T. 1981. Current problems and research related to interactions between marine mammals and fisheries in Norwegian coastal and adjacent waters. *In* ICES Council Meeting 1981.

Bjørndal, T., and Conrad, J. M. 1987. The dynamics of an open access fishery. *Canadian Journal of Economics*: 74-85.

Bjørndal, T., Ussif, A., and Sumaila, U. R. 2004. A bioeconomic analysis of the Norwegian spring spawning herring (NSSH) stock. *Marine Resource Economics*, 19: 353-365.

Boncoeur, J., Alban, F., Ifremer, O. G., and Ifremer, O. T. 2002. Fish, fishers, seals and tourists: economic consequences of creating a marine reserve in a multi-species, multi-activity context. *Natural Resource Modeling*, 15: 387-411.

Borges, L. 2015. The evolution of a discard policy in Europe. *Fish and Fisheries*, 16: 534-540. doi: 10.1111/faf.12062.

Bosetti, V., and Pearce, D. 2003. A study of environmental conflict: the economic value of Grey Seals in southwest England. *Biodiversity and Conservation*, 12: 2361-2392.

Bousquet, N., Chassot, E., Duplisea, D. E., and Hammill, M. O. 2014. Forecasting the Major Influences of Predation and Environment on Cod Recovery in the Northern Gulf of St. Lawrence. *PloS one*, 9.

Bowen, W. 2000. Reconstruction of pinniped diets: accounting for complete digestion of otoliths and cephalopod beaks. *Canadian Journal of Fisheries and Aquatic Sciences*, 57: 898-905.

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

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

Bowen, W. D., Lawson, J. W., and Beck, B. 1993. Seasonal and Geographic-Variation in the Species Composition and Size of Prey Consumed by Gray Seals (*Halichoerus-Grypus*) on the Scotian Shelf. *Canadian Journal of Fisheries and Aquatic Sciences*, 50: 1768-1778. doi: DOI 10.1139/f93-198.

Bowen, W. D., and Lidgard, D. 2013. Marine mammal culling programs: review of effects on predator and prey populations. *Mammal Review*, 43: 207-220.

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

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

Brander, K. M. 2005. Cod recruitment is strongly affected by climate when stock biomass is low. *ICES Journal of Marine Science: Journal du Conseil*, 62: 339-343.

Brasao, A., Duarte, C. C., and Cunha-e-Sa, M. A. 2000. Managing the Northern Atlantic bluefin tuna fisheries: the stability of the UN Fish Stock Agreement Solution. *Marine Resource Economics*, 15: 341-360.

Brown, S. L., Bearhop, S., Harrod, C., and McDonald, R. A. 2012. A review of spatial and temporal variation in grey and common seal diet in the United Kingdom and Ireland. *Journal of the Marine Biological Association of the United Kingdom*, 92: 1711-1722.

Bruckmeier, K., Westerberg, H., and Varjopuro, R. 2013. Baltic Seal Reconciliation in Practice The Seal Conflict and its Mitigation in Sweden and Finland. *Human-Wildlife Conflicts in Europe: Fisheries and Fish-eating Vertebrates as a Model Case*: 34.

Bundy, A. 2005. Structure and functioning of the eastern Scotian Shelf ecosystem before and after the collapse of groundfish stocks in the early 1990s. *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 1453-1473.

Bundy, A., and Fanning, L. P. 2005. Can Atlantic cod (*Gadus morhua*) recover? Exploring trophic explanations for the non-recovery of the cod stock on the eastern Scotian Shelf, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 1474-1489.

Bundy, A., Heymans, J. J., Morissette, L., and Savenkoff, C. 2009. Seals, cod and forage fish: A comparative exploration of variations in the theme of stock collapse and ecosystem change in four Northwest Atlantic ecosystems. *Progress in Oceanography*, 81: 188-206. doi: 10.1016/j.pocean.2009.04.010.

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

Butler, J. R. A., Middlemas, S. J., Graham, I. M., and Harris, R. N. 2011. Perceptions and costs of seal impacts on Atlantic salmon fisheries in the Moray Firth, Scotland: Implications for the adaptive co-management of seal-fishery conflict. *Marine Policy*, 35: 317-323. doi: 10.1016/j.marpol.2010.10.011.

Butler, J. R. A., Middlemas, S. J., McKelvey, S. A., McMyn, I., Leyshon, B., Walker, I., Thompson, P. M., et al. 2008. The Moray Firth Seal Management Plan: an adaptive framework for balancing the conservation of seals, salmon, fisheries and wildlife tourism in the UK. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 18: 1025-1038. doi: 10.1002/aqc.923.

Cardinale, M., and Svedäng, H. 2011. The beauty of simplicity in science: Baltic cod stock improves rapidly in a 'cod hostile' ecosystem state. *Marine Ecology Progress Series*, 425: 297-301.

Chakraborty, K., and Kar, T. K. 2012. Economic perspective of marine reserves in fisheries: A bioeconomic model. *Math Biosci*, 240: 212-222. doi: 10.1016/j.mbs.2012.07.008.

Chaudhuri, K. 1986. A bioeconomic model of harvesting a multispecies fishery. *Ecological Modelling*, 32: 267-279.

Chouinard, G. A., Swain, D. P., Hammill, M. O., and Poirier, G. A. 2005. Covariation between grey seal (*Halichoerus grypus*) abundance and natural mortality of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 1991-2000. doi: 10.1139/f05-107.

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

Christensen, V., Walters, C. J., and Pauly, D. 2005. *Ecopath with Ecosim: a user's guide*. Fisheries Centre, University of British Columbia, Vancouver, 154.

Cissé, A. A., Gourguet, S., Doyen, L., Blanchard, F., and Péreau, J.-C. 2013. A bio-economic model for the ecosystem-based management of the coastal fishery in French Guiana. *Environment and Development Economics*, 18: 245-269.

Clark, C. W. 2006. Fisheries bioeconomics: why is it so widely misunderstood? *Population Ecology*, 48: 95-98.

Cook, R. M. 2013. A fish stock assessment model using survey data when estimates of catch are unreliable. *Fisheries Research*, 143: 1-11.

Cook, R. M., and Heath, M. R. 2005. The implications of warming climate for the management of North Sea demersal fisheries. *ICES Journal of Marine Science: Journal du Conseil*, 62: 1322-1326.

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

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

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

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

Courchamp, F., Woodroffe, R., and Roemer, G. 2003. Removing protected populations to save endangered species. *Science*, 302: 1532-1532.

Cronin, M., Gerritsen, H., and Reid, D. 2012. Evidence of low spatial overlap between grey seals and a specific whitefish fishery off the west coast of Ireland. *Biological Conservation*, 150: 136-142.

Cronin, M., Jessopp, M., Houle, J., and Reid, D. 2014. Fishery-seal interactions in Irish waters: Current perspectives and future research priorities. *Marine Policy*, 44: 120-130.

Cronin, M., Pomeroy, P., and Jessopp, M. 2013. Size and seasonal influences on the foraging range of female grey seals in the northeast Atlantic. *Marine biology*, 160: 531-539.

Da Rocha, J. M., Cerviño, S., and Gutiérrez, M. J. 2010. An endogenous bioeconomic optimization algorithm to evaluate recovery plans: an application to southern hake. *ICES Journal of Marine Science: Journal du Conseil*, 67: 1957-1962.

Delgado, C. L., Wada, N., Rosegrant, M. W., Meijer, S., and Ahmed, M. 2003. *Fish to 2020: Supply and demand in changing global markets*, International Food Policy Research Institute and WorldFish Center.

DeMaster, D. P., Fowler, C. W., Perry, S. L., and Richlen, M. F. 2001. Predation and competition: the impact of fisheries on marine-mammal populations over the next one hundred years. *Journal of Mammalogy*, 82: 641-651.

DFO. 2011. *Impacts of Grey Seals on Fish Populations in Eastern Canada*.

Drinkwater, K. F. 2005. The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES Journal of Marine Science: Journal du Conseil*, 62: 1327-1337. doi: 10.1016/j.icesjms.2005.05.015.

Duck, J., and Morris, C. 2013. Surveys of harbour (common) and grey seals in Orkney, the north coast of Scotland, the Moray Firth and the Firth of Tay in August 2012.

Eero, M., Köster, F. W., and Vinther, M. 2012. Why is the Eastern Baltic cod recovering? *Marine Policy*, 36: 235-240.

El-Shaarawi, A. H., and Piegorisch, W. W. 2001. *Encyclopedia of environmetrics*, John Wiley & Sons.

Engelhard, G. H., Peck, M. A., Rindorf, A., Smout, S. C., van Deurs, M., Raab, K., Andersen, K. H., et al. 2014. Forage fish, their fisheries, and their predators: who drives whom? *ICES Journal of Marine Science: Journal du Conseil*, 71: 90-104.

European Commission 1983. Council Directive of 28 March 1983 concerning the importation into Member States of skins of certain seal pups and products derived therefrom (83/129/EEC). *Official Journal of the European Communities*.

European Commission 1985. Council Directive of 27 September 1985 amending Council Directive 83/129/EEC concerning the importation into Member States of skins of certain seal pups and products derived therefrom (85/444/EEC). *Official Journal of the European Communities*.

European Commission 1989. Council Directive of 8 June 1989 amending Directive 83/129/EEC concerning the importation into Member States of skins of certain seal pups and products derived therefrom (89/370/EEC). *Official Journal of the European Communities*.

European Commission 2015. *The Common Fisheries Policy (CFP)*. [accessed 15/08/2016]. Available from: http://ec.europa.eu/fisheries/cfp/index_en.htm.

FAO. 2011. *Review of the state of world marine fisheries resources*. FAO Fisheries and Aquaculture Technical Paper No. 569, Rome 334 pp.

FAO FishStatJ 2014. *FishStatJ - software for fishery statistical time series*. In FAO Fisheries and Aquaculture Department [online or CD-ROM], 2014 edn., Rome, [accessed 2014]. Available from: <http://www.fao.org/fishery/statistics/software/fishstatj/en>.

Fennell, D. A. 2014. Ecotourism, Routledge.

Fernandes, P. G., Coull, K., Davis, C., Clark, P., Catarino, R., Bailey, N., Fryer, R., et al. 2011. Observations of discards in the Scottish mixed demersal trawl fishery. ICES Journal of Marine Science: Journal du Conseil, 68: 1734-1742.

Finnish Game and Fisheries Research Institute 2015. Seal numbers. [accessed 25/09/2015]. Available from: http://www.rktl.fi/english/game/seals/seal_numbers/.

Fisheries and Oceans Canada DFO 2011-2015 Integrated Fisheries Management Plan for Atlantic Seals. [accessed 03/01/2012]. Available from: <http://www.dfo-mpo.gc.ca/fm-gp/seal-phoque/reports-rapports/mgtplan-planges20112015/mgtplan-planges20112015-eng.htm#c3.7.1>.

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

Fjälling, A., Wahlberg, M., and Westerberg, H. 2006. Acoustic harassment devices reduce seal interaction in the Baltic salmon-trap, net fishery. ICES Journal of Marine Science, 63: 1751-1758. doi: 10.1016/j.icesjms.2006.06.015.

Flaaten, O. 1991. Bioeconomics of sustainable harvest of competing species. Journal of Environmental Economics and Management, 20: 163-180.

Flaaten, O. 1998. On the bioeconomics of predator and prey fishing. Fisheries Research, 37: 179-191.

Flaaten, O., and Stollery, K. 1996. The economic costs of biological predation. Environmental and Resource Economics, 8: 75-95.

Fletcher, R. I. 1978. Time-dependent solutions and efficient parameters for stock-production models. Fishery Bulletin, 76.

Frank, K. T., Petrie, B., Choi, J. S., and Leggett, W. C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science*, 308: 1621-1623. doi: 10.1126/science.1113075.

Frank, K. T., Petrie, B., Fisher, J. A., and Leggett, W. C. 2011. Transient dynamics of an altered large marine ecosystem. *Nature*, 477: 86-89.

Froese, R. 2008. The continuous smooth hockey stick: a newly proposed spawner-recruitment model. *Journal of Applied Ichthyology*, 24: 703-704.

Fu, C. H., Mohn, R., and Fanning, L. P. 2001. Why the Atlantic cod (*Gadus morhua*) stock off eastern Nova Scotia has not recovered. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 1613-1623. doi: DOI 10.1139/cjfas-58-8-1613.

Fulton, E. A., Smith, A. D., Smith, D. C., and van Putten, I. E. 2011. Human behaviour: the key source of uncertainty in fisheries management. *Fish and Fisheries*, 12: 2-17.

Furness, R. 2002. Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea. *ICES Journal of Marine Science*, 59: 261-269. doi: 10.1006/jmsc.2001.1155.

Gårdmark, A., Östman, Ö., Nielsen, A., Lundström, K., Karlsson, O., Pönni, J., and Aho, T. 2012. Does predation by grey seals (*Halichoerus grypus*) affect Bothnian Sea herring stock estimates? *ICES Journal of Marine Science: Journal du Conseil*, 69: 1448-1456.

Gavaris, S. 1988. An adaptive framework for the estimation of population size, Canadian Atlantic Fisheries Scientific Advisory Committee.

Gazit, T., Lidgard, D., and Sykes, K. 2013. Changing Environments: Tracking the Scientific, Socio-political, Legal, and Ethical Currents of the Grey Seal-Cod Debate in Atlantic Canada. *Journal of International Wildlife Law & Policy*, 16: 266-299.

Gilbert, D. J. 1988. Use of a simple age-structured bioeconomic model to estimate optimal long-run surpluses. *Marine Resource Economics*, 5: 23-42.

Gosch, M., Hernandez-Milian, G., Rogan, E., Jessopp, M., and Cronin, M. 2014. Grey seal diet analysis in Ireland highlights the importance of using multiple diagnostic features. *Aquatic Biology*, 20: 155-167.

Gotz, T., and Janik, V. M. 2013. Acoustic deterrent devices to prevent pinniped depredation: efficiency, conservation concerns and possible solutions. *Marine Ecology Progress Series*, 492: 285-+. doi: 10.3354/meps10482.

Graham, I. M., Harris, R. N., Denny, B., Fowden, D., and Pullan, D. 2009. Testing the effectiveness of an acoustic deterrent device for excluding seals from Atlantic salmon rivers in Scotland. *ICES Journal of Marine Science: Journal du Conseil*, 66: 860-864.

Graham, I. M., Harris, R. N., Matejusova, I., and Middlemas, S. J. 2011. Do 'rogue' seals exist? Implications for seal conservation in the UK. *Animal Conservation*, 14: 587-598. doi: 10.1111/j.1469-1795.2011.00469.x.

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

Gruber, C. P. 2014. Social, Economic, and Spatial Perceptions of Gray Seal (*Halichoerus grypus*) Interactions with Commercial Fisheries in Cape Cod, MA. p. 68. Duke University.

Guillen, J., Macher, C., Merzéréaud, M., Bertignac, M., Fifas, S., and Guyader, O. 2013. Estimating MSY and MEY in multi-species and multi-fleet fisheries, consequences and limits: an application to the Bay of Biscay mixed fishery. *Marine Policy*, 40: 64-74.

Hammill, M., Stenson, G., Swain, D., and Benoît, H. 2014. Feeding by grey seals on endangered stocks of Atlantic cod and white hake. *ICES Journal of Marine Science: Journal du Conseil*: fsu123.

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

Hammond, P. S., Grellier, R., and Harris, R. N. 2006. Grey seal diet composition and prey consumption in the North Sea and west of Scotland. *In* Scientific Advice on Matters Related to the Management of Seal Populations: 2006. Ed. by SCOS.

Hannesson, R. 1998. Marine reserves: what would they accomplish? *Marine Resource Economics*, 13: 159-170.

Hardin, G. 1968. The tragedy of the commons. *Science*, 162: 1243-1248.

Harris, R., Harris, C., Duck, C., and Boyd, I. 2014. The effectiveness of a seal scarer at a wild salmon net fishery. *ICES Journal of Marine Science: Journal du Conseil*: fst216.

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

Harvey, C., Cox, S., Essington, T., Hansson, S., and Kitchell, J. 2003. An ecosystem model of food web and fisheries interactions in the Baltic Sea. *ICES Journal of Marine Science*, 60: 939-950. doi: 10.1016/s1054-3139(03)00098-5.

Harvey, V., Hammill, M., Swain, D., Breed, G., Lydersen, C., and Kovacs, K. 2012. Winter foraging by a top predator, the grey seal *Halichoerus grypus*, in relation to the distribution of prey. *Marine Ecology Progress Series*, 462: 273-286.

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

Harwood, J., and Walton, M. 2002. Interaction between seals and commercial fisheries in the North-East Atlantic. Executive summary. European Parliament. Luxemburg.

Hawkins, D. M. 2004. The problem of overfitting. *Journal of chemical information and computer sciences*, 44: 1-12.

Heath, M. R., and Cook, R. M. 2015. Hind-casting the quantity and composition of discards by mixed demersal fisheries in the North Sea. *PloS one*, 10: e0117078.

Heath, M. R., Cook, R. M., Cameron, A. I., Morris, D. J., and Speirs, D. C. 2014a. Cascading ecological effects of eliminating fishery discards. *Nature communications*, 5.

Heath, M. R., Culling, M. A., Crozier, W. W., Fox, C. J., Gurney, W. S. C., Hutchinson, W. F., Nielsen, E. E., et al. 2014b. Combination of genetics and spatial modelling highlights the sensitivity of cod (*Gadus morhua*) population diversity in the North Sea to distributions of fishing. *ICES Journal of Marine Science*, 71: 794-807. doi: 10.1093/icesjms/fst185.

Heath, M. R., Neat, F. C., Pinnegar, J. K., Reid, D. G., Sims, D. W., and Wright, P. J. 2012a. Review of climate change impacts on marine fish and shellfish around the UK and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 22: 337-367.

Heath, M. R., Rasmussen, J., Bailey, M. C., Dunn, J., Fraser, J., Gallego, A., Hay, S. J., et al. 2012b. Larval mortality rates and population dynamics of Lesser Sandeel (*Ammodytes marinus*) in the northwestern North Sea. *Journal of Marine Systems*, 93: 47-57. doi: 10.1016/j.jmarsys.2011.08.010.

Herrmann, M. 1996. Estimating the induced price increase for Canadian Pacific halibut with the introduction of the individual vessel quota program. *Canadian Journal of Agricultural Economics/Revue canadienne d'agroeconomie*, 44: 151-164.

Heymans, J. J., Howell, K. L., Ayers, M., Burrows, M. T., Gordon, J. D. M., Jones, E. G., and Neat, F. 2011. Do we have enough information to apply the ecosystem approach to management of deep-sea fisheries? An example from the West of Scotland. *ICES Journal of Marine Science*, 68: 265-280. doi: 10.1093/icesjms/fsq065.

Hilborn, R. 1985. Fleet dynamics and individual variation: why some people catch more fish than others. *Canadian Journal of Fisheries and Aquatic Sciences*, 42: 2-13.

Hilborn, R., and Walters, C. J. 1987. A general model for simulation of stock and fleet dynamics in spatially heterogeneous fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, 44: 1366-1369.

Hilborn, R., and Walters, C. J. 1992. *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*/Book and Disk, Springer.

HM Government 1970. *Conservation of Seals Act 1970*. Her Majesty's Stationery Office, London.

Hoff, A., and Frost, H. 2008. Modelling combined harvest and effort regulations: the case of the Dutch beam trawl fishery for plaice and sole in the North Sea. *ICES Journal of Marine Science: Journal du Conseil*, 65: 822-831.

Holland, D. S., and Sutinen, J. G. 1999. An empirical model of fleet dynamics in New England trawl fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 253-264.

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

Holma, M., Lindroos, M., and Oinonen, S. 2014. The Economics of Conflicting Interests: Northern Baltic Salmon Fishery Adaption to Gray Seal Abundance. *Natural Resource Modeling*, 27: 275-299. doi: 10.1111/nrm.12034.

Holmes, S. J. 2008. Seal Predation on VIa Cod and its Effect on the Assessment of the VIa Cod Stock. *In Working Documents of the Working Group on the Assessment of Northern Shelf Demersal Stocks (WGNDS) 2008*. Ed. by ICES.

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

Holmes, S. J., Wright, P. J., and Fryer, R. J. 2008. Evidence from survey data for regional variability in cod dynamics in the North Sea and West of Scotland. *ICES Journal of Marine Science: Journal du Conseil*, 65: 206-215.

Houle, J. E., De Castro, F., Cronin, M. A., Farnsworth, K. D., Gosch, M., and Reid, D. G. 2015. Effects of seal predation on a modelled marine fish community and consequences for a commercial fishery. *Journal of Applied Ecology*.

Hoyt, E. 2005. Sustainable ecotourism on Atlantic islands, with special reference to whale watching, marine protected areas and sanctuaries for cetaceans. *In Biology and environment: proceedings of the Royal Irish Academy*, pp. 141-154. JSTOR.

Hritonenko, N., and Yatsenko, Y. 2006. Optimization of harvesting return from age-structured population. *Journal of Bioeconomics*, 8: 167-179.

Hutchings, J. A., and Myers, R. A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 2126-2146.

Hutchings, J. A., and Rangeley, R. W. 2011. Correlates of recovery for Canadian Atlantic cod (*Gadus morhua*). *Canadian Journal of Zoology*, 89: 386-400.

Hutniczak, B. 2012. Recovery of the Eastern Baltic Cod Fishery: Perspectives Revealed through Bioeconomic Modelling. *Journal of Management and Sustainability*, 2. doi: 10.5539/jms.v2n1p3.

Hutton, T., Mardle, S., Pascoe, S., and Clark, R. A. 2004. Modelling fishing location choice within mixed fisheries: English North Sea beam trawlers in 2000 and 2001. *ICES Journal of Marine Science*, 61: 1443-1452.

ICES. 1990. Report of the ICES Advisory Committee on Fishery Management. ICES Cooperative Research Report No. 236.

ICES 2011. Historical Nominal Catches 1950-2010. [accessed 2015]. Available from: <http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx>.

ICES. 2013a. Report of the ICES Advisory Committee 2013. Book 6, 421 pp.

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

ICES. 2013c. Report of the Working Group on Biology and Assessment of Deep-sea Fisheries Resources (WGDEEP). 14-20 March 2013, Copenhagen, Denmark. ICES CM 2013/ACOM:17 963 pp.

ICES. 2013d. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK). 24 - 30 April 2013, ICES Headquarters, Copenhagen. ICES CM 2013/ACOM:13 1435 pp.

ICES. 2014a. Report of the Baltic Fisheries Assessment Working Group (WGBFAS). 3-10 April 2014, ICES HQ, Copenhagen, Denmark. ICES CM 2014/ACOM:10 919 pp.

ICES. 2014b. Report of the Report of the Working Group on Widely Distributed Stocks (WGWIDE). 26 August - 1 September 2014, ICES Headquarters, Copenhagen, Denmark. ICES CM 2014/ACOM:15 938 pp.

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

ICES. 2014d. Report of the Working Group for the Bay of Biscay and the Iberian waters Ecoregion (WGBIE). 7-13 May 2014, Lisbon, Portugal. ICES CM 2014/ACOM:11 714 pp.

ICES 2015a. Official Nominal Catches 2006-2013. [accessed 01/2015]. Available from: <http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx>.

ICES. 2015b. Report of the Herring Assessment Working Group for the Area South of 62°N (HAWG). 10-19 March 2015, ICES HQ, Copenhagen, Denmark. ICES CM 2015/ACOM:06 850 pp.

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

ICES. 2016a. First Interim Report of the International Bottom Trawl Survey Working Group (IBTSWG). 4-8 April 2016, Sète, France. ICES CM 2016/SSGIEOM:24 292 pp.

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

Isomaa, M., Kaitala, V., and Laakso, J. 2013. Baltic cod (*Gadus morhua callarias*) recovery potential under different environment and fishery scenarios. *Ecological Modelling*, 266: 118-125.

Jones, E., McConnell, B., Sparling, C., and Matthiopoulos, J. 2013. Grey and harbour seal usage maps: Sea Mammal Research Unit report to Scottish Government. ICES Document 2150, 36 pp.

Jounela, P., Suuronen, P., Millar, R., and Koljonen, M. 2006. Interactions between grey seal (*Halichoerus grypus*), Atlantic salmon (*Salmo salar*), and harvest controls on the salmon fishery in the Gulf of Bothnia. *ICES Journal of Marine Science*, 63: 936-945. doi: 10.1016/j.icesjms.2006.02.005.

Kar, T. K., and Chakraborty, K. 2010. Bioeconomic modelling of a prey predator system using differential algebraic equations. *International Journal of Engineering, Science and Technology*, 2: 13-34.

Kar, T. K., and Chaudhuri, K. S. 2004. Harvesting in a two-prey one-predator fishery: a bioeconomic model. *The ANZIAM Journal*, 45: 443-456.

Kar, T. K., and Matsuda, H. 2008. A bioeconomic model of a single-species fishery with a marine reserve. *J Environ Manage*, 86: 171-180. doi: 10.1016/j.jenvman.2006.12.001.

Kauhala, K., Kunnasranta, M., and Valtonen, M. 2011. Hallien ravinto Suomen merialueella 2001–2007 – alustava selvitys. *Suomen Riista*, 57: 73-83.

Kauppinen, T., Siira, A., and Suuronen, P. 2005. Temporal and regional patterns in seal-induced catch and gear damage in the coastal trap-net fishery in the northern Baltic Sea: effect of netting material on damage. *Fisheries Research*, 73: 99-109. doi: 10.1016/j.fishres.2005.01.003.

Kell, L. T., Mosqueira, I., Grosjean, P., Fromentin, J. M., Garcia, D., Hillary, R., Jardim, E., et al. 2007. FLR: an open-source framework for the evaluation and development of management strategies. *ICES Journal of Marine Science: Journal du Conseil*, 64: 640-646.

Kellogg, R. L., Easley, J. E., and Johnson, T. 1988. Optimal timing of harvest for the North Carolina bay scallop fishery. *American Journal of Agricultural Economics*, 70: 50-62.

Klimova, A., Phillips, C., Fietz, K., Olsen, M. T., Harwood, J., Amos, W., and Hoffman, J. 2014. Global population structure and demographic history of the grey seal. *Molecular ecology*, 23: 3999-4017.

Knowler, D. 2002. A review of selected bioeconomic models with environmental influences in fisheries. *Journal of Bioeconomics*, 4: 163-181.

Königson, S., Fjälling, A., Berglind, M., and Lunneryd, S. G. 2013. Male gray seals specialize in raiding salmon traps. *Fisheries Research*, 148: 117-123. doi: 10.1016/j.fishres.2013.07.014.

Königson, S., Fjälling, A., and Lunneryd, S.-G. 2007. Grey seal induced catch losses in the herring gillnet fisheries in the northern Baltic. *NAMMCO Scientific Publications*, 6: 203-213.

Königson, S., Fjälling, A., and Lunneryd, S. G. 2005. Impact of grey seals on the herring gillnet fishery along the Swedish Baltic coast. *Institute of Coastal Research, Swedish Board of Fisheries. ICES CM*, 10: 12.

Königson, S., Lovgren, J., Hjelm, J., Ovegard, M., Ljunghager, F., and Lunneryd, S. G. 2015. Seal exclusion devices in cod pots prevent seal bycatch and affect their catchability of cod. *Fisheries Research*, 167: 114-122. doi: 10.1016/j.fishres.2015.01.013.

Kronbak, L. G. 2005. The dynamics of an open-access fishery: Baltic Sea cod. *Marine Resource Economics*, 19: 459-479.

Kronbak, L. G., Nielsen, J. R., Jorgensen, O. A., and Vestergaard, N. 2009. Bio-economic evaluation of implementing trawl fishing gear with different selectivity. *J Environ Manage*, 90: 3665-3674. doi: 10.1016/j.jenvman.2009.07.008.

Lambert, R. A. 2001. Grey seals to cull or not to cull? *In History Today*.

Lambert, R. A. 2002. The grey seal in Britain: a twentieth century history of a nature conservation success. *Environment and History*, 8: 449-474.

Larkin, S. L., and Sylvia, G. 1999. Intrinsic fish characteristics and intraseason production efficiency: a management-level bioeconomic analysis of a commercial fishery. *American Journal of Agricultural Economics*, 81: 29-43.

Laukkanen, M. 2001. A bioeconomic analysis of the northern Baltic salmon fishery: coexistence versus exclusion of competing sequential fisheries. *Environmental and Resource Economics*, 18: 293-315.

Lavigne, D. 1996. Ecological interactions between marine mammals, commercial fisheries, and their prey: unravelling the tangled web. *High-latitude seabirds*, 4: 59-71.

Lavigne, D. 2003. *Marine mammals and fisheries: The role of science in the culling debate*, CSIRO Publishing, Victoria. 31-47 pp.

Lehtonen, E., and Suuronen, P. 2004. Mitigation of seal-induced damage in salmon and whitefish trapnet fisheries by modification of the fish bag. *ICES Journal of Marine Science*, 61: 1195-1200. doi: 10.1016/j.icesjms.2004.06.012.

Lehtonen, E., and Suuronen, P. 2010. Live-capture of grey seals in a modified salmon trap. *Fisheries Research*, 102: 214-216. doi: 10.1016/j.fishres.2009.10.007.

Leonart, J., Maynou, F., Recasens, L., and Franquesa, R. 2003. A bioeconomic model for Mediterranean fisheries, the hake off Catalonia (western Mediterranean) as a case study. *Scientia Marina*, 67: 337-351.

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

Lundström, K. 2012. Assessment of dietary patterns and prey consumption of marine mammals: Grey seals (*Halichoerus grypus*) in the Baltic Sea. *In* Department of Biological and Environmental Sciences, p. 36. University of Gothenburg.

Lundström, K., Hjerne, O., Alexandersson, K., and Karlsson, O. 2007. Estimation of grey seal (*Halichoerus grypus*) diet composition in the Baltic Sea. *NAMMCO Scientific Publications*, 6: 177-196.

Lundström, K., Hjerne, O., Lunneryd, S. G., and Karlsson, O. 2010. Understanding the diet composition of marine mammals: grey seals (*Halichoerus grypus*) in the Baltic Sea. *ICES Journal of Marine Science: Journal du Conseil*, 67: 1230-1239.

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

Lunneryd, S. G., Fjälling, A., and Westerberg, H. 2003. A large-mesh salmon trap: a way of mitigating seal impact on a coastal fishery. *ICES Journal of Marine Science: Journal du Conseil*, 60: 1194-1199.

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

Mackinson, S., Sumaila, U. R., and Pitcher, T. J. 1997. Bioeconomics and catchability: fish and fishers behaviour during stock collapse. *Fisheries Research*, 31: 11-17.

Maravelias, C. D., Damalas, D., Ulrich, C., Katsanevakis, S., and Hoff, A. 2012. Multispecies fisheries management in the Mediterranean Sea: application of the Fcube methodology. *Fisheries Management and Ecology*, 19: 189-199.

Marchal, P. 2005. Technological developments and tactical adaptations of important EU fleets (TECTAC). Final report of the EU project NQ5RS-2002-019.

Marine Environmental Mapping Programme 2015. BGS SeaBed Sediment (250K) Map.

Marine Management Organisation. 2012. UK Sea Fisheries Statistics 2011.

Massey, D. M., Newbold, S. C., and Gentner, B. 2006. Valuing water quality changes using a bioeconomic model of a coastal recreational fishery. *Journal of Environmental Economics and Management*, 52: 482-500.

Matejusova, I., Doig, F., Middlemas, S. J., Mackay, S., Douglas, A., Armstrong, J. D., Cunningham, C. O., et al. 2008. Using quantitative real-time PCR to detect salmonid prey

in scats of grey *Halichoerus grypus* and harbour *Phoca vitulina* seals in Scotland - an experimental and field study. *Journal of Applied Ecology*, 45: 632-640. doi: 10.1111/j.1365-2664.2007.01429.x.

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

Matulich, S. C., Mittelhammer, R. C., and Reberte, C. 1996. Toward a more complete model of individual transferable fishing quotas: Implications of incorporating the processing sector. *Journal of Environmental Economics and Management*, 31: 112.

McConnell, K. E., and Strand, I. E. 1989. Benefits from commercial fisheries when demand and supply depend on water quality. *Journal of Environmental Economics and Management*, 17: 284-292.

Mesnil, B., and Rochet, M.-J. 2010. A continuous hockey stick stock-recruit model for estimating MSY reference points. *ICES Journal of Marine Science: Journal du Conseil*: 1780-1784. doi: 10.1093/icesjms/fsq055.

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

Millar, C. P., and Fryer, R. J. 2005. Revised estimates of annual discards-at-age for cod, haddock, whiting and saithe in ICES sub-area IV and division VIa. *Fisheries Research Services Internal Report*, 15.

Millar, R. B., and Fryer, R. J. 1999. Estimating the size-selection curves of towed gears, traps, nets and hooks. *Reviews in Fish Biology and Fisheries*, 9: 89-116.

Minister of Supply and Services Canada 1986. *Seals and sealing in Canada: Report of the Royal Commission*. 73 pp.

Ministry of Agriculture and Forestry 2007. *Management Plan for the Finnish Seal Populations in the Baltic Sea*. Ministry of Agriculture and Forestry.

Mohn, R., and Bowen, W. 1996. Grey seal predation on the eastern Scotian Shelf: modelling the impact on Atlantic cod. *Canadian Journal of Fisheries and Aquatic Sciences*, 53: 2722-2738.

Moore, P. G. 2003. Seals and fisheries in the Clyde Sea area (Scotland): traditional knowledge informs science. *Fisheries Research*, 63: 51-61. doi: 10.1016/s0165-7836(03)00003-1.

Morissette, L., Christensen, V., and Pauly, D. 2012. Marine mammal impacts in exploited ecosystems: would large scale culling benefit fisheries? *PloS one*, 7: e43966.

Morizur, Y., Berrow, S. D., Tregenza, N. J. C., Couperus, A. S., and Pouvreau, S. 1999. Incidental catches of marine-mammals in pelagic trawl fisheries of the northeast Atlantic. *Fisheries Research*, 41: 297-307.

Myers, R. A. 2001. Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. *ICES Journal of Marine Science: Journal du Conseil*, 58: 937-951.

Myers, R. A., and Barrowman, N. J. 1996. Is fish recruitment related to spawner abundance? *Fishery Bulletin*, 94: 707-724.

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

Myers, R. A., Hutchings, J. A., and Barrowman, N. J. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecological Applications*, 7: 91-106.

Myers, R. A., and Pepin, P. 1994. Recruitment variability and oceanographic stability. *Fisheries Oceanography*, 3: 246-255.

Neubauer, P., Jensen, O. P., Hutchings, J. A., and Baum, J. K. 2013. Resilience and recovery of overexploited marine populations. *Science*, 340: 347-349.

Nøstbakken, L., Thebaud, O., and Sørensen, L.-C. 2011. Investment behaviour and capacity adjustment in fisheries: a survey of the literature. *Marine Resource Economics*, 26: 95-117.

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

Oksanen, S. M., Ahola, M. P., Lehtonen, E., and Kunnasranta, M. 2014. Using movement data of Baltic grey seals to examine foraging-site fidelity: implications for seal-fishery conflict mitigation. *Marine Ecology Progress Series*, 507: 297-308.

Önal, H., McCarl, B. A., Griffin, W. L., Matlock, G., and Clark, J. 1991. A bioeconomic analysis of the Texas shrimp fishery and its optimal management. *American Journal of Agricultural Economics*, 73: 1161-1170.

Ostrom, E. 2008. *Tragedy of the Commons*. The New Palgrave Dictionary of Economics.

Ouellet, P., Savenkoff, C., Benoît, H. P., and Galbraith, P. S. 2016. A comparison of recent trends in demersal fish biomass and their potential drivers for three ecoregions of the Gulf of St Lawrence, Canada. *ICES Journal of Marine Science: Journal du Conseil*, 73: 329-344.

Overholtz, W. J., and Link, J. S. 2007. Consumption impacts by marine mammals, fish, and seabirds on the Gulf of Maine-Georges Bank Atlantic herring (*Clupea harengus*) complex during the years 1977-2002. *ICES Journal of Marine Science: Journal du Conseil*, 64: 83-96.

Pal, D., Mahapatra, G. S., and Samanta, G. P. 2012. Optimal harvesting of prey-predator system with interval biological parameters: A bioeconomic model. *Mathematical Biosciences*.

Parsons, E. C. M. 2003. Seal management in Scotland: tourist perceptions and the possible impacts on the Scottish tourism industry.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. 1998. Fishing down marine food webs. *Science*, 279: 860-863.

Perring, E. 2001. The causes and impact of changes in fish stocks in the waters around Fair Isle during the twentieth century. *Scottish Geographical Journal*, 117: 117-137. doi: 10.1080/00369220118737116.

Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Le Bris, A., Mills, K. E., Nye, J. A., et al. 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science*, 350: 809-812.

Pezzey, J. C. V., Roberts, C. M., and Urdal, B. T. 2000. A simple bioeconomic model of a marine reserve. *Ecological Economics*, 33: 77-91.

Pitcher, T. J. 1995. The impact of pelagic fish behaviour on fisheries. *Scientia Marina*, 59.

Pope, J. G., and Shepherd, J. G. 1982. A simple method for the consistent interpretation of catch-at-age data. *Journal du Conseil*, 40: 176-184.

Prelezo, R., Accadia, P., Andersen, J. L., Andersen, B. S., Buisman, E., Little, A., Nielsen, J. R., et al. 2012. A review of EU bio-economic models for fisheries: the value of a diversity of models. *Marine Policy*, 36: 423-431.

Puga, R., Vázquez, S. H., Martínez, J. L., and de León, M. E. 2005. Bioeconomic modelling and risk assessment of the Cuban fishery for spiny lobster *Panulirus argus*. *Fisheries Research*, 75: 149-163. doi: 10.1016/j.fishres.2005.03.014.

Quinn II, T. J., and Deriso, R. B. 1999. *Quantitative fish dynamics*, Oxford University Press.

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

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

Rijnsdorp, A. D., Daan, N., and Dekker, W. 2006. Partial fishing mortality per fishing trip: a useful indicator of effective fishing effort in mixed demersal fisheries. *ICES Journal of Marine Science: Journal du Conseil*, 63: 556-566.

Rose, G. A. 2004. Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years. *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 1553-1557.

Russell, D. J., Brasseur, S. M., Thompson, D., Hastie, G. D., Janik, V. M., Aarts, G., McClintock, B. T., et al. 2014. Marine mammals trace anthropogenic structures at sea. *Current Biology*, 24: R638-R639.

Salz, P., Buisman, E., Soma, K., Frost, H., Accadia, P., and Prellezo, R. 2011. FISHRENT: bio-economic simulation and optimisation model for fisheries, LEI Wageningen UR.

Sana, S. S., Purohit, D., and Chaudhuri, K. 2012. Joint project of fishery and poultry – A bioeconomic model. *Applied Mathematical Modelling*, 36: 72-86. doi: 10.1016/j.apm.2011.04.031.

Sanchirico, J. N., and Wilen, J. E. 1999. Bioeconomics of spatial exploitation in a patchy environment. *Journal of Environmental Economics and Management*, 37: 129-150.

Sanchirico, J. N., and Wilen, J. E. 2001. A Bioeconomic Model of Marine Reserve Creation. *Journal of Environmental Economics and Management*, 42: 257-276. doi: 10.1006/jeem.2000.1162.

Sardà, F., Coll, M., Heymans, J. J., and Stergiou, K. I. 2015. Overlooked impacts and challenges of the new European discard ban. *Fish and Fisheries*, 16: 175-180.

Schaefer, M. B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries, Inter-American Tropical Tuna Commission.

Scottish Fishermen's Organisation. 2013. Production and marketing plan 2015.

Scottish Government 2015a. Fish and Shellfish. [accessed 24/02/2015]. Available from: <http://www.gov.scot/Topics/marine/marine-environment/species/fish>.

Scottish Government 2015b. Regulating Fisheries in Scotland. Available from: <http://www.gov.scot/Topics/marine/Compliance/Regulation>.

Scottish Parliament 2010. Marine (Scotland) Act 2010 (asp5). The Stationery Office.

Simons, S. L., Bartelings, H., Hamon, K. G., Kempf, A. J., Döring, R., and Temming, A. 2014. Integrating stochastic age-structured population dynamics into complex fisheries economic models for management evaluations: the North Sea saithe fishery as a case study. *ICES Journal of Marine Science: Journal du Conseil*, 71: 1638-1652.

Sinclair, A. R. E., Pech, R. P., Dickman, C. R., Hik, D., Mahon, P., and Newsome, A. E. 1998. Predicting effects of predation on conservation of endangered prey. *Conservation Biology*, 12: 564-575.

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

Smout, S., Rindorf, A., Hammond, P. S., Harwood, J., and Matthiopoulos, J. 2013. Modelling prey consumption and switching by UK grey seals. *ICES Journal of Marine Science: Journal du Conseil*.

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

Sparholt, H. 1994. Fish species interactions in the Baltic Sea. *Dana*, 10: 131-162.

Speirs, D. C., Guirey, E. J., Gurney, W. S. C., and Heath, M. R. 2010. A length-structured partial ecosystem model for cod in the North Sea. *Fisheries Research*, 106: 474-494. doi: 10.1016/j.fishres.2010.09.023.

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

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

STECF. 2013. The 2013 Annual Economic Report on the EU Fishing Fleet (STECF-13-15). Luxembourg, EUR 26158 EN, JRC 84745 302 pp.

STECF. 2015a. The 2015 Annual Economic Report on the EU Fishing Fleet (EWG 15-03 and EWG 15-07). Varese, Italy, JRC97371.

STECF. 2015b. Evaluation of Fisheries Dependent Information (STECF-15-12). Luxembourg, EUR 27416 EN, JRC 97365 799 pp.

Stewart, C., Iverson, S., and Field, C. 2014. Testing for a change in diet using fatty acid signatures. *Environmental and Ecological Statistics*: 1-18.

Stratoudakis, Y., Fryer, R. J., Cook, R. M., and Pierce, G. J. 1999. Fish discarded from Scottish demersal vessels: estimators of total discards and annual estimates for targeted gadoids. *ICES Journal of Marine Science: Journal du Conseil*, 56: 592-605.

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

Suuronen, P., and Lehtonen, E. 2012. The role of salmonids in the diet of grey and ringed seals in the Bothnian Bay, northern Baltic Sea. *Fisheries Research*, 125: 283-288.

Suuronen, P., Siira, A., Kauppinen, T., Riikonen, R., Lehtonen, E., and Harjunpää, H. 2006. Reduction of seal-induced catch and gear damage by modification of trap-net design: Design principles for a seal-safe trap-net. *Fisheries Research*, 79: 129-138. doi: 10.1016/j.fishres.2006.02.014.

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

Swain, D. P., Benoit, H. P., and Hammill, M. O. 2015. Spatial distribution of fishes in a Northwest Atlantic ecosystem in relation to risk of predation by a marine mammal. *Journal of Animal Ecology*, 84: 1286-1298. doi: 10.1111/1365-2656.12391.

Swain, D. P., and Chouinard, G. A. 2008. Predicted extirpation of the dominant demersal fish in a large marine ecosystem: Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences*, 65: 2315-2319.

Swain, D. P., Jonsen, I. D., Simon, J. E., and Davies, T. D. 2013. Contrasting decadal trends in mortality between large and small individuals in skate populations in Atlantic Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 70: 74-89. doi: 10.1139/cjfas-2012-0179.

Swain, D. P., and Mohn, R. K. 2012. Forage fish and the factors governing recovery of Atlantic cod (*Gadus morhua*) on the eastern Scotian Shelf. *Canadian Journal of Fisheries and Aquatic Sciences*, 69: 997-1001.

Tahvonen, O. 2009. Economics of harvesting age-structured fish populations. *Journal of Environmental Economics and Management*, 58: 281-299. doi: 10.1016/j.jeem.2009.02.001.

The IUCN Red List of Threatened Species 2015. *Gadus morhua*. [accessed 07/10/2015]. Available from: <http://www.iucnredlist.org/details/summary/8784/0>.

Thomas, L. 2012. Estimating the size of the UK grey seal population between 1984 and 2011.

Thomas, L. 2013. Estimating the size of the UK grey seal population between 1984 and 2012, using established and draft revised priors.

Thomas, L. 2014. Estimating the size of the UK grey seal population between 1984 and 2013, using established and draft revised priors.

Thomas, L., Hammill, M. O., and Bowen, W. D. 2011. Estimated Size of the Northwest Atlantic Grey Seal Population 1977-2010. p. iv + 23. Ed. by DFO Can. Sci. Advis. Sec. Res. Doc. 2011/017. Fisheries and Oceans Canada, Science.

Thompson, D., Lonergan, M., and Duck, C. 2005. Population dynamics of harbour seals *Phoca vitulina* in England: monitoring growth and catastrophic declines. *Journal of Applied Ecology*, 42: 638-648.

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

Thorson, J. T., Minto, C., Mente-Vera, C. V., Kleisner, K. M., Longo, C., and Jacobson, L. 2013. A new role for effort dynamics in the theory of harvested populations and data-poor stock assessment. *Canadian Journal of Fisheries and Aquatic Sciences*, 70: 1829-1844.

Tollit, D., Steward, M., Thompson, P., Pierce, G., Santos, M., and Hughes, S. 1997. Species and size differences in the digestion of otoliths and beaks: implications for estimates of pinniped diet composition. *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 105-119.

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

Ulrich, C., Andersen, B. S., Sparre, P. J., and Nielsen, J. R. 2007. TEMAS: fleet-based bio-economic simulation software to evaluate management strategies accounting for fleet behaviour. *ICES Journal of Marine Science: Journal du Conseil*, 64: 647-651.

Ulrich, C., Le Gallic, B., Dunn, M. R., and Gascuel, D. 2002a. A multi-species multi-fleet bioeconomic simulation model for the English Channel artisanal fisheries. *Fisheries Research*, 58: 379-401.

Ulrich, C., Pascoe, S., Sparre, P. J., Wilde, J.-W. D., and Marchal, P. 2002b. Influence of trends in fishing power on bioeconomics in the North Sea flatfish fishery regulated by catches or by effort quotas. *Canadian Journal of Fisheries and Aquatic Sciences*, 59: 829-843.

van Deurs, M., Koski, M., and Rindorf, A. 2013. Does copepod size determine food consumption of particulate feeding fish? *ICES Journal of Marine Science: Journal du Conseil*: fst090.

van Putten, I. E., Kulmala, S., Thébaud, O., Dowling, N., Hamon, K. G., Hutton, T., and Pascoe, S. 2012. Theories and behavioural drivers underlying fleet dynamics models. *Fish and Fisheries*, 13: 216-235.

Varjopuro, R. 2011. Co-existence of seals and fisheries? Adaptation of a coastal fishery for recovery of the Baltic grey seal. *Marine Policy*, 35: 450-456. doi: 10.1016/j.marpol.2010.10.023.

Vermard, Y., Andersen, B. S., Ulrich-Rescan, C., and Sparre, P. J. 2005. Application du modèle TEMAS a l'étude bioéconomique des pêcheries de poissons plats en Mer du Nord. *In Actes du 7ieme forum halieumétrique*, pp. 21-23.

Votier, S. C., Bicknell, A., Cox, S. L., Scales, K. L., and Patrick, S. C. 2013. A bird's eye view of discard reforms: bird-borne cameras reveal seabird/fishery interactions.

Walters, C. J., and Ludwig, D. 1981. Effects of measurement errors on the assessment of stock-recruitment relationships. *Canadian Journal of Fisheries and Aquatic Sciences*, 38: 704-710.

Wanless, S., Harris, M. P., Redman, P., and Speakman, J. R. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series*, 294: 8.

Wanless, S., Wright, P. J., Harris, M. P., and Elston, D. A. 2004. Evidence for decrease in size of lesser sandeels *Ammodytes marinus* in a North Sea aggregation over a 30-yr period. *Marine Ecology Progress Series*, 279: 237-246.

Warburton, C., Parsons, E., Woods-Ballard, A., Hughes, A., and Johnston, P. 2001. Whale-watching in West Scotland. *Hebidean Whale and Dolphin Trust*.

Werner, T. B., Northridge, S., Press, K. M., and Young, N. 2015. Mitigating bycatch and depredation of marine mammals in longline fisheries Introduction. *ICES Journal of Marine Science*, 72: 1576-1586. doi: 10.1093/icesjms/fsv092.

Wilén, J. E., Smith, M. D., Lockwood, D., and Botsford, L. W. 2002. Avoiding surprises: incorporating fisherman behavior into management models. *Bulletin of Marine Science*, 70: 553-575.

Woods-Ballard, A., Parsons, E., Hughes, A., Velandar, K., Ladle, R., and Warburton, C. 2003. The sustainability of whale-watching in Scotland. *Journal of Sustainable Tourism*, 11: 40-55.

Wright, P. J., Neat, F. C., Gibb, F. M., Gibb, I. M., and Thordarson, H. 2006. Evidence for metapopulation structuring in cod from the west of Scotland and North Sea. *Journal of Fish Biology*, 69: 181-199. doi: 10.1111/j.1095-8649.2006.01262.x.

Yodzis, P. 2001. Must top predators be culled for the sake of fisheries? *Trends in Ecology & Evolution*, 16: 78-84.

Yoshimoto, S. S., and Clarke, R. P. 1993. Comparing dynamic versions of the Schaefer and Fox Production models and their application to lobster fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, 50: 181-189.