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Bycatch of a protected species, the Atlantic grey seal (*Haliochoerus grypus*, Fabricius 1791), in static net fisheries: untangling the problem

Thesis presented by

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Declaration

This is to certify that the work I am submitting is my own and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism.

Signed:

Cian Luck

Cian Luck

Acknowledgments

These past four years, I have been exceedingly lucky to be supported by such brilliant supervisors, colleagues, collaborators, friends, and family. This thesis would not have been possible without them, or half as much fun.

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Abstract

As fisheries management has moved towards a more ecosystem-based approach, research has increasingly focused on understanding the impacts of fishing on the wider ecosystem. Fisheries bycatch, the incidental catch of non-targeted animals, represents the dominant anthropogenic threat facing many marine species worldwide, having already pushed some populations and species towards extinction. In Western Europe, an unknown number of grey seals (*Halichoerus grypus*) are bycaught annually, predominantly in fisheries using static nets. Despite growing concerns surrounding interactions between seals and fisheries, which have largely focused on damage to fishers' catches, our understanding of the mechanisms involved in seal bycatch, and the potential impact it may have on grey seal populations, remains extremely limited, thus precluding an ecosystem approach to fisheries management. This thesis aims to address key information gaps regarding the cause and effect of grey seal bycatch in static net fisheries.

Firstly, I aimed to identify novel drivers of seal bycatch by analysing an extensive dataset of at-sea observations of seal bycatch. While mesh size and distance to the closest major grey seal colony were found to significantly affect bycatch rates, this is the first study to demonstrate that water turbidity also plays an important role, suggesting that making nets more detectable to seals may be effective in mitigating seal bycatch. These results are presented in chapter 2.

In chapter 3, I demonstrated a novel methodology for estimating total bycatch of a protected species at a national level when only sparse observational data are available. The results of this analysis provided the first annual estimates of seal bycatch across all static net fishing vessels operating in Irish waters. Between 2011 and 2016, an average of 329 seals were estimated to be caught each year, with confidence intervals ranging from fewer than 5 seals per year to more than 800, potentially exceeding sustainable limits.

In chapter 4, Hidden Markov Models were applied to tracking data from 164 grey seals tagged in Ireland, the UK, and northern France, combined with locational data of concurrent static net fishing activity, to study the behaviour of seals near nets.

Overall, seals were found to be more likely to transition from travel to foraging behaviour with increasing proximity to fishing nets, suggesting that where seals and nets overlapped, direct interactions were likely to occur.

Finally, in chapter 5, I applied knowledge gained in previous chapters to examine the potential impact of bycatch on the national population of grey seals breeding in Ireland, using Population Viability Analysis. A range of bycatch scenarios were simulated to explore the full range of plausible bycatch levels (based on the findings of chapter 3), with additional scenarios testing the effect of age or sex-bias in bycatch mortality, the potential mitigating effect of immigration of seals from outside of Ireland, and potential colony-specific impacts of bycatch. Higher levels of bycatch resulted in reduced population growth, and extirpation of the national population once bycatch exceeded 700 seals per year. Populations were most sensitive to bycatch of female seals and more robust to removals of males and juveniles. Recruitment of 400 seals per year from colonies outside of Ireland allowed the national population to persist despite worst-case scenario bycatch levels. Colonies in the south and southwest of Ireland may be most vulnerable to bycatch pressure due to high levels of bycatch in adjacent waters.

Prior to this study we had an extremely limited understanding of the drivers and mechanisms involved in grey seal bycatch, and no knowledge of what total bycatch levels were, or whether or not they were sustainable. This research has addressed these critical knowledge gaps and provided fundamental information for management of seal-fishery conflicts. However, key knowledge gaps remain and improved monitoring of bycatch and fishing effort, particularly in inshore fisheries, and more frequent monitoring of the grey seal breeding population, are needed to ensure the conservation status of grey seals in Ireland and the sustainability of static net fisheries.

Chapter 1: General Introduction

Image: Collecting biometric data of a recently bycaught seal near the Blasket Islands, Co Kerry.

1.1 An ecosystem approach to fisheries management

Humans have harvested animals from the sea for at least 40,000 years (O'Connor et al. 2011). In the late 19th century, the development of fossil-fuelled fishing vessels allowed industrialised fleets to expand their range and access greater numbers of fish (Pauly et al. 2005; Swartz et al. 2010). As technology improved, more fish were caught (Pauly et al. 2003), however, as once-abundant stocks became depleted, fisheries began targeting fish in new areas (Swartz et al. 2010), at deeper depths (Morato et al. 2006), and lower trophic levels (Pauly et al. 1998). This resulted in fewer refugia where fish were not exposed to fishing. Today, industrial fishing occurs in more than 55% of the global ocean area, with a spatial extent four times that of agriculture (Kroodsma et al. 2018). Eventually the rate of expansion of global fisheries could no longer compensate for depletions of fish stocks already accessed, and in the 1980s, after decades of increasing catches, landings began to decline (Pauly et al. 2003, 2005). Globally, fish stocks declined by 38% between 1970 and 2007 (Hutchings et al. 2010), and total biomass of large predatory fish is presently only 10% of pre-industrial levels (Myers & Worm 2003).

Overfishing can significantly impact marine ecosystems, as depleting a species to such an extent that it no longer fulfils its ecological role can potentially leave an ecosystem more vulnerable to environmental pressures including eutrophication, disease transmission, or establishment of invasive species (Redford 1992; Jackson et al. 2001; McCauley et al. 2015). Effective fisheries management has enabled approximately half of the world's fish stocks to recover to above target levels (Hilborn et al. 2020). However, the other half of global fish stocks are less intensively managed or poorly assessed, and many depleted stocks have failed to recover as a result (Hutchings 2000; Hilborn et al. 2020). Traditionally, fisheries management has focused on maintaining single species fish stocks at a level that allows for the maximum sustainable yield (MSY) to be harvested from the stock indefinitely. A single stock or species approach to fisheries management ignores the potential impact of fishing on the wider ecosystem and risks adversely affecting other fisheries or causing significant shifts in ecosystem structure (Trochta et al. 2018). As fisheries science has progressed, the calculation of MSY has evolved as experts developed a more holistic, precautionary definition of stock sustainability (Quinn & Collie 2005).

In 1995, the Food and Agriculture Organisation of the United Nations (FAO) produced the Code of Conduct for Responsible Fisheries, which outlined 19 principles as standards of behaviour for responsible fisheries management (FAO 1995). These general principles included statements such as "States and users of living aquatic resources should conserve aquatic ecosystems" and "Management measures should not only ensure the conservation of target species but also of species belonging to the same ecosystem or associated or dependent upon the target species". This outlined a need to move away from managing single fish stocks in isolation and instead adopting an Ecosystem Approach to Fisheries Management (EAFM; Garcia & Cochrane 2005). EAFM is a broad, encompassing term, but critically aims to account for the impact of fishing on the wider ecosystem, and the effect of ecosystem dynamics on the fishery (FAO 2003; Hall & Mainprize 2004; Garcia & Cochrane 2005).

1.2 Interactions between fisheries and large marine predators

Central to EAFM is the interaction between fishing and non-target species. Encounters between large marine predators and fisheries often result in interactions that are deleterious for predators and or fisheries.

1.2.1 Biological interactions

Biological interactions, also referred to as indirect interactions, describe the competition between predators and fisheries for a shared resource (Northridge & Hofman 1999). Cury et al. (2011) quantified the effect of variation in prey biomass on global seabird population dynamics and estimated that seabirds required one third of the available prey biomass to sustain populations over the long term. Global populations of seabirds have declined by an estimated 70% since the 1950s (Paleczny et al. 2015). As the estimated food consumption by seabirds has declined over this time, biomass removal by fisheries has increased, and resource competition between seabirds and fisheries has intensified (Grémillet et al. 2018).

The extent to which prey consumption by predators affects fisheries catch is unclear. Globally, marine mammals are estimated to consume approximately four times as much biomass as fisheries capture, and seabirds about the same as fisheries (de L. Brooke 2004; Kaschner & Pauly 2005). However, competition in a given area may be low as predators target different species (Trites et al. 1997; Kaschner et al. 2006; Morissette et al. 2012), size classes (Houle et al. 2016), or trophic levels to fisheries (Morissette et al. 2012). Nonetheless, the failure of cod stocks in the northwest Atlantic has been at least partially attributed to predation pressure by grey seals (*Halichoerus grypus*) and harp seals (*Pagophilus groenlandicus*; O'Boyle & Sinclair 2012). Competition for fish, whether real or perceived, remains a persistent source of conflict between conservationists and fishers (Kaschner & Pauly 2005).

By the end of the 21st century, competition with fisheries is predicted to cause local extinctions of marine mammal populations and reduce species richness, particularly in coastal environments, where species with relatively restricted ranges will be most impacted (DeMaster et al. 2001; Karamanlidis et al. 2008). While marine mammals depend on large quantities of prey, a large proportion of marine mammal diet consists of prey from lower trophic levels, thus limiting the extent of resource competition (Trites et al. 1997; Kaschner et al. 2006). However, as fisheries increasingly target species at lower trophic levels, they could potentially place more pressure on marine mammal populations as competition for primary production increases (Trites et al. 1997; Pauly et al. 1998).

1.2.2 Operational interactions

Operational interactions, also known as direct interactions, include predators removing or damaging fish from nets or lines (known as depredation), damaging gear, or becoming incidentally caught as bycatch (Northridge & Hofman 1999). Depredation of target catch by marine mammals, sharks and seabirds has become a more important issue in fisheries management as the cumulative number of fisheries reporting depredation has increased in recent decades (Hamer et al. 2012; Mitchell et al. 2018; Tixier et al. 2020b). As fisheries have expanded and many fish stocks have declined it is possible that once-tolerable levels of depredation have now become unsustainable, or depleted prey resources have caused predators to engage in depredation more frequently (Tixier et al. 2020b). Tixier et al. (2020b) reviewed the literature on fisheries depredation by large marine predators and found it occurs throughout the world's oceans but has been reported most frequently in the northeast Atlantic. Passive fishing gears such as longlines or static nets, which expose captured fish to predators for longer periods of time than active gears such as trawls, are most susceptible to depredation (Tixier et al. 2020b). Pinnipeds and odontocetes were the most commonly reported depredating taxa, and while both interacted with a wide range of fishing technologies, pinniped depredation was most prevalent for static net fisheries while odontocetes primarily targeted longlines (Tixier et al. 2020b).

Depredation can be costly to fishers as predators remove or damage catch beyond a point that it can be sold (Peterson & Carothers 2013; Tixier et al. 2020a, 2020b). Depredation by grey seals and harbour seals (*Phoca vitulina*) in static net fisheries off eastern Canada in the 1980s was estimated to cost $60,000 USD per year (Farmer & Billard 1984), while presently in the Southern Ocean, killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) damage or remove an estimated $15 million USD worth of Patagonian toothfish (*Dissostichus eleginoides*) from commercial longline fisheries each year (Tixier et al. 2020a). Depredation incurs further costs when fishers must deploy additional gear to compensate for losses or move fishing operations to avoid depredating predators. Peterson et al. (2014) estimated that depredation by killer whales cost demersal longline fishing vessels an average of $433 USD per depredated set in fuel spent deploying additional gear, and roughly $1000 USD per depredated day in additional fuel, food, and opportunity loss. The undocumented loss of fish through depredation can adversely affect stock assessment and setting of appropriate quotas, as accounting for depredation of sablefish (*Anoplopoma fimbria*) in Alaskan fisheries resulted in a 1% reduction in the recommended quota for the fishery (Peterson & Hanselman 2017).

Depredation can provide predators with a source of easily accessed food at a reduced energetic cost. However, removing fish from lines or nets may increase the likelihood of predators becoming entangled (Read 2008; Hamer et al. 2012; Tixier et al. 2020b). This risk is highlighted by observations of some species purposely entering nets and foraging during fishing operations, such as the case of bottlenose dolphins (*Tursiops truncatus*) and fur seals (*Arctocephalus* sp.) foraging within demersal and midwater trawls in Australian fisheries (Jaiteh et al. 2013; Lyle et al. 2016). Retaliatory killing is another negative consequence of depredation for marine predators, which might involve the deliberate killing of predators by fishers during depredation events or random encounters with predator species known or perceived to depredate their catch (Tixier et al. 2020b). In the Mediterranean Sea, bottlenose dolphins were seen as pests by fishers, and as recently as the 1950s bounties were paid for the deliberate killing of dolphins (Bearzi et al. 2008).

Bycatch represents the dominant anthropogenic threat to the conservation of many marine predator populations (Wallace et al. 2010; Avila et al. 2018; Gray & Kennelly 2018; Dias et al. 2019). Air-breathing taxa such as marine mammals, turtles, and seabirds are particularly vulnerable to bycatch and, as many species are long-lived and slow to reproduce, populations can be extremely sensitive to additive mortality (e.g. Wallace et al. 2010; Anderson et al. 2011; Reeves et al. 2013; Lewison et al. 2014). Bycatch, particularly in longline fisheries, is recognised as one of the three most important threats to seabirds, affecting 28% of seabird species (Dias et al. 2019), and killing an estimated 160,000 (minimum) seabirds annually (Anderson et al. 2011). Six of the seven species of marine turtle are listed as Vulnerable, Endangered, or Critically Endangered according to the IUCN Red List (www.iucnredlist.org) and bycatch mortality is recognised as a major conservation threat (Wallace et al. 2011). Between 1990 and 2008, Wallace et al. (2011) estimated that approximately 85,000 turtles were caught in gillnets, longlines, and trawl fisheries, but the authors suggest that total bycatch was likely one to two orders of magnitude higher than the reported total. Global bycatch of marine mammals is likely in the hundreds of thousands, with the majority occurring in static net fisheries (Read et al. 2006; Lewison et al. 2014). Bycatch in static nets is known to affect 75%

of odontocete species, 64% of mysticetes, and 66% of pinnipeds (Reeves et al. 2013), and some species have been pushed close to extinction as a result. The Yangtze River dolphin or baiji (*Lipotes vexillifer*) was the first species of cetacean driven to extinction by bycatch (Turvey et al. 2007), and the vaquita (*Phocoena sinus*), Mexico's endemic porpoise, is likely to follow (Taylor et al. 2017). In 1997 the total number of vaquita was estimated at about 567 individuals, but due to unsustainable levels of bycatch in static net fisheries, fewer than 19 remain (Jaramillo-Legorreta et al. 2019).

1.3 Interactions between seals and static net fisheries

Seal-fishery interactions are a particularly contentious issue in global fisheries as growing seal populations, decreasing catch, and perceived high levels of interaction have led to frequent calls from the fishing industry for seal culls (Lavigne 2003; Bowen & Lidgard 2013; Cronin et al. 2014). Depredation by seals has been reported for 21 species (63% of all pinniped species) across 112 fisheries, and was most prevalent in the north Atlantic and eastern Pacific (Tixier et al. 2020b). Seals mostly target static nets and trap fisheries, partially or fully removing fish from nets (Wickens 1995; Cosgrove et al. 2015), and damaging or entering traps to access fish inside (Campbell et al. 2008; Königson et al. 2013). Grey seals and harbour seals are the two species most widely reported in depredation events (Tixier et al. 2020b).

Bycatch is recognised as the dominant anthropogenic threat to pinnipeds, with 66% of seal species recorded as bycatch in at least 25 countries, the majority of which occurred in static net fisheries (Woodley & Lavigne 1991; Reeves et al. 2013). Bycatch has contributed to the declines of northern fur seals (*Callorhinus ursinus*) and harbour seals in the northern Pacific, and harp seals in the Barents Sea, while having had detrimental impacts on other species including harbour seals in Alaska and Newfoundland, grey seals in the Baltic Sea, and the endangered Mediterranean (*Monachus schauinslandi*) and Hawaiian monk seals (*Monachus monachus*; Woodley & Lavigne 1991; Kovacs et al. 2012). Hundreds and possibly thousands of grey seals and harbour seals are bycaught in the north Atlantic each year (Reeves et al. 2013).

1.3.1 Grey seals and static net fisheries in the Northeast Atlantic

Direct interactions between grey seals and fisheries in the northeast Atlantic have led to widespread seal-fishery conflicts (Cronin et al. 2014; Vincent et al. 2016; Cox et al. 2020). In Ireland, grey seals have been known to depredate fish, particularly in static net fisheries (Cronin et al. 2014). Fishers have expressed concern that growing numbers of seals have led to smaller catches and increased levels of depredation, making static net fishing financially non-viable (Cronin et al. 2014). This has led to frequent calls for seal culls, and in 2004 an illegal cull of pups occurred at the Blasket Islands colony, Co Kerry. However, our understanding of the extent to which seals and fisheries interact in Irish waters, directly or indirectly, remains limited (Cronin et al. 2014).

Diet studies have indicated that some predation by grey seals of commercially important species, such as blue whiting (*Micromesistius poutassou*) and horse mackerel (*Trachurus trachurus*), may occur to the southwest and southeast of Ireland (Gosch et al. 2019). However a size and trait-based dynamic community model of the Celtic Sea, constructed by Houle et al. (2016), suggested that total annual consumption of fish by both grey seals and harbour seals was an order of magnitude less than what was removed through fishing. Based on this model, seal predation did not significantly affect the spawning stock biomass of 90% of the fish species landed by commercial fisheries, and quadrupling seal predation had little effect on landings.

Preliminary reports suggested that grey seals had the most direct interactions with static-net fisheries operating within 12 nautical miles of the coast (Cronin et al. 2014). A pilot study identified high levels of depredation and bycatch in static net fisheries operating off the west and southwest of Ireland (Cosgrove et al. 2015, 2016). These studies showed that the rate of depredation was affected by the depth at which nets were set, the timing of hauling, and in some fisheries, the duration of the soak period (Cosgrove et al. 2015), while bycatch was influenced by mesh size, depth, and target species (Cosgrove et al. 2016). This study, using dedicated observers, provided the most comprehensive dataset available on direct seal-fishery interactions in static net fisheries operating in Irish waters, but was nonetheless limited to three vessels over a 12 month period.

Vessel Monitoring System (VMS) technology transmits the location of fishing vessels at regular intervals. Since 2005, VMS has been mandatory on-board all fishing vessels operating in European waters, greater than 15m in length, and in 2012 this was expanded to include all vessels larger than 12m. By comparing the distribution of fishing effort and movement of grey seals fitted with GPS tags, studies have shown varying levels of spatial and temporal overlap between seals and fisheries in Irish waters. Cronin et al. (2012) found evidence of low spatial overlap between eight female grey seals tagged on the Blasket Islands and the offshore whitefish fleet operating to the west of Ireland, suggesting that the potential for interaction in this fishery was low. In the Celtic and Irish Seas, grey seals tagged at Raven Point, Co Wexford, similarly did not overlap with fishing vessels using active gears, but did show significant overlap with vessels using passive gears, again indicating potentially high levels of interaction between seals and static nets (Cronin et al. 2016).

1.3.2 Study species: Grey seals (*Halichoerus grypus*)

Grey seals are distributed across the north Atlantic with three recognised population centres in the Northwest and Northeast Atlantic, and the Baltic Sea (figure 1). Differences in mitochondrial DNA exist between the three population centres, but the difference between the Northeast Atlantic and Baltic populations is less than between the Northwest Atlantic population and the others (Klimova et al. 2014). Throughout their range, grey seal numbers have increased in recent decades, although the Baltic Sea population has yet to recover from hunting in the early 20th century (Harding et al. 2007; NOAA 2019; Russell et al. 2019). Grey seals are sexually dimorphic, with adult males being substantially larger than females, and grey seals in the Northwest Atlantic being slightly larger than those in Europe (Jefferson et al. 2015).

Grey seals come ashore each year to breed. In the Northwest Atlantic and Baltic Sea populations, this occurs in late winter to early spring, while in the Northeast Atlantic breeding primarily occurs in autumn (Davies 1957). Grey seals are polygynous and display a large degree of philopatry and breeding site fidelity, in some cases returning to within metres of where they were born to breed (Pomeroy et al. 2000). Mothers give birth to a dependent white-coated pup which is suckled for 15-21 days before undergoing a post-weaning fast lasting between 9 and 40 days (Bennett et al. 2007). Recruitment into the breeding population occurs at about 5 years for females and 10 years for males (Harwood & Prime 1978).

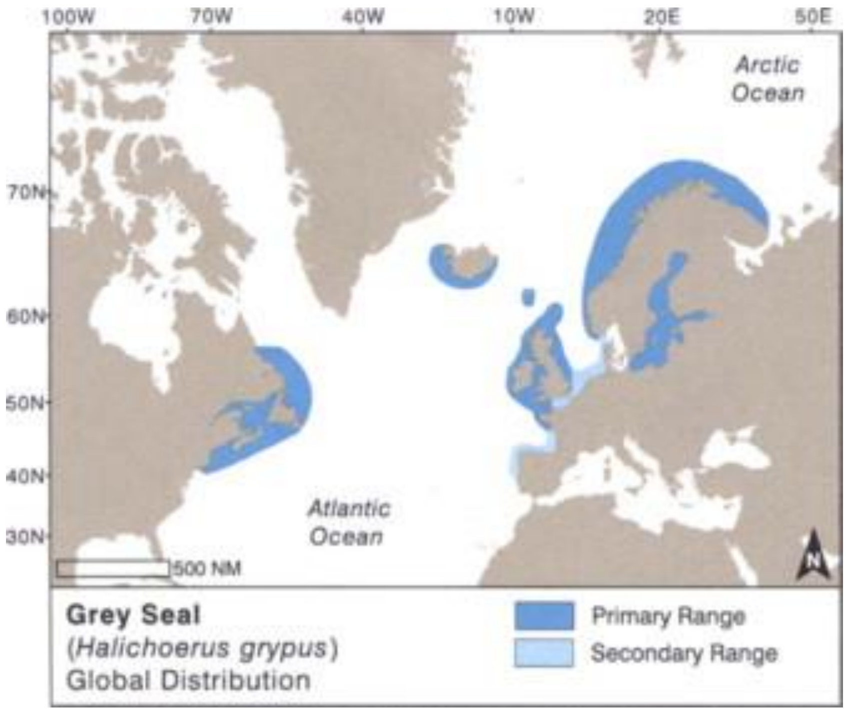

Figure 1: Global distribution of grey seals (from Jefferson et al. 2015).

As generalist predators, grey seals consume a wide variety of prey species, their diets largely influenced by the local and seasonal abundance of prey (Benoit & Bowen 1990; Hammond et al. 1994; Bowen et al. 2006; Gosch et al. 2019). Grey seals feed on both pelagic and demersal prey, regularly diving to the benthos to forage (McConnell et al. 1999; Jessopp et al. 2013; Vincent et al. 2016). Grey seals can dive to 450m but the majority of dives are much shallower, with average dive depths of 57m in males and 49m in females (Beck et al. 2003; Jessopp et al. 2013). Outside of the breeding season, adults regularly make discrete foraging trips, mostly within the continental shelf, commuting between preferred foraging grounds and haulout locations (Russell et al. 2015). Foraging trips can cover hundreds of kilometres, but grey seals are typically coastal foragers, with a mean foraging distance of 50km from shore (Mcconnell et al. 1999; Cronin et al. 2013).

In Europe, grey seals are listed as Annex II species under the EU Habitats Directive (92/43/EEC), which obliges Ireland to ensure that populations are maintained at "favourable conservation status". The UK is home to approximately 38% of the global grey seal population, with most of these concentrated in colonies around Scotland (Russell et al. 2019). Ireland is home to a smaller population representing around 6% of grey seals in western Europe (Ó Cadhla et al. 2013). In the UK, the grey seal population grew rapidly between the mid-1980s when surveys began and the mid-1990s, when pup production and population growth began to slow (Russell et al. 2019; Thomas et al. 2019). Now, colonies in the North Sea region continue to grow, while those in the Inner Hebrides, Outer Hebrides, and Orkneys appear to have reached carrying capacity (Thomas et al. 2019). In Ireland, population surveys have been carried out less frequently, but aerial surveys of the breeding population showed that the all-age population in the Republic of Ireland increased from between 5,509 and 7,083 grey seals in 2005 to between 7,284 and 9,365 seals in the 2009-2012 survey (Ó Cadhla et al. 2007, 2013). Similarly, based on thermal-imaging surveys carried out in August, summer counts of grey seals hauled out at major haulout sites steadily increased from 1,309 in 2003, to 2,964 in 2011/2012, to 3,698 in 2017/2018 (Morris & Duck 2019). Approximately 84% of pups are born at seven major breeding colonies around Ireland, with the largest of these along the west coast, including colonies at the Inishkea Island Group, Northwest Galway, and Blasket Islands (figure 2). Tracking studies have shown that grey seals, fitted with GPS tags, regularly moved between haulouts in Ireland and the UK (figure 2).

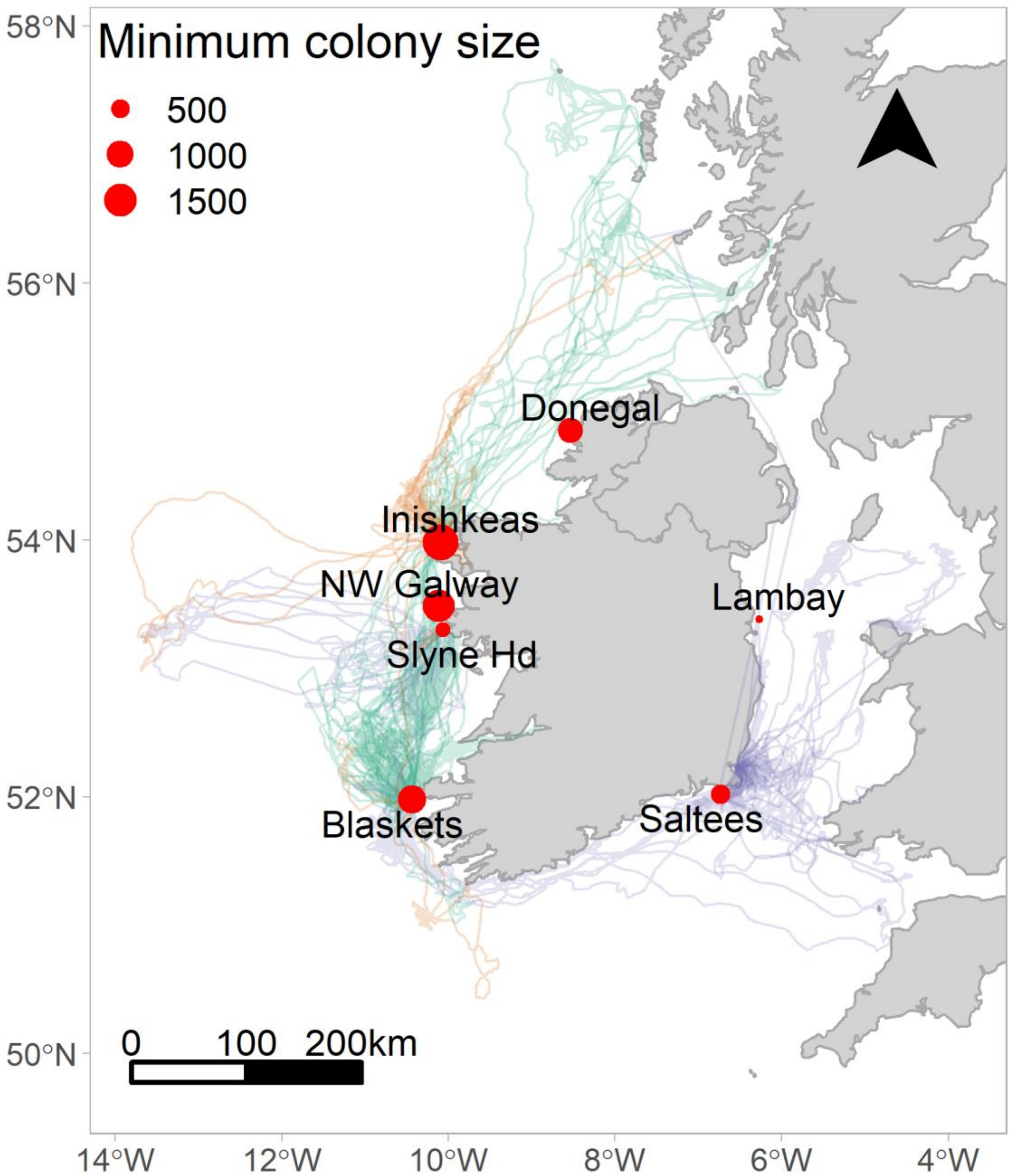

Figure 2: Map of major breeding colonies of grey seals in the Republic of Ireland. Coloured lines indicate movements of grey seals fitted with GPS tags at the Inishkeas (orange), Blasket Islands (green), and Wexford Harbour (purple).

1.3.3 Study area: Ireland and Western Europe

The bathymetry to the west of Ireland includes a large area of continental shelf, which slopes gently to about 200m before dropping to much deeper depths of the abyssal plain, while the Celtic and Irish Sea are shallow (< 200m) throughout (figure 3). These waters include numerous productive fishing grounds and on an average day more than 1000 fishing vessels are active in the waters around Ireland (Gerritsen & Lordan 2014). The Irish fishing industry directly employs approximately 3000 people, generating nearly €600 million in 2018, approximately 0.2% GDP (BIM 2020). The national fishing fleet consists of roughly 2000 registered vessels, the majority of which belong to the "polyvalent general" and "polyvalent potting" fleet segments. These multi-purpose vessels include small-scale inshore vessels using mostly static gear, and larger offshore vessels using a mixture of gear types. Non-Irish European fishing vessels also fish in Irish waters as under the EU Common Fisheries Policy (EU1380/2013) all EU fishing vessels are granted equal access to EU waters. The most profitable species landed in Ireland include mackerel (*Scomber scombrus*), monkfish (*Lophius* sp.), and Dublin Bay Prawn (*Nephrops norvegicus*; BIM 2020).

All fishing vessels larger than 10m in length must submit logbooks detailing the type of gear used, where and when fishing took place, and total catch composition. Since 2005, vessels greater than 15m in length operating in European waters must carry Vessel Monitoring System technology, providing spatial and temporal data on fishing activity. In 2012, this regulation was expanded to include all vessels over 12m in length. Smaller vessels, however, which make up the vast majority of vessels registered in Ireland and fish primarily in inshore waters, are subject to less stringent regulation than larger vessels. Vessels less than 12m in length (86% of registered vessels in 2021) are not required to carry VMS or any tracking technology, and vessels smaller than 10m (74% of registered vessels in 2021) are not required to submit logbooks.

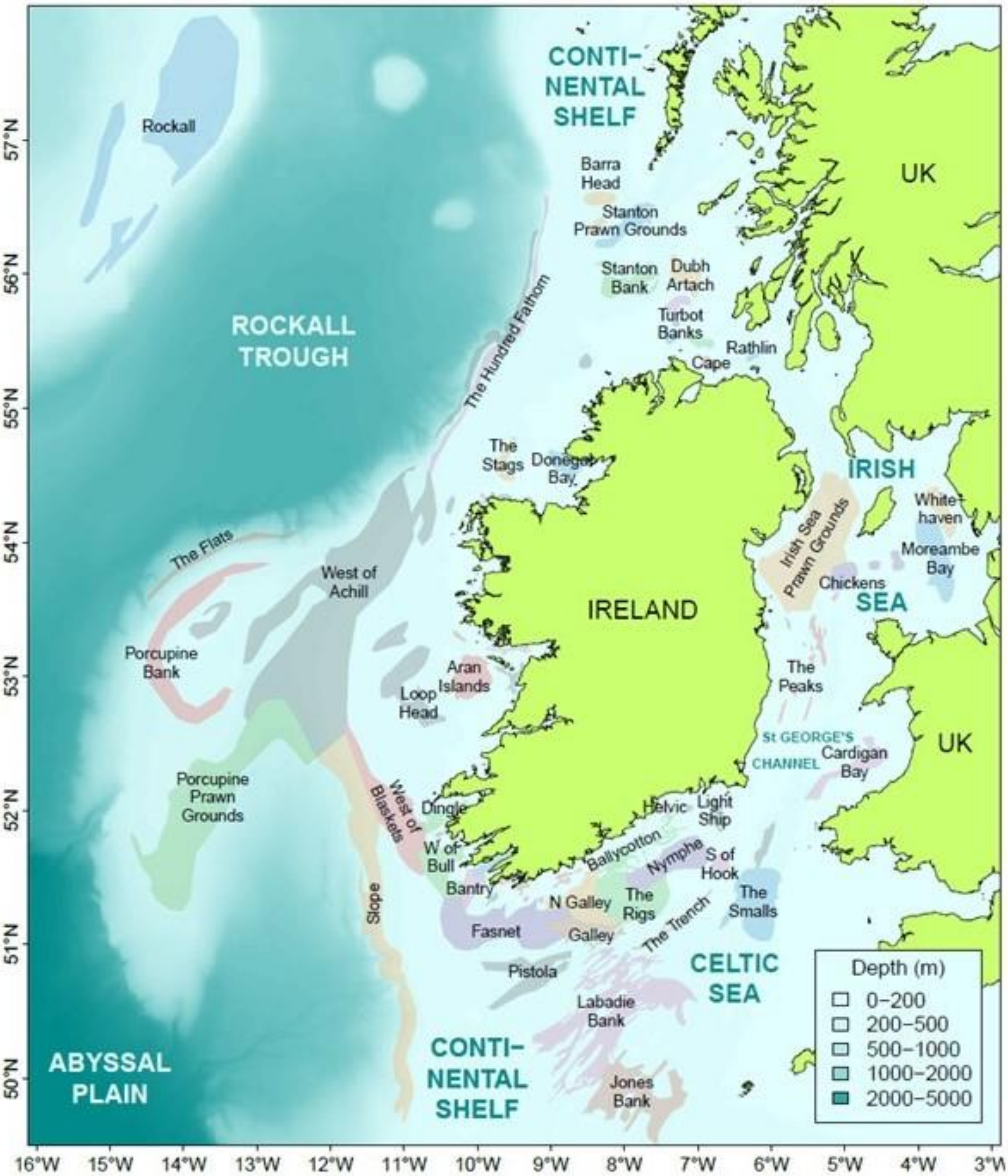

Figure 3: Major fishing grounds surrounding Ireland. Shaded fishing areas are delineated based on analysis of Vessel Monitoring System (VMS) data (Gerritsen & Lordan 2014).

1.4 Information gaps in seal-fishery interactions

As outlined by Northridge et al. (2017a), the development of novel mitigation strategies for reducing bycatch is dependent on identifying new environmental or gear-related factors causing animals to become entangled. Cosgrove et al. (2016) identified potential drivers of seal bycatch based on an analysis of observer data collected from three static net fishing vessels. There is a clear need to gather more data covering a greater number of vessels, over a broader geographic range and a longer time period to identify novel drivers of seal bycatch which may allow for development of effective mitigation strategies in the future.

An important question in seal-fishery interactions is how seals might interact with nets when they are left to soak unattended. With the application of state-space modelling to biotelemetry data, it is possible to infer the behavioural states of seals based on their movements at sea (Carter et al. 2016; Bennison et al. 2017; Patterson et al. 2017). Coupled with the increased availability of vessel tracking data from sources such as Global Fishing Watch, allowing us to estimate where static nets have likely been deployed, there is now an opportunity to identify overlap between seals and static nets in near real-time and explore potential anthropogenic influences on seal behaviour.

Furthermore, the potential pressure placed on the population by bycatch mortality remains unquantified. Without estimating the total number of seals annually removed as bycatch, we cannot exclude the possibility that bycatch may be placing an unsustainable pressure on population viability. Addressing this data gap is essential to Ireland meeting its obligations under EU policy.

1.5 Aims and thesis outline

Given significant knowledge gaps regarding seal-fisheries interactions, particularly around quantifying bycatch rates and effects on populations, I aimed to address key gaps in our understanding of the cause and effect of grey seal bycatch in static net fisheries.

In chapter 2, I aimed to identify the drivers of observed spatial and temporal trends in the rate of seal bycatch in static net fisheries.

In chapter 3, I produced the first estimates of seal bycatch across all static net fisheries operating in Irish waters by applying the results of chapter 2 to fishing effort data based on logbooks, and using expert knowledge to address information gaps in the logbook data.

In chapter 4, I examined the spatial overlap between grey seals and static net fisheries in near real-time, and the potential effect of proximity to nets on seal behaviour. This analysis applied Hidden Markov Models (HMMs) to tracking data from over 160 grey seals tagged in Ireland, the UK, and northern France to identify the locations of foraging behaviour at sea, and used Automatic Identification System (AIS) data to identify the likely locations of static nets.

In chapter 5, I explored the potential effect of bycatch on the population of grey seals breeding in the Republic of Ireland through Population Viability Analysis (PVA). Multiple scenarios were constructed to explore the full range of plausible bycatch levels identified in chapter 3 on the national population, before creating additional scenarios to test how immigration of seals from outside of Ireland, biases in bycatch mortality, and colony-specific mortality levels might alter the impact of bycatch on the population.

Finally, chapter 6 provided a synthesis of the results from each preceding chapter, discussing the key findings and limitations of the study, and outlining how best to build on this thesis in future research.

Chapter 2: Drivers of spatiotemporal variability in bycatch of a top marine predator: first evidence for the role of water turbidity in protected species bycatch

This chapter was published in the Journal of Applied Ecology. The text has been modified slightly to improve continuity in the thesis.

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Author contributions: **C.L.** and M.C. conceived the project outline and designed the methodology; **C.L.**, M.G., K.H., O.T. and R.C. collected and sourced the data; **C.L.** led the data analysis and writing of the manuscript with much input from M.J., E.R. and M.C. All authors contributed critically to the drafts and gave final approval for publication.

Image: Grey seals and one harbour seal bycaught in a static net off Co. Mayo, 2011. Photo by Martha Gosch.

2.1 Abstract

Bycatch of protected species in static net fisheries is a global conservation concern and is currently considered the dominant anthropogenic threat facing many marine mammal species. Effective bycatch mitigation remains challenging, contingent on an understanding of the underlying mechanisms that cause individuals to become entangled. I combined data collected by scientific observers and fishers to identify predictors of seal bycatch in static net fisheries along the west, southwest, and south coasts of Ireland. First, I analysed the broad regional and seasonal trends in seal bycatch before identifying environmental variables that could explain these patterns. Based on negative binomial generalised linear mixed effects models, seal bycatch significantly varied with season, and decreased with greater distance to major seal colonies and in clearer, less turbid water. Our results suggest that distance to major seal colonies was a significant driver of spatial variation in seal bycatch, and water turbidity a major driver of seasonal trends. These findings will enable us to identify future bycatch risk and target mitigation measures effectively. This is the first study to identify the effect of water turbidity on bycatch of a protected marine species. Increasing net visibility in turbid waters may provide a novel approach to mitigating against protected species bycatch in static net fisheries.

2.2 Introduction

As fisheries management moves towards a more ecosystem-based approach, bycatch of non-targeted species has become a significant issue (Lewison et al. 2004a; Moore et al. 2008; Cronin et al. 2014). Air-breathing animals are particularly vulnerable, and bycatch of protected species of marine mammals (Reeves et al. 2013), seabirds (Žydelis et al. 2013), and marine turtles (Wallace et al. 2010) is now a major conservation concern. Previous studies of protected species bycatch have focused on quantifying and assessing the population effects of bycatch (e.g. Lewison & Crowder 2003; Orphanides 2010; Brown et al. 2014), highlighting the need for management. More recent focus has been placed on testing the efficacy of bycatch mitigation measures (Melvin et al. 1999; Wang et al. 2010; Orphanides & Palka 2013), although Northridge et al. (2017a) suggest that many of these have now been exhausted. The development of new mitigation measures is likely dependent on an improved understanding of the underlying causes and mechanisms of bycatch, however, relatively few studies have examined these to date.

Among pinnipeds, bycatch in static net fisheries is widespread on a global scale and is the dominant anthropogenic threat to seals worldwide (Woodley & Lavigne 1991; Read 2008; Kovacs et al. 2012; Reeves et al. 2013). Globally, 66% of seal species have been recorded as bycatch in 25 countries, and in the North Atlantic alone, thousands are caught in static nets each year (Reeves et al. 2013). While previous studies have reduced seal bycatch in static salmon traps (Westerberg et al. 2007) and cod pots (Königson et al. 2015) by modifying the gear to exclude seals, no effective mitigation exists for reducing seal bycatch in static net fisheries. Understanding the underlying causes of seal entanglement is essential for effective mitigation measures to be designed and implemented.

Ireland is home to populations of grey seals (*Halichoerus grypus*) and harbour (*Phoca vitulina*) seals at the edge of both species' range in Northwest Europe. Both species are protected under National and European legislation and both have been recorded as bycatch in Irish fisheries, although grey seals have reportedly been caught more frequently (Berrow et al. 1998; Cosgrove et al. 2016).

This study aims to identify reliable and informative predictors of seal bycatch; enabling us to predict future bycatch risk and develop improved and novel mitigation strategies. I aim to do this by analysing a large dataset of fishing effort and seal bycatch observations recorded by fishers and scientific observers. Firstly, I aim to explore the broad spatial and temporal trends in seal bycatch before identifying the environmental variables that may be causing these trends. This will allow more refined, targeted, and effective mitigation to be developed in the future.

2.3 Materials and Methods

Dedicated observer programmes, examining interactions between seals and static net fisheries, were carried out on inshore fishing vessels off the west (county Mayo) and southwest coasts (county Kerry) of Ireland. Additional data were collected by fishers operating in the southwest (county Kerry) and south (county Cork) of the country. Data from the west coast were previously published by Cosgrove et al. (2016). Thirteen fishing vessels were included in the study; three based in the west, nine in the southwest, and one in the south. Each recorded haul was assigned to a study region based on the location of the net, independent of the home-port of the vessel (Figure 1).

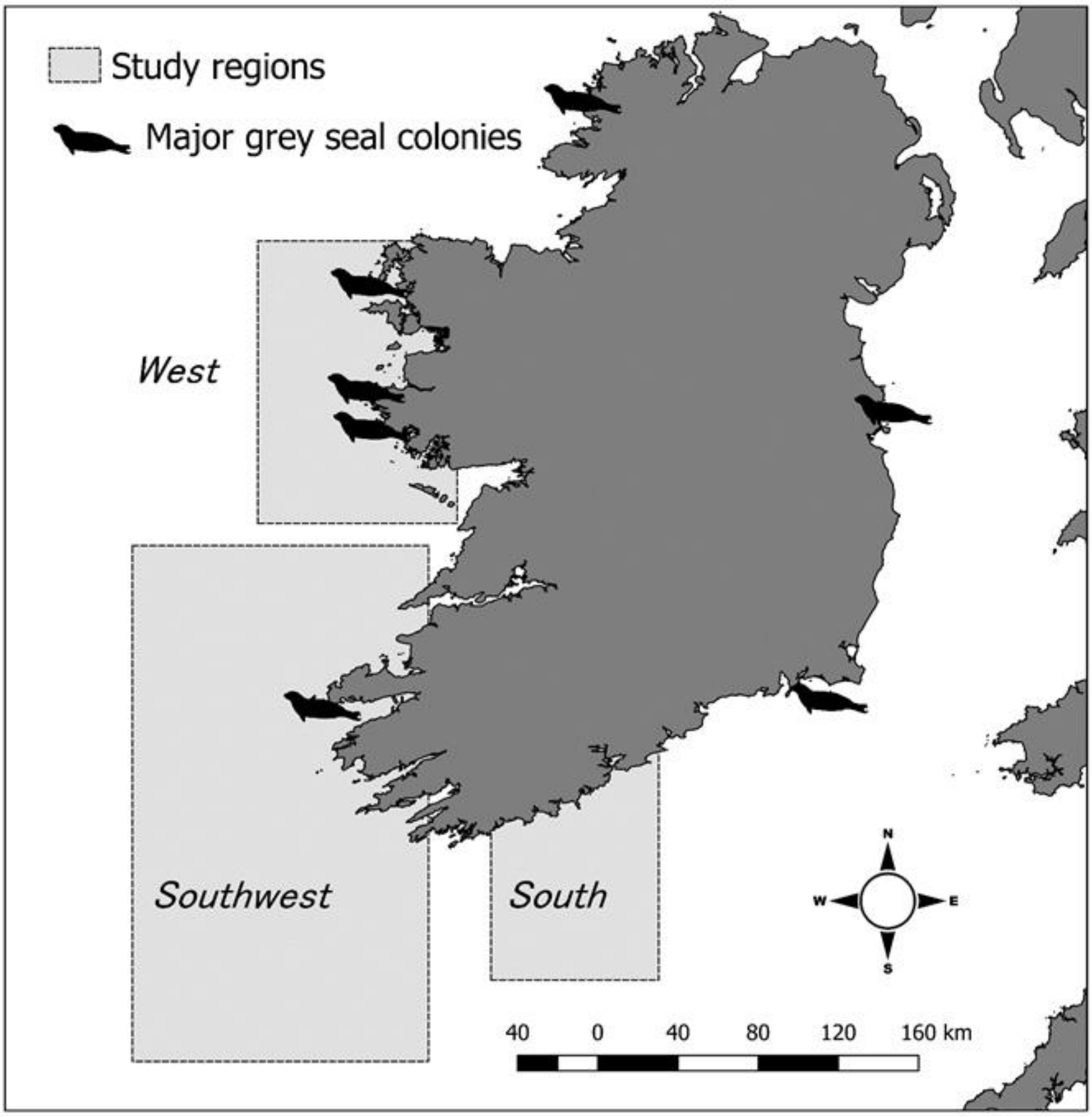

Figure 1: Location and extent of fishing areas within the designated regions of this study, and locations of the seven largest breeding populations of grey seals around the coast of Ireland.

Vessels used a combination of entangling nets, which were deployed for several days, and targeted similar commercial species (Table 1). Illustrations of the types of gillnet and entangling nets observed in this study can be found in Gabriel et al. (2008). The nets in this study, hereafter referred to as "gillnets", "tangle", "trammel", and "spider" nets, are all forms of gillnet/entangling net as described by the Food and Agricultural Organisation of the United Nations (FAO), and differed primarily in mesh size (Table 2). All nets were bottom-set with lead bottom lines and polypropylene headropes to keep the nets vertical in the water. Some gillnets were fitted with plastic floats on the headropes for extra buoyancy. All nets were single walled with the exception of trammel nets which were three-walled (the outer walls having a larger mesh size). Spider nets were similar to tangle nets but with a larger mesh size, and were used primarily to target spider crabs (*Maja squinado*). The data recorded by both observers and fishers included the date the nets were shot and hauled, GPS location, net type, mesh size, catch, and bycatch. Observers collected additional data on the species, sex, and size of bycaught seals when possible.

Table 1: Fishing effort recorded in each study region

Region	**Data collected by**		**Number of vessels**	**Number of hauls**	**Timeline recorded**	**Primary target species**
	Observers	Fishers				
West	X		3	185	Jun 2011 – Jul 2012	Monkfish (*Lophius piscatorius*), Crawfish (*Palinurus elephas*)
Southwest	X	X	10	740	Aug 2017 – Dec 2018	Crawfish (*Palinurus elephas*)
South	X	X	2	2318	Jan 2010 – Oct 2016	Monkfish (*Lophius piscatorius*), Spider crab (*Maja squinado*)

Table 2: Gillnets and entangling nets used.

Net type	Mesh size (cm)	Outer mesh size (cm)	Mean set length (km (SE))	Mean soak time (days (SE))	Used by fishing vessels in:		
					West	Southwest	South
Gill	14	NA	0.872 (0.072)	0.943 (0.036)	X		X
Tangle	27	NA	0.835 (0.050)	3.979 (0.113)	X	X	X
Trammel	27	81	0.671 (0.059)	2.810 (0.042)	X		X
Spider	35.5	NA	0.684 (0.040)	3.250 (0.148)			X

Bathymetry data, extracted from a harmonised digital terrain model produced by the European Marine Observation and Data Network (EMODnet), available at: http://portal.emodnet-bathymetry.eu/, was used to estimate the depth at which nets were set. As all of the nets used in this study were bottom-set nets, the depth of the sea floor was used as the depth at which the nets were set. The depth in metres was then averaged along the length of each net.

Data on water turbidity were sourced from the European Space Agency GlobColour project (http://www.globcolour.info/), which provides a continuous set of merged level three (L3) Ocean Colour products. Turbidity was represented as Secchi Disc Depth (SDD) in metres (the depth at which a calibrated black and white disc is still visible from the surface), calculated using the Morel algorithm (Morel et al. 2007). Low values of SDD indicate high turbidity and high SDD values indicate low turbidity. These data were downloaded as 8-day composites at 4km^2 spatial resolution. Similar to depth, values of water turbidity were averaged along the length of each net, and averaged between shoot and haul dates.

The distance from each fishing net to each of the seven major grey seal breeding colonies in Ireland was calculated as a proxy for seal density in the area. To account for colony size, distance was inversely weighted by dividing each distance by the estimated proportion of the national breeding population of grey seals in the colony, according to Ó Cadhla et al. (2013). Thus, proximity to a large colony was weighted more heavily than the same distance to a smaller colony. The lowest scaled distance was then selected for each haul as the distance to nearest colony. I focused on these colonies, which represent 84% of the national breeding population of grey seals (Ó Cadhla et al. 2013; Figure 1), because of their greater size relative to other colonies, the larger foraging range of grey seals relative to harbour seals (Cronin et al. 2014; Jones et al. 2015), and the reported higher incidences of grey seal rather than harbour seal bycatch (Cosgrove et al. 2016; Northridge et al. 2017b). This approach assumes that seal density declines linearly with distance to colony. While this is a valid assumption for the purposes of this analysis (e.g. Jones et al. 2015), in reality, the distribution of seals is more likely to be habitat-mediated, or follow consistent corridors between foraging grounds or distant colonies (Cronin et al. 2012, 2016; Jessopp et al. 2013; Jones et al. 2015).

Two negative binomial generalised linear mixed effect models were developed to identify predictors of seal bycatch. The first included region and season as predictor variables, to test for broad spatial and temporal trends in bycatch. In the second model, distance to major seal colony and water turbidity were substituted for region and season respectively. The non-independence of these variables (Figure 2) precluded them from being included in the same model, but it was considered that these variables may have accounted for a large proportion of spatial and temporal variation in seal bycatch, and that continuous variables such as these would allow for more refined bycatch prediction and mitigation.

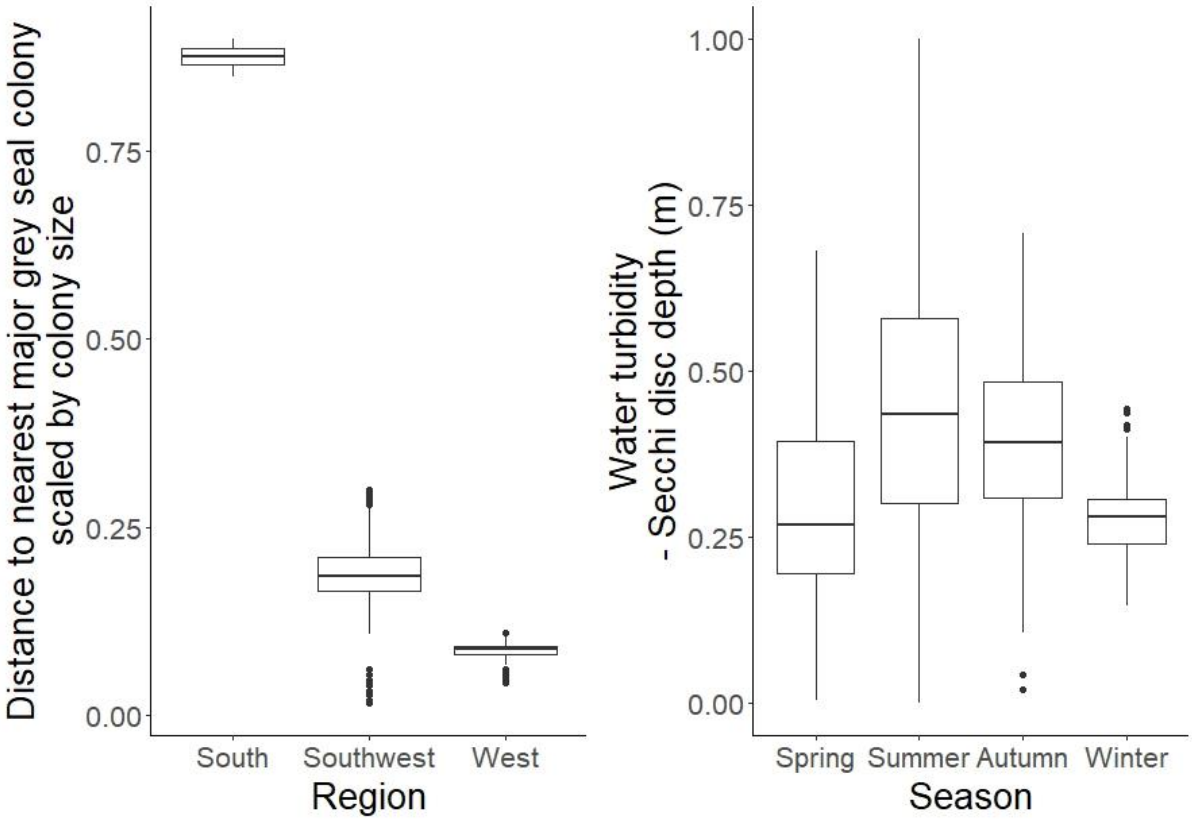

Figure 2: Distance to nearest major grey seal colony across each study region, and water turbidity across seasons. Distance to colony has been rescaled by dividing distance by the proportion of the national estimated grey seal population present at the colony according to O'Cadhla et al. (2013). Distance and water turbidity values were then rescaled once more to between zero and one.

The number of seals caught per haul was included in each model as the response variable. A standard unit of effort was calculated by multiplying the length of each net in km by the number of days which the net was left to soak in the water (any nets left to soak for less than a day were assigned a soak time of 0.5). This effort term was included as an offset in each model. The rate of seal bycatch, or seals per unit effort (SPUE), could then be calculated as the number of seals caught divided by the effort term. Because some predictor variables included in the models were not recorded or available for each observation in the dataset, including different variables resulted in a different subset of the data being used to build the model. To compare model outputs, both models were built on the same subset of the data. Continuous predictors were rescaled to between zero and one, to improve model convergence and compare predictor effect sizes.

Table 3: Predictor variables included in negative binomial generalised linear mixed effect models of seals bycaught per haul as a function of regional and seasonal predictors and continuous predictors.

Predictor variables	**Effect**	**Rationale**
Regional/Seasonal model only		
Region	Fixed	To account for regional variability
Season	Fixed	To account for seasonal variability
Continuous model only		
Distance to major seal colony – scaled by colony size	Fixed	Seals may be more likely to encounter nets that are set close to major haulouts
Turbidity – Secchi disc depth (m)	Fixed	May affect the ability of seals to detect a net underwater
All models		
Mesh size (cm)	Fixed	Different mesh sizes may affect the likelihood of a seal becoming entangled
Depth	Fixed	Seals may be more likely to encounter nets at certain depths and/or nets may be less visible at depth
Vessel ID	Random	To account for unexplained inter-vessel variability
Year	Random	To account for inter-annual variability
Effort – net length (km) * soak time (days)	Offset	To account for variation in fishing effort between observations (hauls)

All environmental data were processed using a combination of Quantum GIS (QGIS) and the *raster* package in R (R Core Team 2018), and all statistical analysis was carried out in R. The variables included in each model are summarised in Table 3. For categorical predictors the south was specified as the reference region and spring as the reference season. The seasons were defined as spring (Mar – May), summer (Jun – Aug), autumn (Sep – Nov), and winter (Dec – Feb). For model selection, the *'dredge'* function from the *MuMIn* package was used to explore all possible permutations of each model. A confidence set of models was then defined, including all those within six second-order Akaike Information Criterion (AICc) of the most optimal models, excluding any models with better-fitting (lower AICc), nested equivalents within the confidence set (Richards 2008; Arnold 2010; Grueber et al. 2011). Pseudo-R^2 values were calculated to provide an estimate of model fit and the model's ability to predict the occurrence of bycatch was assessed by calculating the Area Under the receiver operating Curve (AUC).

2.4 Results

2.4.1 Fishing effort

Between 2010 and 2017, 3308 hauls of static nets were recorded by observers and fishers on board 13 vessels along the west, southwest, and southern coasts of Ireland (Table 1). Of the total hauls, 14.7% involved gill nets, 76.7% involved tangle or trammel nets, and 8.6% involved spider nets. In the south region, which included a complete time-series of data, tangle, trammel, and spider nets were used primarily in summer, whereas gill nets were used mostly in winter. Soak time was, on average, three days, with the exception of gill nets, which were usually left in the water for less than a day.

2.4.2 Bycatch

In total, 257 seals were caught in 197 hauls, providing a mean rate of seal bycatch (SPUE ± SE) of 0.038 ± 0.006. Of these 197 hauls, 81% involved a single seal becoming caught and the most seals caught in a single net was seven. Regionally, SPUE was highest in the west, lowest in the south and seasonally highest in winter and spring (Figure S1). Observers measured 122 bycaught seals, all from the west and southwest fisheries, although the sex and species were not positively identified for all. Of the bycaught seals, length (measured from nose to end of tail), ranged from 96 - 185cm, (mean length 142cm SE 18cm), and where sex and species were identified, included 23 males and 15 females, and 63 grey seals versus 10 harbour seals.

2.4.3 Earth observation data

Due to the patchiness of satellite coverage, particularly in winter when increased cloud cover blocks satellite observations, turbidity values were extracted for 1585 (48%) of the hauls. This subset of the original data included 73 hauls in which 103 seals were bycaught. Turbidity varied seasonally, with the lowest mean SDD occurring in winter and spring (Figure 2).

2.4.4 Model outputs: Predictors of seal bycatch

2.4.4.1 Regional/Seasonal model

Model selection resulted in four models within six AICc of the lowest score. The model with the lowest AICc was nested within the three next best models. Therefore these more complex models were considered less informative and were excluded from further analysis. The remaining model included mesh size and season as predictor variables. Region and depth were both retained in two of the initial four models, however, each of these were excluded as a consequence of a better-fitting, nested model existing within the confidence set (Appendix S2). With only one model remaining, no model averaging was carried out. The number of seals caught per haul increased significantly with increasing mesh size ($P < 0.001$) and was significantly lower in summer ($P < 0.001$) and autumn ($P < 0.01$, table 4), relative to spring. The lognormal conditional R^2 value of the model was 0.58 and when used to predict the occurrence of seal bycatch on the study data, the model provided an AUC score of 0.60.

2.4.4.2 Continuous model

Model selection resulted in six models within six AICc of the lowest score, four of which were included in model averaging (Appendix S2). Mesh size was retained in all four models with a relative importance of 1.00. Turbidity (relative importance: 0.90) and distance to colony (relative importance: 0.62) were retained in two models each. Depth was retained in two of the initial six models, however, each of these were excluded as a consequence of better-fitting, nested models existing within the confidence set. As such, depth was not included in the averaged model. Based on conditional model averaged parameter estimates, the number of seals caught per haul significantly increased with increasing mesh size ($P < 0.01$), decreased in less turbid waters (i.e. as SDD increased; $P < 0.05$) and at greater distances from major grey seal colonies ($P < 0.01$, Table 4). The lognormal conditional R^2 value of the model was 0.87, and when used to predict the occurrence of seal bycatch on the study data, the model provided an AUC score of 0.51.

Table 4: Model averaged estimates, with standard errors (SE), 95% confidence intervals (CI), and P values for the number of seals caught per haul, as a function of broad regional and seasonal predictors and more refined continuous predictors.

Regional/Seasonal model

Predictor variables	Estimate	SE	Lower CI	Upper CI	P
Intercept	-3.9395	1.01	-14.406	-2.662	**< 0.001**
Season: Summer	-1.8576	0.3902	-3.088	-1.442	**< 0.001**
Season: Autumn	-1.8452	0.6388	-4.840	-1.939	**< 0.01**
Season: Winter	0.5073	0.5842	-0.844	1.593	0.385
Mesh size	3.8215	1.1396	-0.311	4.717	**< 0.001**

Continuous model

Predictor variables	Estimate	SE	Lower CI	Upper CI	P
Intercept	-3.313	1.266	-5.796	-0.830	**< 0.01**
Distance to colony (scaled)	-2.618	1.011	-4.601	-0.635	**< 0.01**
Turbidity (Secchi disc depth)	-2.063	0.853	-3.735	-0.390	**< 0.05**
Mesh size	3.092	1.119	0.897	5.286	**< 0.01**

Significant P values highlighted in bold. Estimates were only calculated for variables occurring in the confidence set of models (Appendix S2). Estimate values indicate the change in seals per haul as continuous predictor variables increase by one unit, or for the specified category of a categorical predictor variable when compared to the baseline category indicated. The estimate for turbidity refers to Secchi disc depth, which is an inverse measure of water turbidity. Conditional rather than full average results of model averaging are presented here. Continuous predictor variables have been rescaled to between zero and one.

2.5 Discussion

Developing effective mitigation for the bycatch of protected species is reliant on understanding its causal factors. Including broad predictors of bycatch, such as region or season, may provide a good model fit, but though the model may account for a large amount of the variance in the data, the actual causes of bycatch remain unexplained. This may still be informative for conservation but at best enables broad-stroke mitigation measures, such as fishing restrictions over large areas or entire seasons, which are economically costly and unlikely to be adopted readily by industry. Only by identifying the underlying variables driving these trends in bycatch can we hope to develop more refined and effective mitigation. Mesh size and depth have previously been demonstrated to be important factors for bycatch across numerous taxa (Peckham et al. 2007; Žydelis et al. 2009; Orphanides 2010; Cosgrove et al. 2016), but to our knowledge this is the first study to quantify the effect of proximity of nets to major colonies, and the first to demonstrate an effect of water turbidity on the rate of bycatch of seals, or any protected species.

Regionally, seal bycatch was highest in the west and lowest in the south, though the analysis failed to identify region as an important predictor of bycatch. Scaled distance to colony was, however, retained in the model selection process and was shown to have a significant effect on seal bycatch. This, perhaps unsurprisingly, suggests that distance to colony was a stronger driver of the observed spatial variation in seal bycatch than the broadly defined regions. The western region encompassed the Inishkea Islands, Ireland’s largest grey seal breeding colony, whereas the closest major colony to the southern region was the Blasket Islands, over 120km distant (see Chapter 1, Figure 2). Nets set in the west subsequently had the lowest mean rescaled distances to colony (Figure 2) and our refined model showed that this had a significant effect on seal bycatch. This is likely a result of nets being exposed to higher numbers of seals closer to major haulouts. Indeed, seals have been shown to forage predominantly within 50km of their haulouts (Cronin et al. 2013) and Hamer and

Goldsworthy (2006) found that the number of seals observed at the surface during fishing operations, which was assumed proportional to bycatch risk, increased as distance to the nearest breeding colony decreased.

Seasonally, seal bycatch was highest in winter and spring, and lowest in summer and autumn. There are several possible reasons for this. Cronin et al. (2013) showed that seals in Ireland increased their time spent at sea post-breeding and pre-moult, which might have led to higher encounter rates between seals and any given net. Seal pups, which were born in autumn, may be more likely to become entangled due to their inexperience foraging near nets and their small body sizes relative to the size of the net mesh. The majority of seals bycaught in the west and southwest were juveniles (based on size), similar to what was observed in previous studies along the south coast of Ireland (Rogan et al. 2001). While these seals were only approximately aged by body size, few if any were small enough to be considered recently born pups, and though juvenile seals may be inexperienced foraging near nets, this would not fully explain the seasonality of bycatch as juveniles, rather than pups, are exposed to nets year round. Alternatively, water turbidity shows a similar seasonality to the rate of seal bycatch and our results show that there is a strong and significant correlation between the two. Furthermore, there is biological justification for why water turbidity may affect the likelihood of a seal becoming entangled in a net. Seals rely primarily on vision and tactile senses to locate prey underwater (Schusterman et al. 2000). While seals possess excellent vision underwater (Hanke et al. 2009), the visual acuity of seals has been shown to deteriorate rapidly with even moderate increases in water turbidity (Weiffen et al. 2006). Seals also possess vibrissae with exceptional tactile senses. Vibrissae can respond to faint movements in the water (Dehnhardt et al. 1998; Hanke et al. 2013), and can follow the hydrodynamic trails of submersibles (Dehnhardt & Hanke 2010), other seals (Schulte-Pelkum et al. 2007) and presumably fish (Wieskotten et al. 2010). However, in these cases, seals are responding to hydrodynamic stimuli generated by moving objects. Given that these stimuli are persistent but short-ranged by their physical nature (Bleckmann 1994), it is less likely that a static net would generate sufficient hydrodynamic stimuli to warn a seal of a net until it was in close proximity (Dehnhardt et al. 2003), highlighting the importance of vision in avoiding nets.

Considering that different sized mesh is used to target different species of fish, it is perhaps unsurprising that mesh size may also be selective to non-target species, including seals. Similar to Cosgrove et al. (2016) who focused on static net fisheries along the west coast, I found that seal bycatch increased with mesh size across a larger spatial scale and larger range of mesh sizes. Larger mesh sizes have been linked to increased rates of turtle (Murray 2009), seabird (Dagys & Žydelis 2002), and cetacean bycatch (Orphanides 2010). However, for some species, bycatch rates may again decline once mesh size exceeds a certain threshold (Ainley et al. 1981; Orphanides 2010). Based on our results it appears that nets with smaller mesh sizes (e.g. gillnets) may be too fine to easily entangle seals and, with mesh sizes up to 35.5cm, no upper threshold at which bycatch decreased was evident.

The analysis by Cosgrove et al. (2016), which included data from the west coast fishing area in this study, found that the rate of seal bycatch increased with increasing water depth. However, our analysis, which included data from a wider geographical area, found no significant relationship between depth and seal bycatch. The depth at which nets are set has been shown to have varying effects on protected species bycatch. Turtles are often caught primarily in deeper waters (Peckham et al. 2007), seabirds are usually caught in shallow waters (Žydelis et al. 2009; Bellebaum et al. 2013), and harbour porpoises have been caught primarily in shallow waters (Bjørge et al. 2013) but also specifically at intermediate depths (Orphanides 2010). The effect of depth on protected species bycatch may be species-specific but also influenced by the region and habitat in which the study takes place. This is likely why the effect of depth on seal bycatch, as observed by Cosgrove et al. (2016) in the west coast fishing area, was no longer significant at a larger spatial scale.

This research suggests that several opportunities exist for mitigation of seal bycatch in static fishing gear. Unlike other protected species that range widely, seals regularly haul out in large numbers at predictable locations. This is advantageous for conservation as this research shows that focusing any necessary fishing restrictions close to major colonies, particularly during moult and breeding seasons, could effectively reduce seal bycatch while being less restrictive to fishing efforts over larger spatial scales. Hazen et al. (2018) showed that targeted dynamic area closures could achieve similar conservation goals for bycaught species, while excluding fishing from areas 2 to 10 times smaller than static, non-targeted closures.

To our knowledge, no previous studies have tested, let alone found a significant link, between the turbidity of water and bycatch of protected species. Martin and Crawford (2015) applied a sensory ecology perspective to the literature on protected species bycatch and concluded that these species are being caught “because they simply do not see the nets”, and that to reduce bycatch, nets need to be made more visible. This provides a novel avenue of potential mitigation for seal bycatch, without introducing temporal or spatial restrictions on fishing effort. Changing the twine colour of nets has had mixed effects in reducing cetacean bycatch (e.g. Frady et al. 1994; Kot et al. 2012), and Martin and Crawford (2015) caution against the use of lights on nets, as these may disrupt the dark adaptation of underwater foragers. Visual deterrents, however, including replacing the top portion of a net with thicker twine and adding shark shapes to a net, have proven effective at reducing seabird and turtle bycatch (Melvin et al. 1999; Wang et al. 2010). While no comparable visual deterrents have been tested as a means of reducing seal bycatch, Martin and Crawford (2015) suggest that adding visual “warning panels” has the potential to increase net visibility for seals, and reduce bycatch. However, the effect of fitting nets with visual alerts on seal bycatch, seal depredation, and fish catches would require further study.

The FAO recommend a maximum threshold for mesh size in static nets to reduce turtle bycatch (FAO Fisheries and Aquaculture Department 2009), and this research provides a strong argument for focusing mitigation measures for seal bycatch on larger meshed static nets (tangle, trammel, and spider nets).

A major challenge in the study of protected species bycatch is the rarity of bycatch events relative to fishing effort, and the scale of the observer effort required to detect them. From the 2017 report of the ICES working group on bycatch of protected species a total of 443 individuals (including 38 seals) were recorded as bycatch from 6646 observer days spent at sea, although most of this effort focused on vessels using ‘active gear’ e.g. trawlers (in compliance with the EU 812 Regulation (Council Regulation (EC) No 812/2004)), where bycatch rates are lower compared to those using static gear (ICES 2017). Nonetheless, the rarity of bycatch events means that a dedicated observer programme could spend considerable effort at sea and observe little to no bycatch. Indeed, Reeves et al. (2013) found that world-wide, complete time series of marine mammal bycatch events were rare. In the absence of expensive and time-costly observer schemes, some studies have used official logbooks to substitute or complement vessel-based observers recording bycatch (e.g. Baum et al. 2003; Hamer 2007). However, without comparable observer schemes for cross-referencing, logbook data are likely to under-report protected species bycatch (Hamer et al. 2013). Reconciling the expertise of scientists with the tacit knowledge of fishers can be a powerful tool in fisheries assessments (Paterson 2010; Mackinson et al. 2011; Bentley et al. 2019), and this study is an encouraging sign of how incorporating fishers’ knowledge into research can inform effective mitigation.

In conclusion, this study explores the spatial and temporal trends in bycatch of seals in static net fisheries, and identifies distance to colony and water turbidity as possible drivers of these trends. Quantifying these effects will allow us to identify fisheries, regions, and seasons where the risk of seal bycatch is highest. This will allow us to target and refine future mitigation measures, and maximise conservation of this bycaught species. Additionally, this study identifies new potential mitigation approaches, through increasing net visibility in turbid waters, which could reduce seal bycatch without requiring spatial or temporal restrictions on fishing.

Chapter 3: Estimating protected species bycatch from limited observer coverage: a case study of seal bycatch in static net fisheries

This chapter was published in Global Ecology and Conservation. The text has been modified slightly to improve continuity in the thesis.

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Author contributions: **C.L.** and M.C. conceived the project outline and **C.L.** designed the methodology; C.L, O.T., and R.C. collected and sourced the data; **C.L.** led the data analysis and writing of the manuscript with much input from M.J., E.R. and M.C. All authors contributed critically to the drafts and gave final approval for publication.

Image: A grey seal, entangled around the neck, on the Blasket Islands, Co Kerry. Photo by Jolene Cronin.

3.1 Abstract

Fisheries bycatch represents a major anthropogenic threat to marine megafauna worldwide. To identify populations at risk, it is essential to estimate the total number of individuals removed from a population as bycatch. However, estimating total bycatch remains challenging due to the often-limited scope of monitoring programmes. In this study, I aimed to maximise the value of limited bycatch data collected by scientific observers and self-reported by fishers to provide estimates of total seal bycatch for static net fisheries operating in Irish waters. Bycatch rate was modelled as a function of known predictors of seal bycatch, and this model was then used to predict bycatch rates throughout the Irish Exclusive Economic Zone. Annual estimates of seal bycatch, from 2011 to 2016, ranged between 202 (90% CI: 2-433) and 349 (90% CI: 6-833) seals per annum. Estimated bycatch exceeded the precautionary threshold of Potential Biological Removal (PBR = 165-218; $F_r = 0.5$) for the national grey seal population but was below less conservative threshold values (PBR = 330-437; $F_r = 1.0$), with confidence intervals spanning both. Further research on the population structure of grey seals in the Northeast Atlantic is needed to set appropriate bycatch thresholds. Nonetheless, this study shows that by utilising predictive models to maximise the value of limited bycatch observer effort, we can produce informative estimates of protected species bycatch and highlight areas of high bycatch risk. This is presented as a case study for maritime nations with comparatively limited bycatch data to fill key data gaps in protected species bycatch worldwide.

3.2 Introduction

The incidental catch of non-targeted species by fisheries, known as bycatch, is recognised as a major threat to marine species worldwide (Wallace et al. 2010; Anderson et al. 2011; Lewison et al. 2014; Dias et al. 2019). Air-breathing megafauna, including marine mammals, turtles and seabirds, are particularly vulnerable to this kind of mortality and have been recorded as bycatch in over 90 countries (e.g. Wallace et al. 2010; Anderson et al. 2011; Reeves et al. 2013; Lewison et al. 2014; Dias et al. 2019). The majority of these bycatch events have involved static entangling nets and longline fisheries (Wallace et al. 2010; Žydelis et al. 2013; Lewison et al. 2014; Brownell et al. 2019).

For many endangered species, including the vaquita (*Phocoena sinus*; Taylor et al. 2017), Mediterranean monk seal (*Monachus monachus*; Karamanlidis et al. 2008), and several albatross species (Pardo et al. 2017), bycatch represents the dominant risk to population and species survival. To assess the conservation status of protected populations and enable effective mitigation for endangered species, we must first estimate the proportion of a population that is being removed by fisheries as bycatch (Soykan et al. 2008). Typically, this is achieved by first assessing the bycatch rate through on-board observations by dedicated scientific observers, then extrapolating observed bycatch levels to include the total fishing effort within a population's range or management area. Bycatch estimates can then be compared to threshold values to assess if the population can sustain the estimated level of mortality without failing to meet conservation or management targets (Wade 1998; Lonergan 2011; Curtis et al. 2015).

However, estimating the total number of individuals caught across an entire fishing fleet is challenging due to low observer coverage and a paucity of detailed data on the distribution of fishing effort. Scientific observers provide the best means of estimating bycatch rates at sea, however, the over-dispersed nature of bycatch in some fisheries often necessitates high observer effort to detect bycatch events (Babcock et al. 2003; Barlow & Berkson 2012); low observer effort in a given area can, by chance, result in atypically high or low bycatch rates (Rogan & Mackey 2007; Sims et al. 2008; Wakefield et al. 2018); and even large-scale observer programmes may only include a small proportion of the total fishing effort in a given area (Lewison et al. 2004b; Moore et al. 2008). Unless observer coverage includes 100% of the fishing effort in a given area, we must assume that the observed fishing effort is representative of the unobserved, and the more limited the observer coverage the broader the assumptions made (Wakefield et al. 2018). Logbooks remain the most comprehensive source of information on catch and effort by fishing vessels. However, beyond where and when fishing occurred, much of the key information required to estimate bycatch such as gear type, fishing effort and mesh sizes

(Cosgrove et al. 2016; Northridge et al. 2017a; Chapter 2), is lacking or unreliably reported.

Grey seals (*Halichoerus grypus*) are distributed across the North Atlantic with three recognised population centres in the Northwest and Northeast Atlantic, and the Baltic Sea. In Europe, this species is protected as an Annex II species under the European Union Habitats Directive (92/43/EEC), which obliges member states to ensure populations are maintained at "favourable conservation status". Home to approximately 38% of the global grey seal population, the United Kingdom (UK) provides annual estimates of total seal bycatch by UK vessels, based on observer data (Northridge et al. 2017b; Russell et al. 2019). The UK however, is the only European country with a long-running, dedicated observer programme for bycatch of protected, endangered or threatened species (ICES 2018), and considerable data gaps exist regarding bycatch levels among non-UK fishing fleets and those operating in neighbouring countries, including the Republic of Ireland. Irelands' population of grey seals, on the western edge of the Northeast Atlantic population's range, is estimated to be between 7284 and 9365 individuals, representing approximately 6% of grey seals in Western Europe (Ó Cadhla et al. 2013; OSPAR COMMISSION 2017). Recent research has highlighted the risk of seal bycatch in specific static net fisheries in Irish waters (Cosgrove et al. 2016; Chapter 2), however, estimating levels of bycatch mortality has not been possible to date due to limited observer coverage and key information gaps in logbook data.

In this study, I aim to address critical gaps in understanding the scale and sustainability of bycatch of Northeast Atlantic grey seals by estimating the level of seal bycatch across all static net fisheries operating within the Irish Exclusive Economic Zone (EEZ; figure 1). To maximise the value of limited observer data, a predictive mode of seal bycatch including known drivers of seal bycatch is developed, and then applied to fishing effort data reported in logbooks. Expert knowledge is used to infer key missing or unreliably reported information in the logbooks. This is presented as an approach that could be used by maritime nations with comparably limited bycatch data to do more with less, and fill key information gaps required to assess protected species bycatch globally. Finally, these estimates are compared to those produced by simple extrapolation of observed bycatch rates to total fishing effort for comparison.

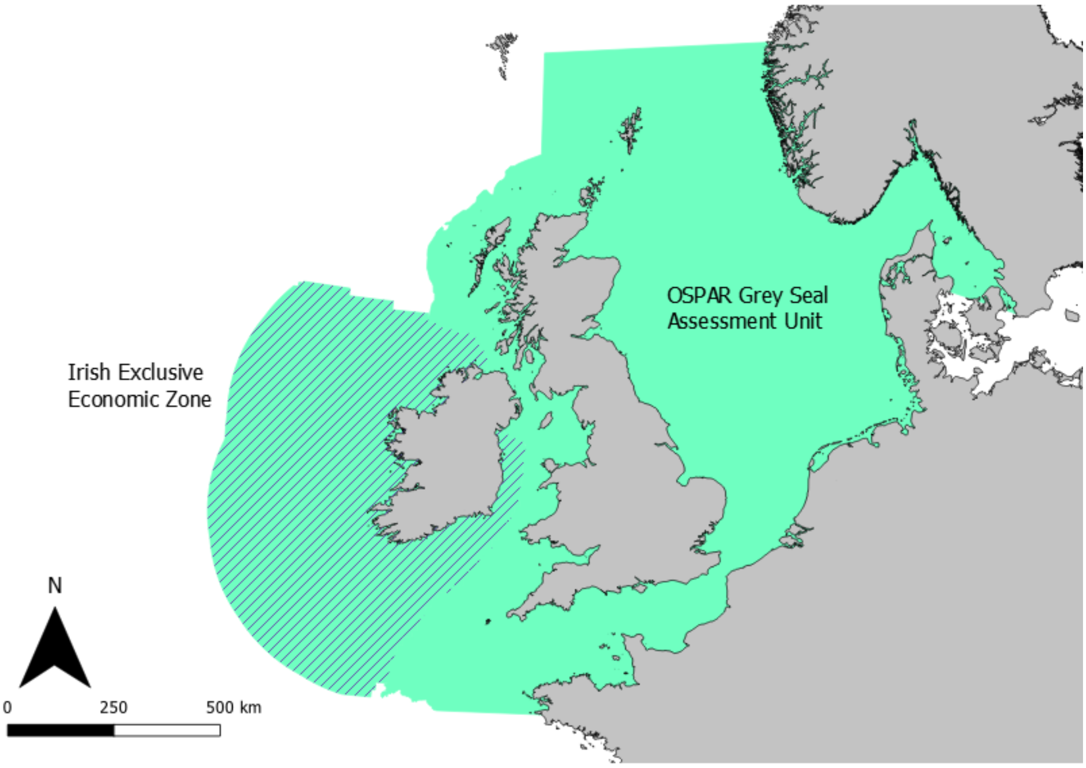

Figure 1: Map of the OSPAR Grey Seal Assessment Unit in green, inclusive of the Irish EEZ delineated by the striated pattern.

3.3 Methods

3.3.1 Observed effort and bycatch data

Observations of seal bycatch were recorded by scientific observers and self-reported by skippers on fishing vessels off the west, southwest, and south coasts of Ireland, between January 2010 and December 2018. These data comprised 3118 hauls from 17 vessels ranging in size from <10m to 22m length, and accounted for approximately 1.3% of the total reported static net fishing effort within the Irish EEZ over that time. Data were collected as part of separate research programmes along the west and south-west coasts of Ireland, including on-board observations of bycatch by scientific observers and self-reported data by skippers when observers were not present, and one extensive dataset of self-reported data on fishing effort and catch composition, including seal bycatch, in the south of Ireland (table 1). The presence or absence of a scientific observer was included in our analysis to control for potential bias in self-reported versus observer-collected bycatch data. All fishing vessels used forms of gillnet/entangling nets, as described by the Food and Agricultural Organisation of the United Nations (FAO). The nets used in this study could broadly be classified as "gillnets", "tangle", and "trammel" which differed primarily in mesh size (table 2). All nets were set on the sea floor (bottom-set) with weighted lead lines and buoyant head ropes to keep the nets vertical in the water. Some, but not all, gillnets were fitted with plastic floats on the head ropes for extra buoyancy. All nets comprised a single net wall, with the exception of trammel nets, which were three-walled (the mesh size of the outer net walls being substantially larger than the central net).

Recorded data included the date the nets were shot and hauled, GPS location at the beginning and end of each haul, net type, mesh size, catch, and bycatch composition. The net length was taken as the distance between start and end locations of a haul in metres and was measured using the "sf" package (Pebesma 2018) in the statistical framework R (R core team 2018). Any net lengths longer than 10km (n = 120) were assumed errors and were removed from the dataset.

The rate of seal bycatch or seals per unit effort (SPUE) was defined as:

$$SPUE = \frac{number\ of\ seals\ caught}{net\ length\ (km) \times soak\ time\ (days)}$$

The majority of data included the dates the nets were shot and hauled but not the times. Therefore, nets soaked for less than a day were assigned a soak time of 0.5 days.

Table 1: Description of bycatch data collection programmes included in this study.

Data collection programme	Data collected by	Number of hauls	Number of vessels	Vessel size range	Number of seals caught
Interactions between seals and entangling net fisheries (see Cosgrove et al. 2016)	Observers	358	3	12-22m	71
Bycatch monitoring programme, led by the Marine Institute of Ireland (ongoing)	Observers Fishers	63 477	3 10	< 12m < 12m	9 45
Personal fishing records from static net fisher	Fishers	2220	1	< 12m	132

Table 2: Description of nets included in bycatch data collection programmes.

Net type	Mesh size (cm)	Outer mesh size (cm)	Set length (km) – Mean (± SE); Median	Soak time (days) – Mean (± SE); Median	SPUE – Mean (± SE)
Gillnet	14	NA	2.41 (± 0.09); 1.00	0.94 (± 0.04); 1	0.015 (0.009)
Tangle	≥ 27	NA	1.20 (± 0.03); 0.71	5.04 (± 0.10); 4	0.031 (0.006)
Trammel	27	81	0.72 (± 0.06); 0.52	2.91 (± 0.046); 3	0.055 (0.010)

3.3.2 Fishing effort data

3.3.2.1 EU fishing effort

Data on European fishing effort were downloaded from the Joint Research Centre data dissemination tool of the European Commission Scientific, Technical and Economic Committee for Fisheries (STECF; see https://stecf.jrc.ec.europa.eu/data-dissemination). STECF effort data were based on logbooks for vessels over 10m in length only, as vessels smaller than 10m are not required to keep logbooks. Fishing effort was reported as hours fished and was spatially aggregated by ICES statistical rectangles and temporally by quarter and year. Data could be further differentiated between net type (gillnet or trammel), vessel length category, and vessel home country. Only ICES rectangles that were at least partly within the Irish EEZ were included in the analysis (see figure 2), and fishing effort from Irish vessels were excluded, as these were accounted for in more detailed national logbooks.

3.3.2.2 National fishing effort

The Marine Institute, Ireland, provided aggregated and anonymised logbook data for Irish vessels, which included location (aggregated to ICES statistical rectangles), net type, species landed, and fishing effort in days fished per trip. Only logbook entries from Irish vessels were included. As with EU fishing data, ICES rectangles that were at least partly within the Irish EEZ were included in the analysis (figure 2).

3.3.3 Inferring gear type

National and STECF logbook data aggregate gear types differently, but both essentially define all static nets as gillnets (all non-trammel nets) or trammel nets. This was a critical impediment to this analysis as studies have shown mesh size and net type to have significant effects on seal bycatch rates (Cosgrove et al. 2016; Northridge et al. 2017a; Chapter 2), and it was believed that combining gears would lead to considerable over and underestimation of bycatch in certain fisheries. To differentiate between gillnet and tangle net effort, I examined the species landed, and through consultation with fisheries experts, identified a number of indicator species which were most likely caught with a certain net type (table 3). For each logbook entry, it was assumed that nets listed as trammel nets were indeed trammels. For nets listed as “gillnets” I identified the top three species landed by weight per logbook entry, and first attempted to infer the net type from the top species landed. If the top species did not include any “indicator” species, I then looked to the second species landed by weight, and then the third if necessary. For national logbook data, this was carried out on a trip-by-trip basis, however, the STECF aggregate landings and effort data as separate datasets. For each STECF record, effort was matched to landings first by combination of ICES rectangle, vessel nationality, vessel length category, quarter, and year. If no gear type could be inferred from these landings, data were then matched by rectangle, nationality, quarter, and year only, and then if necessary, by rectangle, quarter, and year only. Some species, such as shrimp or shellfish, were unlikely to have been caught with static nets, and these records (<1% of data) were excluded from analysis, as they were assumed a result of mislabelled gear types. Less than 4% of logbook entries could not be assigned a net type and for these I took the precautionary assumption that unknown nets were tangle nets, as these have been found to have higher levels of seal bycatch in Irish waters (Cosgrove et al. 2016; Chapter 2).

Table 3: Landed species, as listed in logbook entries, used as indicator species to differentiate between gillnets and tangle nets.

Indicator species landed, as listed in logbooks	**Inferred gear type**
Cod, Haddock, Hake, Pollack, Saithe	Gillnet
Monkfish, Skates and rays, Black Sole, Turbot, Brill, Spiny Lobsters	Tangle net
Nephrops, Scallop, Shrimp, Whelk	Exclusive of static nets

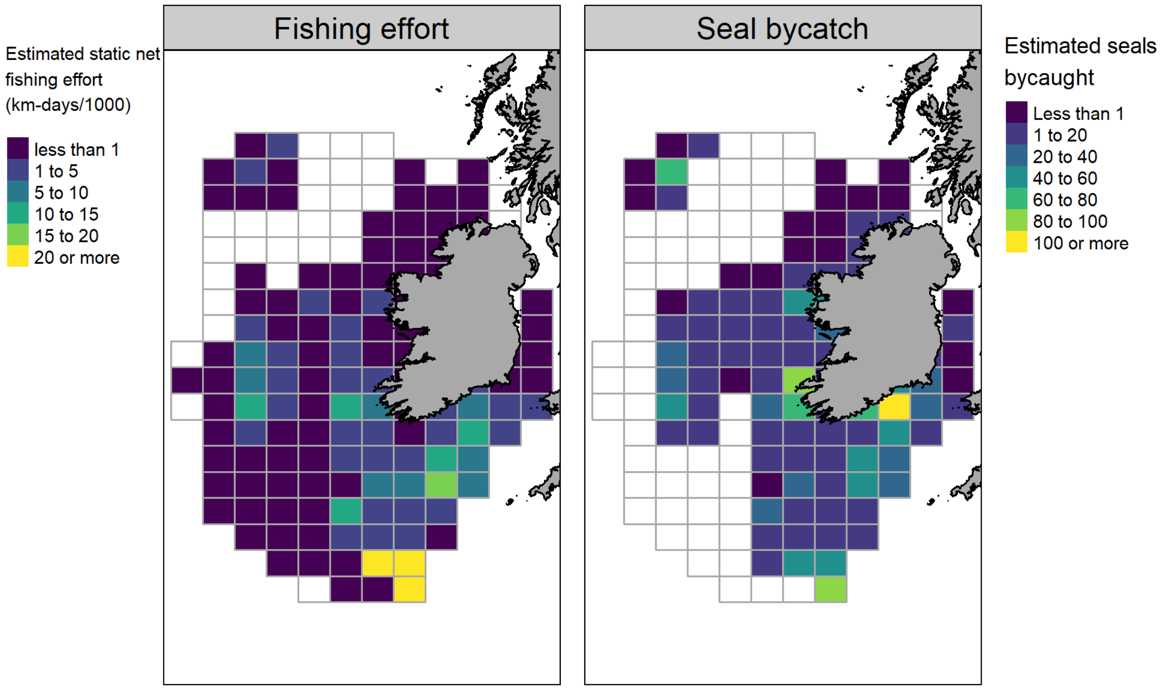

Figure 2: Static net fishing effort, based on logbook records, within the Irish Exclusive Economic Zone (EEZ) and estimated total levels of seal bycatch between 2011 and 2016.

3.3.4 Geo-processing

Following chapter 2, data on water turbidity and seal density were included in the analysis, as these were found to significantly affect seal bycatch rates. Water turbidity was sourced from the European Space Agency GlobColour project (see http://www.globcolour.info/), as 8-day composites at 4km^2 spatial resolution. Turbidity was averaged along the length of each observed net and across each statistical rectangle. For observed nets, values were also averaged between shoot and haul dates where necessary. Seal density was estimated by calculating the minimum distance from each fishing net (observer data) or the centroid of each ICES rectangle (logbook data) to each of the seven major grey seal breeding colonies in Ireland, and dividing by the estimated proportion of the national breeding population (according to Ó Cadhla et al. 2013) at each site. Thus, proximity to a large colony was weighted more heavily than the same distance to a smaller colony. The lowest scaled distance was selected for each haul or rectangle as the distance to nearest colony. I focused on grey seal colonies because of their greater size relative to harbour seal

(*Phoca vitulina*) colonies, the larger foraging range of grey seals relative to harbour seals (Cronin et al. 2014), and the higher incidences of grey seal bycatch in static nets (Cosgrove et al. 2016; Northridge et al. 2017b). Bathymetry data from a gridded global terrain model produced by General Bathymetric Chart of the Oceans data portal (https://www.gebco.net/data_and_products/gridded_bathymetry_data/) was used to estimate the depth at which nets were set and the minimum depth within each ICES statistical rectangle.

3.3.5 Predicting bycatch rates

A negative binomial generalised linear mixed effects model (GLMM) was used to construct a predictive model of seal bycatch as a function of predictors known to affect seal bycatch rates (Chapter 2), modified to only include predictor variables that could be applied to logbook data. The rate of seal bycatch per hundred units of effort (SPUE), rounded to the nearest integer, was included as the response variable to allow for a negative binomial distribution.

$$\log(SPUE \times 100) = Dist + SDD + Net + \ Obs + \ (1|vessel\ ID) + \ (1|year)$$

Where, $Dist$ is the minimum, scaled distance to colony, SDD is water turbidity as Secchi disc depth in metres, Net is the type of net (i.e. gillnet, tangle, or trammel) and Obs the presence/absence of an observer, both included as categorical predictors. $(1|vessel\ ID)$ and $(1|year)$ were included as random effects to account for inter-vessel and inter-annual variation. $Dist$ and SDD were square-root transformed to allow for model convergence. Backwards step-wise model selection was used based on second-order Akaike information criterion (AICc), and then the final model was used to predict the rate of seal bycatch across all reported fishing effort. Mean gear-specific bycatch rates for gillnets, tangle nets and trammel nets were also calculated for comparative purposes.

3.3.6 Extrapolating to fleet level

Once the rate of bycatch had been estimated, extrapolating the total number of seals caught within the EEZ became a relatively simple calculation of bycatch rate multiplied by fishing effort. The logbook data included the number of days fished per trip, the number of nets and the total length of nets deployed. However, in the national logbooks some fields were left mostly blank (net length) or filled with inconsistent or implausible values (number of nets, which ranged from 2 to 475) and were therefore considered unreliable. In these cases, the net lengths entered in the logbooks were replaced with the median observed net lengths and soak times, per net type (table 2), and for the number of nets deployed per day of fishing effort I first calculated the medians per vessel, before calculating the median of these values to at least partially account for inter-vessel variation. Some of the extreme values of the reported number of days fished per trip were considered unlikely to be true (e.g. 72 days fished) and any outliers exceeding the 99th percentile (~1% of the data) were replaced with the median reported value. Effort in km-days was then calculated as:

$$E_{km-days} = D \; * N_{npd} \; * L_{(g,t,tr)} * S_{(g,t,tr)}$$

Where D is the number of days fished, as reported in the logbooks, N_{npd} is the median of the median number of nets deployed per day by each observed fishing vessel, $L_{(g,t,tr)}$ is the median observed net length in km, and $S_{(g,t,tr)}$ is the median soak time in days for gillnets (g), tangle (t), or trammel (tr) nets. The STECF provided fishing effort as hours fished, so for the EU fleet fishing effort in km-days was estimated as (E_H = sum of STECF fishing effort in hours fished):

$$E_{km-days} = \frac{E_H}{24} * N_{npd} \; * L_{(g,t,tr)} * S_{(g,t,tr)}$$

Total bycatch was then estimated by multiplying fishing effort by the predicted bycatch rates according to the GLMM ($E_{km-days} * SPUE_{GLMM}$). For comparison, total bycatch was also estimated as the product of fishing effort and mean observed gear-specific bycatch rates ($E_{km-days} * \overline{SPUE}_{(g,t,tr)}$), hereafter referred to as the "applied average" method.

3.3.7 Confidence limits

Bootstrapping, or random resampling of observer data with replacement, was used to generate confidence limits around bycatch estimates. I resampled the subset of observer data usable in the predictive GLMM 1000 times, recalculated the mean bycatch rates, and refitted the GLMM to each iteration. The 5th and 95th percentiles of these bycatch estimates were taken as the 90% confidence interval for bycatch estimates.

3.3.8 Potential Biological Removal

In the absence of an agreed bycatch limit within EU waters and defined management units for European grey seals, estimates of total bycatch were compared to thresholds of Potential Biological Removal (PBR) for the national grey seal population. PBR is enshrined in the Marine Mammal Protection Act of the USA, which requires mitigation measures to be enacted when "incidental mortality and serious injuries" caused by human activities exceed PBR (Wade 1998; Taylor et al. 2000). This is designed to allow protected populations to maintain at least half of their estimated population size, given no human-caused mortality. PBR is calculated as:

$$PBR = N_{min} * \frac{R_{max}}{2} * F_r$$

Where N_{min} is the minimum population estimate, R_{max} is the intrinsic growth potential for the population (0.12 is the standard value for pinnipeds), and F_r is a recovery statistic set to between 0.1 and 1.0. By using the minimum population estimate in the calculation of PBR, greater uncertainty in population size will lead to wider confidence intervals and lower bycatch limits. The most recent assessments of the national breeding population of grey seals in the Republic of Ireland provided N_{min}, carried out by Ó Cadhla et al. (2007, 2013). These assessments used counts of new-born pups and production estimation models to estimate total pup production, and then used standard ratio estimates to produce all-age population estimates. Lower values of F_r (e.g. F_r = 0.1) allow for depleted populations to recover quickly; the default value of 0.5 is recommended to allow for bias in estimates of population size, structure, growth rates, and bycatch removals; while greater knowledge and certainty around these estimates may allow for a higher F_r value to be used (Taylor et al. 2000). The most appropriate value of F_r may also depend on specific management objectives for the population, and for this reason, bycatch estimates are presented relative to the full range of PBR values, with F_r ranging from 0.1 to 1.0.

Bycatch estimates are inclusive of both grey seals and harbour seals, however, due to few observations of harbour seal bycatch, and the more inshore distribution and reduced interconnectivity between haul-out sites of harbour seals relative to grey seals (Cronin 2011; Russell et al. 2015; Vincent et al. 2017; Sayer et al. 2019), the majority of bycaught seals were assumed to be grey seals. As it was assumed that seals became entangled while the nets were set on the seafloor, only estimates of bycatch from ICES rectangles with a minimum depth of 500m or less were included, given the deepest recorded dive by a grey seal in Irish waters of 455m (Jessopp et al. 2013).

3.4 Results

3.4.1 Observed effort and bycatch

The number of nets deployed per day across all vessels ranged from one to eleven. The median nets per day varied considerably between vessels, ranging between one and seven. The median of these values was two nets per day. The median net length of gillnets was longer than that of tangle and trammel nets and gillnets had the shortest median soak time (table 2). Seal bycatch was recorded in 197 (6.3%) of the observed hauls, and 257 seals were bycaught in total. Of these, 63 were identified as grey seals, and 10 as harbour seals. Observed SPUE ranged from 0.000 to 13.726, with a median of 0.000 and a mean of 0.040 (± 0.005 SE). SPUE was lowest in gillnets and highest in trammel nets (table 2). Bycatch data were recorded in 35 of the 166 ICES statistical rectangles within the Irish EEZ, and incidences of bycatch were recorded in seven. The highest mean rates of observed SPUE occurred close to shore, particularly along the west coast, at the northern extent of the observer coverage (figure 3).

3.4.2 Fishing effort

Between 2011 and 2016, logbooks reported static net fishing activity in 124 of the 157 ICES rectangles within the Irish EEZ (figure 2). This involved vessels from nine European countries, with French (43%), English (23%), and Irish (21%) vessels responsible for most of the effort. The highest levels of static net fishing were recorded in the Celtic Sea.

3.4.3 Predicting bycatch rates

The predictive model failed to converge with both vessel ID and year included as random effects, so year was excluded and the presence/absence of an observer was not retained in model selection, resulting in a final model with a lognormal conditional R^2 value of 0.24 (table 4). The GLMM predicted values of SPUE between 0.000 and 0.300, with a mean of 0.013 (figure 4). Figure 3 shows the spatial distribution of predicted values of SPUE relative to what was recorded by observers, and the applied average bycatch rates. The GLMM predictions failed to replicate the highest levels of SPUE observed on the west coast, but rather generally predicted moderately high rates of bycatch close to shore and major grey seal colonies, whereas the applied average approach resulted in intermediate bycatch rates applied throughout the study area.

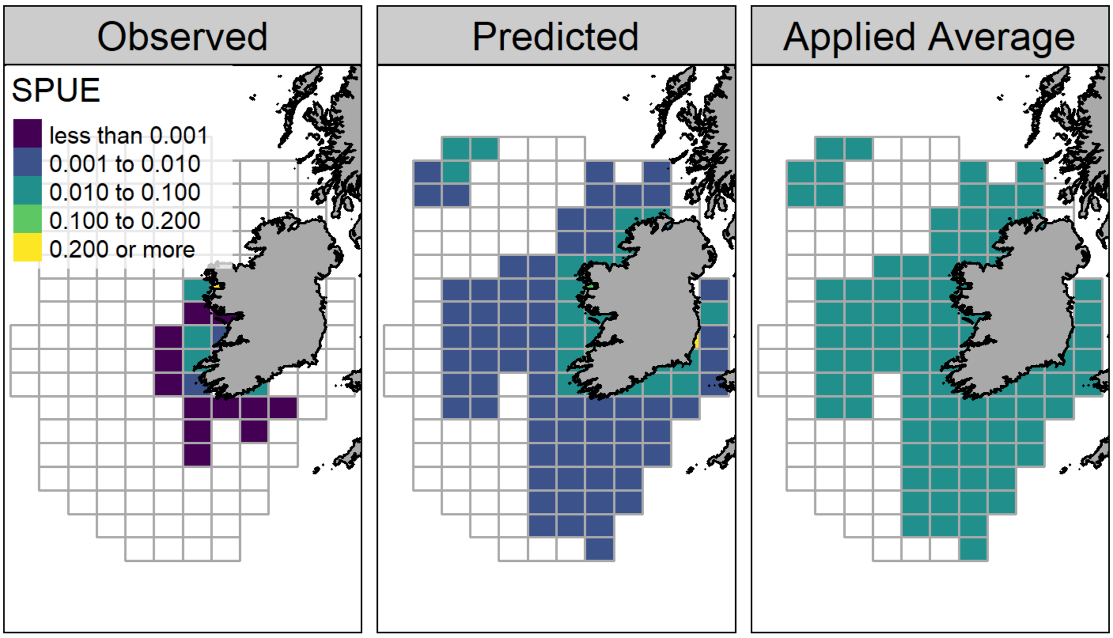

Figure 3: Mean observed seal bycatch per unit effort (SPUE; “Observed”), predicted rates of SPUE using a generalised linear mixed effects model (“Predicted”), and mean gear-specific rates of SPUE applied throughout the EEZ (“Applied Average”). Empty cells indicate areas with no observed or reported fishing effort and all plots share the same colour scale for SPUE.

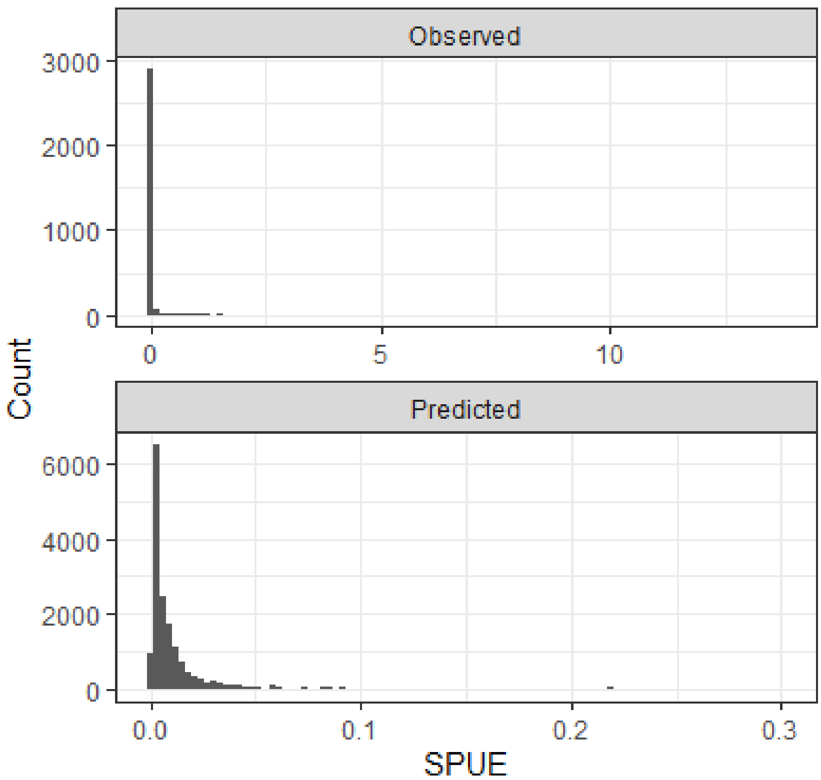

Figure 4: Observed values of seal bycatch per unit effort (SPUE) relative to predicted values of SPUE across the entire static net fishing fleet within the Irish EEZ.

Table 4: Model averaged estimates, with standard errors (SE), 90% confidence intervals (CI), z values and P values for seal bycatch per unit effort (SPUE) as a function of known predictors of seal bycatch, fitted with a negative binomial generalised linear mixed effects model (GLMM).

	Estimate	**SE**	**Lower CI**	**Upper CI**	**z**	**P**
Intercept	5.608	2.838	0.979	10.412	1.976	< 0.05
Net type: tangle	1.393	1.172	-1.137	3.098	1.188	0.235
Net type: trammel	0.752	1.166	-1.774	2.356	0.645	0.519
Secchi disc depth	-1.815	0.708	-3.008	-0.664	-2.562	< 0.05
Distance to colony	-0.028	0.045	-0.112	0.043	-0.629	0.530

3.4.4 Total seal bycatch within Irish EEZ

The predictive model resulted in estimates of annual total seal bycatch that ranged between 202 (90% CI: 3-433) and 349 (90% CI: 6-833), with no clear trend over time (figure 5). The lower bycatch estimates in 2013 coincided with a one-year decrease in reported fishing activity by French vessels using gillnets in the Irish EEZ. These annual estimates exceeded the default value of PBR (165-218; $F_r = 0.5$) for the national grey seal population but were below the least conservative PBR (330-437; $F_r = 1.0$) values, albeit with overlapping confidence intervals (figure 5). Alternatively, using the applied average method resulted in bycatch estimates that exceeded the least conservative value of PBR by almost 300% (figure 5).

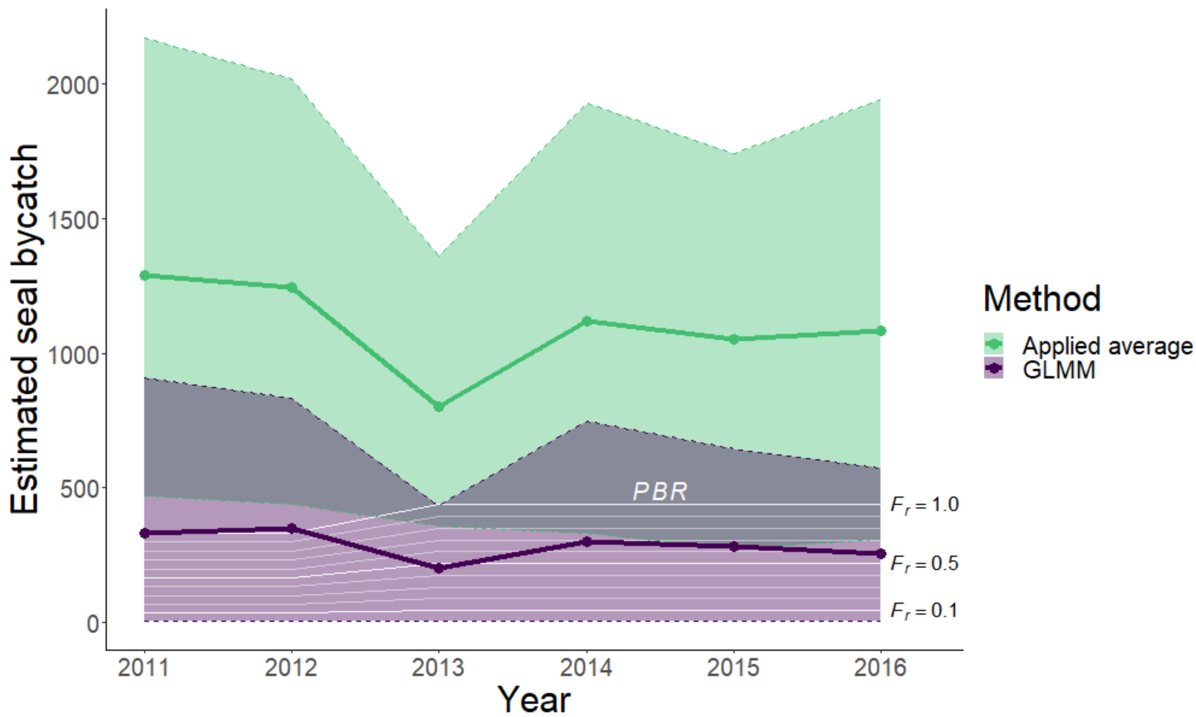

Figure 5: Estimated levels of seal bycatch across all static net fisheries within the Irish EEZ between 2011 and 2016. Point estimates (solid lines) and associated 90% confidence intervals (shaded area) were produced by applying predicted (GLMM) and gear-specific mean (applied average) bycatch rates to fisheries logbook data. White lines indicate the Potential Biological Removal (PBR) thresholds for the Irish grey seal population, with an F_r statistic ranging between the minimum (0.1) and maximum (1.0) values, in increments of 0.1.

3.5 Discussion

Using a predictive model and expert knowledge allowed me to produce estimates of total seal bycatch in Irish waters from limited observer data, the first of their kind. More direct bycatch extrapolation methodologies have proven effective elsewhere, such as in the UK where observed metiér-specific bycatch rates are applied to logbook data (e.g. Northridge et al. 2017b), but this relies on extensive on-board data collection to estimate bycatch rates across a wide range of detailed fishing metiérs. This approach is less suitable in regions with limited observer data across a smaller range of fisheries, and coarse resolution of fishing effort data, that occurs in the majority of marine jurisdictions globally. The observed mean seal bycatch rate recorded in the Irish observer programme was 7.5 times higher than what has been observed in the UK (Northridge et al. 2017b), potentially driven by a smaller sample size but comparatively high observer effort on board inshore fisheries in Ireland, close to major seal haul-outs.

Relative to the modelled bycatch rates, applying mean observed rates across the entire EEZ generally underestimated bycatch in inshore areas while overestimating bycatch further offshore (figure 3), and inflated overall bycatch estimates compared to using the predictive model (figure 5). Whereas applying average bycatch rates assumed a spatially independent relationship between observed and unobserved bycatch, the GLMM method assumed that the observed effects of known predictors of seal bycatch were consistent across observed and unobserved fishing effort (Chapter 2). This method provided a more informative distribution of bycatch risk (figure 3) and allowed me to produce predictions of bycatch rates in response to changing environmental variables (in this case, water turbidity). Given the growing importance of developing dynamic management strategies to protect highly mobile marine species (Dunn et al. 2016; Maxwell et al. 2020), if policy makers wished to reduce bycatch to specified levels, this could provide an invaluable tool for identifying areas or seasons of high bycatch risk to target mitigation measures accordingly.

The national population of grey seals was first assessed by means of a comprehensive national survey effort during the 2005 breeding season and repeated in 2013 (Ó Cadhla et al. 2007, 2013). The most recent survey provides supporting evidence of grey seal population growth since the 1990s, but cautions that "robust statistical data on grey seal population viability or trends in Ireland are not available at present" (Ó Cadhla et al. 2013). The choice of which F_r value to use depends on the population status and the management objective for the population. There are currently no bycatch limits for grey seals within the EU and the criteria for "favourable conservation status" are poorly defined, leading to unclear management objectives for protected seal populations. PBR provides a precautionary reference point/limit for non-natural mortality designed to allow marine mammal populations to reach a maximum net productivity level, or approximately 50-70% of the carrying capacity for the population (Wade 1998). These results do not simplistically define bycatch estimates as sustainable or unsustainable, especially considering the relatively wide confidence intervals, but rather highlight that, with the information presently available, bycatch may represent a significant pressure on the national grey seal population.

For any bycatch limit reference point such as PBR to be effective, it is critical that we identify demographically independent management units within a species range, and manage such units independently (Taylor 1997; Curtis et al. 2015). If the minimum population size used in PBR represents the total of multiple distinct populations, then even the most conservative estimates of PBR may fail to prevent local depletions at this level. Genetic analysis provides an important means of delineating discrete populations (DeYoung & Honeycutt 2005), however, to date this has not been applied to grey seals at a broad geographic scale in Western Europe. Animal movements can provide a hint at population structure, but tagged grey seals have been shown to regularly move between major colonies around Ireland, the UK, and France (Jessopp et al. 2013; Vincent et al. 2017; Carter et al. 2020), providing no clear evidence of demographic isolation. In the absence of such information, the OSPAR Commission define an Assessment Unit for grey seals in Western Europe that extends from the Atlantic margin to the greater North Sea area, inclusive of Irish waters (OSPAR

COMMISSION 2017; figure 1). Future studies on the genetic structure of grey seals in Western Europe will be critical to identifying discrete management units and setting the most appropriate bycatch limits possible.

Providing estimates of bycatch mortality is essential for an ecosystem approach to fisheries management (Garcia & Cochrane 2005; Bellido et al. 2011). The major obstacle to providing usable estimates is the many uncertainties in the data and assumptions required. This study makes every effort to make justifiable assumptions in response to the absence of detailed data, but it is nonetheless vital that estimates are considered within the context of this uncertainty. One potential source of overestimation could be that bycatch observer programmes with limited resources may focus their observer efforts on fisheries that would be expected to experience bycatch. Without a balanced distribution of observer effort across “low” and “high” risk fisheries, it is possible that applying simple means of bycatch rates from this subset of fisheries could overestimate bycatch when applied to the wider fleet. Alternatively, by identifying the gear-specific and environmental drivers of bycatch, then using these to predict bycatch rates, as done in this study, the risk of overestimating bycatch in “low” risk fisheries is reduced.

Nonetheless, if we take a precautionary approach to fisheries management, we must consider that given the remaining data uncertainties, we cannot exclude the possibility that even the highest estimates may still underestimate total levels of bycatch. EU logbook data underestimate fishing effort from smaller vessels, as only vessels larger than 10m in length are obligated to submit logbooks. Consequently, these data fail to capture the fishing effort of 75% of the currently registered Irish fishing vessels smaller than 10m in length. This is arguably the most important data gap to consider as smaller vessels are typically restricted to inshore waters, with potentially high levels of bycatch, even in excess of larger fisheries (Peckham et al. 2007; Alfaro-Shigueto et al. 2011; Doherty et al. 2014). Fishing activity by small-scale fisheries is poorly monitored globally, and unless this fishing effort can be accounted for, best estimates will most likely underestimate total levels of bycatch (Lewison et al. 2014).

A key assumption of observer programmes is that unobserved fishing activity can be inferred from the observed, and observed activities approximate to a random and representative subsample of all activities (Benoît & Allard 2009). However, observer data may not accurately reflect fishing practice, as the presence of an observer may encourage fishers to change their behaviour while the observer is present (observer bias), and the distribution of observers may be determined more strongly by logistical constraints than experimental design (deployment bias; Benoît & Allard 2009; Faunce & Barbeaux 2011; Amande et al. 2012). Observer coverage may be further biased if a programme targets only fisheries with expected high rates of bycatch, or conversely if fisheries with the highest levels of bycatch are less agreeable to facilitating observers on board (Cotter & Pilling 2007; Benoît & Allard 2009). This study utilises a large amount of bycatch data self-reported by skippers. While it is encouraging that a potential observer effect was not detectable in the data, numerous examples exist in the literature to suggest that self-reporting may underestimate bycatch rates relative to observer-collected data (e.g. Allen et al. 2002; Bremner et al. 2009). As such, we should remember that the fishing activity observed in this study might not reflect the fishing activity of the wider fleet, and "observed" bycatch rates should be treated as minima.

Lastly, observers can only record what they can see and may entirely miss incidences of bycatch where animals fall out of nets or escape with serious injuries (Gilman et al. 2005; Benoît & Allard 2009). As such, the estimates presented here, all of which were built on observer and self-reported data, may underrepresent this additional bycatch mortality. Peltier et al. (2016) analysed the distribution of stranded common dolphins (*Delphinus delphis*) along the Bay of Biscay and modelled the drift patterns of dolphin carcasses to estimate the total number of bycaught dolphins, inclusive of unobservable bycatch and robust to observer bias. Bycatch estimates inferred in this way suggested unsustainable levels of bycatch; thousands of dolphins per year, compared to the more sustainable estimate, based on limited observer data, of 550 dolphins caught annually.

In conclusion, this study presents a methodological framework for estimating bycatch mortality from limited observer data, demonstrating that by using (1) sufficient observational data of bycatch events to identify reliable bycatch predictors, (2) fisheries logbook data to estimate fishing effort, and (3) expert knowledge to address key data gaps, plausible and informative bycatch estimates can be produced. While dedicated scientific observer programmes remain the most reliable means of estimating bycatch rates at sea, the global rarity of extensive, long-running programmes too often precludes the estimation of bycatch mortality by traditional means. Unable to quantify this anthropogenic pressure, it remains challenging to identify populations or species at risk. Therefore, it is vital that we develop complementary methodologies to maximise the value of the limited data that does exist, providing an important starting point for an ecosystem-based approach to fisheries management, bycatch mitigation, and addressing key data gaps in our understanding of fisheries bycatch worldwide.

Chapter 4: The co-occurrence of seal foraging behaviour and static net fishing activity

Target journal for publication: Journal of Applied Ecology

Image: An adult male grey seal fitted with GPS tag on the Inishkea Islands, Co Mayo, 2019. Photo by Ash Bennison.

4.1 Abstract

Grey seal (*Halichoerus grypus*) interactions with static net fisheries are a contentious issue, as seals are known to depredate catch and become entangled as bycatch. Previous studies of grey seal tracking data identified significant spatial overlap between seals and fishing vessels using passive gears in the Celtic and Irish Seas. However, this overlap occurred over several months, providing little insight into temporal overlap and encounter rates between seals and nets. In this study Hidden Markov Models (HMMs) were applied to tracking data from over 160 grey seals tagged in the UK, Ireland, and France, to identify the likely location of seal foraging activity. Vessel tracking data were used to infer the concurrent locations of static nets, and distance to the nearest net was incorporated in HMMs as a covariate effect on state transition probabilities. In doing so, this analysis aimed to examine the co-occurrence of foraging and fishing effort by seals and static net fishing vessels, and the potential effect of proximity to fishing nets on grey seal behaviour. Additional covariate effects included region and seal sex. Both the Akaike (AIC) and Bayesian Information Criterion (BIC) were used in model selection, and the models selected by each criterion were presented as a confidence set of plausible models. Both models selected by AIC and BIC converged on three behavioural states inferred as “foraging”, “travel”, and “rest” which was included as a known state. The model selected by BIC retained distance to net as the only covariate effect, and showed that grey seals were most likely to switch from travel to foraging behaviour within 1km of static nets, with the effect size decreasing at greater distances. The AIC-selected model included a three-way interaction between distance to net, sex, and region, and showed that the effect of distance to net varied with sex and region. This study shows that grey seals are likely to forage near static nets which may increase the risk of direct fishery interaction, but this effect may be influenced by intrinsic factors, such as the sex of the seal, and extrinsic factors, including the distribution of fishing effort in a given area.

4.2 Introduction

Where marine predators and commercial fisheries co-occur, interactions can take place that are detrimental to animals, fisheries, or both (Read 2008; Grémillet et al. 2018; Guerra 2019; Tixier et al. 2020b). Indirect interactions encompass the competition for shared resources, namely fish (Trites et al. 1997; Matthiopoulos et al. 2008; Rountos et al. 2015; Houle et al. 2016), while direct interactions include depredation of commercial catch (Mandelman et al. 2008; Cosgrove et al. 2015; Towers et al. 2019), damage to fishing gear (Kauppinen et al. 2005; Brotons et al. 2008; Panagopoulou et al. 2017), and accidental entanglement in gear, known as bycatch (Moore et al. 2008; Reeves et al. 2013; Žydelis et al. 2013; Brownell et al. 2019). Direct fishery interactions pose an immediate threat to many populations of marine predators (Read 2008; Žydelis et al. 2013; Brownell et al. 2019). Of these, bycatch represents the most acute anthropogenic threat (Karamanlidis et al. 2008; Lewison et al. 2014; Taylor et al. 2017), while depredation can reduce the value of catch, dis-incentivise conservation and lead to retaliatory measures by fishers (Mandelman et al. 2008; Read 2008; Hamer et al. 2012; Tixier et al. 2020b). As the range of commercial fisheries have expanded (Swartz et al. 2010; Kroodsma et al. 2018), and some populations of marine predators have recovered from commercial exploitation (Magera et al. 2013), direct predator-fishery interactions have become more prevalent (Guerra 2019; Tixier et al. 2020b). Conflicts between marine predators and fisheries have become a globally reported issue, presenting a major challenge to sustainable fisheries management (Hamer & Goldsworthy 2006; Wallace et al. 2010; Lewison et al. 2014; Dias et al. 2019; Tixier et al. 2020b).

The intensity of interactions will depend on the extent to which predators and fisheries overlap in time and space (Matthiopoulos et al. 2008). Comparing the spatiotemporal overlap of predators and fishing activity can identify areas where interactions are likely to occur (Roe et al. 2014; Cronin et al. 2016; Pikesley et al. 2018; Clay et al. 2019) and allow us to explore changes in animal behaviour in relation to fishing activity (Pirotta et al. 2018; van Beest et al. 2019; Collet & Weimerskirch 2020). With recent advances in GPS tracking technology (Evans et al. 2013; Wilmers et al. 2015) and increased availability of locational data on fishing activity (Kroodsma et al. 2018), we can explore spatial interactions between marine predators and fisheries at increasingly fine spatial and temporal scales (Bodey et al. 2014; van Beest et al. 2019; Clark et al. 2020). Hidden Markov Models (HMMs) provide a means of analysing the movement patterns of tracked animals to infer the underlying behavioural states of animals at sea (Carter et al. 2016; Zucchini et al. 2016; Patterson et al. 2017). Additionally, the application of machine-learning algorithms to Automatic Identification System (AIS) data of fishing vessel locations has provided new insights into precisely where and when vessels are fishing (Kroodsma et al. 2018; Rô Me Guietid et al. 2019). By comparing the at-sea movements and inferred behaviour of marine predators with the concurrent distribution of fishing activity we can identify behavioural responses of predators to fishing vessels (Bodey et al. 2014; Clark et al. 2020) and correlations between behaviour and activity belonging to specific fisheries (van Beest et al. 2019).

In Europe, grey seals (*Halichoerus grypus*) have been shown to depredate fish (Quick et al. 2004; Königson et al. 2013; Cosgrove et al. 2015; Tixier et al. 2020b), damage fishing gear (Cronin et al. 2014; Olsen et al. 2018), and become entangled in nets as bycatch (Vanhatalo et al. 2014; Cosgrove et al. 2016; Northridge et al. 2017b; Chapter 2). This has led to regular requests from the fishing industry for management of the seal population, however, our understanding of the extent of interactions between seals and fisheries in Europe remains limited (Cronin 2011; Cronin et al. 2014). Cronin et al. (2012, 2016) compared the at-sea distribution of 19 grey seals tagged in the southwest and southeast of Ireland with Vessel Monitoring System (VMS) data of fishing activity. They found little evidence for overlap between seals and demersal fisheries to the west of Ireland (Cronin et al. 2012), but in the Irish and Celtic Seas, seals significantly overlapped with fishing vessels using static gear (Cronin et al. 2016). However, this spatial overlap occurred at a broad temporal scale over several months. Alternatively, van Beest et al. (2019) explored the spatial interactions between grey seals and static net fisheries in the Baltic Sea in near real-time and found that the likelihood of seals foraging increased close to fishing nets, although seals spent less than 3.3% of their time within 5km of nets. The authors suggest that this relatively low level of interaction may be a result of missing information regarding the location of fishing nets and a small sample size of seals, including no adult males which are known to have the highest degree of direct interactions with Baltic Sea fisheries (Königson et al. 2013; Kauhala et al. 2015; van Beest et al. 2019).

In this study, I applied HMMs to an extensive dataset of tracking data from 164 grey seals tagged in Western Europe to classify seal behaviour in relation to static net fishing activity. In static net fisheries, interactions with predators often occur at night or when nets are left unattended by vessels (Tixier et al. 2020b). Therefore, by identifying where seals are likely foraging in relation to locations where fishing vessels have likely set nets, in near synchronous time, I aimed to explore not just the co-occurrence of seals and fishing vessels, but the relationship between seal foraging and the likely location of static nets. This will provide new insight into the likelihood of grey seals encountering and directly interacting with static nets.

4.3 Methods

4.3.1 Seal capture and tag deployment

Between March 2013 and May 2019, 164 grey seals (87 males and 77 females) were captured and fitted with Fastloc GPS tags at 25 locations in Ireland, the UK, and France (figure 1, table S1). The tags were attached to the seals' fur with quick-setting epoxy or cyanoacrylate superglue and positioned at the base of the skull (McConnell et al. 1999). Tags typically detached with the old fur during the annual moult, thus to maximise the duration of tag attachment, seals were tagged towards the end of the moult (April-May) when the seals often came ashore in large numbers.

The programming and design of the tags varied between deployments as the technology was developed, but each tag was programmed to attempt a location fix every 10 to 30 minutes. Not all location fixes were successful as they were dependent on the seal's head being above water at the time the tag attempted a fix. The most recent deployments in 2019 included tags that upon unsuccessful location fixes, attempted another fix as soon as the tag was next above water. In addition to GPS positions, tags transmitted two-hourly summaries of behaviour, including the proportion of time spent by the seal either hauled-out, at the surface, or diving (as inferred by on-board conductivity and pressure sensors). A recorded dive began when the inbuilt depth sensor recorded a depth exceeding 1.5m for more than 8 seconds, and ended when the seal returned to less than 1.5m depth.

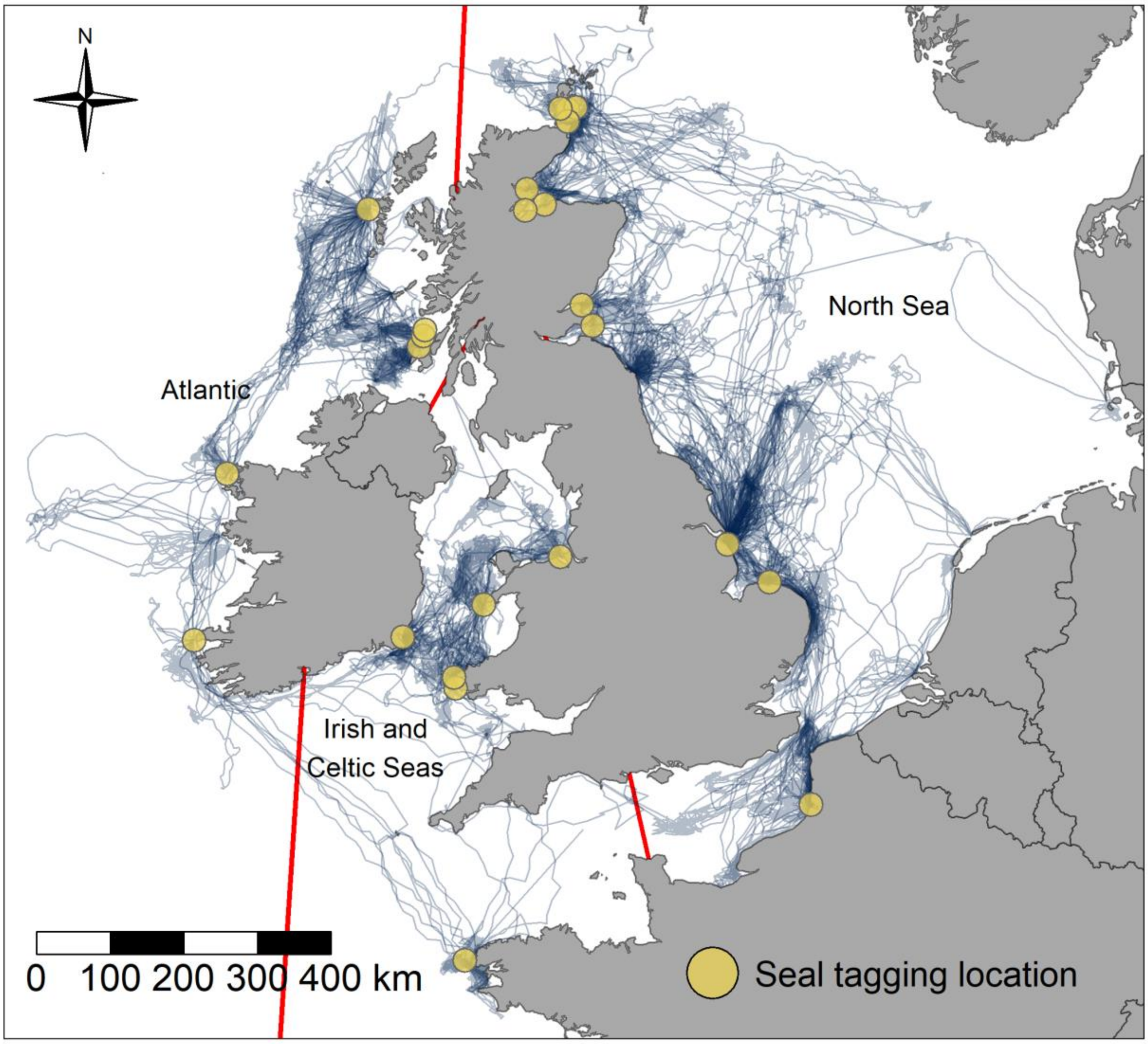

Figure 1: At-sea distribution of 124 grey seals tagged at 24 locations around the UK, Ireland, and France between 2012 and 2019.

4.3.2 Processing of telemetry data

Following Russell et al. (2015) I identified and removed erroneous location fixes which were obtained with less than 5 satellites or had a residual error value of exactly zero or more than 25. The remaining positions were then interpolated to a regular two-hour time interval, using linear interpolation, synchronised with the end of each behavioural summary interval. For marine animals travelling around 2.5 km h^{-1}, Dujon et al. (2014) suggest that robust estimates of speed and direction can be obtained using location intervals of 1-6 hours, and Carter et al. (2020) were able to infer realistic behaviours from grey seal tracks interpolated to two hour intervals. Following Dujon et al. (2014), interpolated positions more than six hours removed from an actual location fix were considered "unreliable" and excluded from further analysis.

4.3.3 Distance to static net fishing activity

AIS data from commercial fishing vessels, provided by Global Fishing Watch (GFW), was used to identify locations of static net fishing activity. GFW apply machine-learning algorithms to satellite-derived AIS data to identify the fishing activity (in hours fished) and primary gear-type of commercial fishing vessels (Merten et al. 2016). These data are provided as daily grids at 0.01° x 0.01° spatial resolution. Only locations in which a vessel identified by GFW as primarily using "set gillnets" or "fixed gear" was actively fishing, between -16° and 10°W, and 45° and 62°N, were included. The length of time that static nets are typically left to "soak" unattended varies with gear-type and target species, but can range from a number of hours to a number of days (e.g. Northridge et al. 2017b; Chapter 2). Without knowing if the fishing activity inferred by GFW represented the deployment or recovery of nets, I measured the minimum Euclidean distance between each seal location and the closest fishing activity that occurred within 3 days of the seal being at that position (in chapter 2, a mean soak time of 3 days ± 0.1 SE was observed in large mesh tangle nets), and inferred this as the distance to the nearest potential location of a fishing net.

4.3.4 Hidden Markov Model

HMMs were used to differentiate between behavioural states in seals in relation to static net fishing activity. A number of studies have used HMMs to infer discrete behavioural states in pinniped tracking data (Jonsen et al. 2005; Michelot et al. 2017; van Beest et al. 2019; Carter et al. 2020), often differentiating between two behavioural states (travel and foraging). High step lengths (the Euclidean distance travelled between successive GPS locations in a given time interval) with low turning angles are generally attributed to travelling behaviour whereas short step lengths and high turning angles are attributed to foraging (e.g. Patterson et al. 2008). However, studies have also shown that seals may spend considerable time at the sea surface, which likely represents resting related to food digestion (Sparling et al. 2007). HMMs based on step lengths and turning angles alone, could misinterpret this behaviour as foraging, thus overestimating foraging activity (Russell et al. 2015; Carter et al. 2016). I differentiated between time intervals (t) spent resting at the surface or hauled out (resting state $Z_t = R$) and diving (foraging and travelling states; $Z_t \in \{F, Tr\}$) based on the proportion of each two-hour time interval spent diving ($\omega_{d,t}$) according to the tag summary data (Russell et al. 2015). Seals must periodically surface to breathe, and have been found to spend a maximum of 88.8% of a two-hour interval diving (Russell et al. 2015, Carter et al. 2020). Following these studies, the threshold for assigning rest and diving states was set at half of the maximum possible proportion of time spent diving, such that $Z_t = R$ when $\omega_{d,t} < 0.444$ and $Z_t \in \{F, Tr\}$ when $\omega_{d,t} \geq 0.444$.

A three-state multivariate, discrete-time HMM (Zucchini et al. 2016) was then fitted, with resting included as a "known state". The remaining intervals with low step lengths and high turning angles were inferred as foraging, and intervals with high step lengths and low turning angles as travelling. This was carried out using the package *momentuHMM* (McClintock & Michelot 2018) in R (R Core Team, 2018). Step lengths were assumed to follow a Weibull distribution, and turning angles to follow a wrapped Cauchy distribution. "Unreliable" intervals (see "Processing of telemetry data" above) were removed from the dataset prior to fitting the HMM, and each seal track was divided into segments uninterrupted by unreliable intervals. Only track segments with a minimum of ten valid intervals were included in the HMM.

Grey seal behaviour has been shown to vary with intrinsic (e.g. sex) and extrinsic (e.g. region, season) factors (Russell et al. 2015; Carter et al. 2017), and seals may adapt their behaviours to changes in environmental conditions and prey availability (van Beest et al. 2019). As the seals in this study were tagged at numerous locations over a large geographical range, the foraging areas available to the seals were divided into three broad regions, based on the distribution of tracks, and the region in which each interpolated seal location occurred was appended to the tracking data (figure 1). This variable was then included as a covariate effect on the state-dependent parameter distributions, allowing for inter-regional variation in movement characteristics.

Using this model structure, I then tested the inclusion of various combinations of covariate effects on state transition probabilities, to explore the potential effect of proximity to fishing activity on the likelihood of seals switching to “foraging” behaviour. These covariates included the sex of the seal (two-level factor), the region in which the behaviour occurred (three-level factor), and distance to net, coded as a binomial factor of whether or not the behaviour occurred within a given distance threshold (1km, 2km, 5km, 10km, 20km, or 50km) of a potential net location. Starting with a fully-saturated model, including a three-way interaction between distance to net, sex, and region, multiple models were run, each time including a different threshold value for distance to net. Preliminary analysis suggested that a threshold value of 1km would enable me to detect an effect of distance to net on state transition probabilities. I then constructed a total of 12 models including all possible combinations of the three covariates that were considered biologically plausible, including distance to net as a binomial factor with a threshold distance of 1km. Only locations within 200km of a fishing location were included to ensure a similar range of values between each sex-region group. For model selection, the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) was calculated for each model. As the AIC is known to more heavily favour complex models with additional covariates, while the BIC penalises model complexity more heavily, I presented the models selected by each criterion as a confidence set of reasonable models, and explore the covariate effects of each (Zucchini et al. 2016; van Beest et al. 2019). From this set of final models, the most probable sequences of behavioural states were extracted using the Viterbi algorithm (Zucchini et al. 2016), and models were re-run using the full-range of distance threshold values.

4.4 Results

Between 2012 and 2019, the highest levels of static net fishing activity occurred to the south of Ireland and the UK, particularly in the eastern English Channel, along the French coast (figure 2). The distance between interpolated seal locations and static nets ranged from less than 1km to nearly 1000km (figure 3), with a median distance of 74km. Approximately 6% of interpolated seal locations were within 5km of a potential static net location and 10% within 10km (figure 3a).

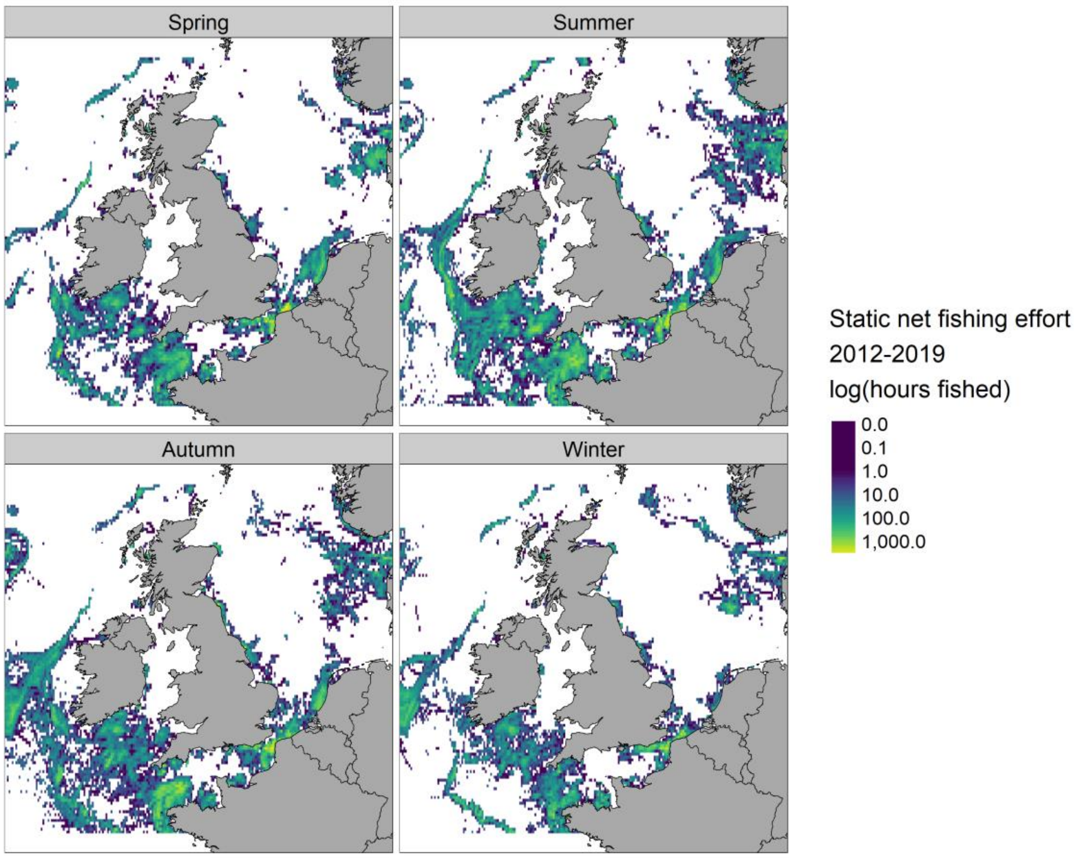

Figure 2: Distribution of static net fishing effort around the UK, Ireland, and northern France between 2012 and 2019, based on AIS data provided by Global Fishing Watch.

Model selection using the AIC resulted in a model including a three-way interaction between distance to net, sex, and region on the state transition probabilities. Alternatively, the BIC selected a model including distance to net as the only covariate effect on state transition probabilities (table 1). Both models converged on similar state-dependent distributions for step length and turning angle (figures S2-S5), with state 1 (inferred travel) having longer step lengths and lower turning angles than states 2 (inferred foraging) and 3 (rest as a known state). Activity budgets resulting from both models were broadly similar. The activity budget resulting from the AIC-selected model (proportion of time spent traveling = 0.33, foraging = 0.37, rest = 0.30) was very similar to that of the BIC-selected model (traveling = 0.33, foraging = 0.36, rest = 0.30), both including a distance threshold of 1km. Approximately 7% of intervals inferred as foraging (both models) were within 5km of static nets and 9% within 10km (figure 3b). An example track coloured by state predictions from the AIC-selected model is shown in figure 4.

Table 1: Log-likelihood and Akaike Information Criterion (AIC) scores for nested HMMs including distance and sex as covariates (d=distance, r=region, s=sex). * indicates an interaction between covariates, and the best models identified by AIC and BIC are highlighted in grey.

Model	loglik	AIC	Δ AIC	BIC	Δ BIC
~ d*s*r	-417103	**819287.7**	**0**	834311	15083.5
~ d*s + r	-413904	819518.6	230.9	827913.9	8686.4
~ d + s + r	-416888	819525.9	238.2	833881.1	14653.6
~ d*r + s	-410989	819534.6	246.9	822083.8	2856.3
~ s + r	-410913	819658.4	370.7	821932.1	2704.6
~ d + r	-413779	821912.3	2624.6	827664	8436.5
~ r	-409786	822054	2766.3	819678.1	450.6
~ d*s	-413768	827621.8	8334.1	827641.6	8414.1
~ s + d	-409706	827634.3	8346.6	819518.4	290.9
~ s	-409709	827874.1	8586.4	819524.4	296.9
~ d	-409561	833841.4	14553.7	**819227.5**	**0**
~ null	-409715	834261.2	14973.5	819535.6	308.1

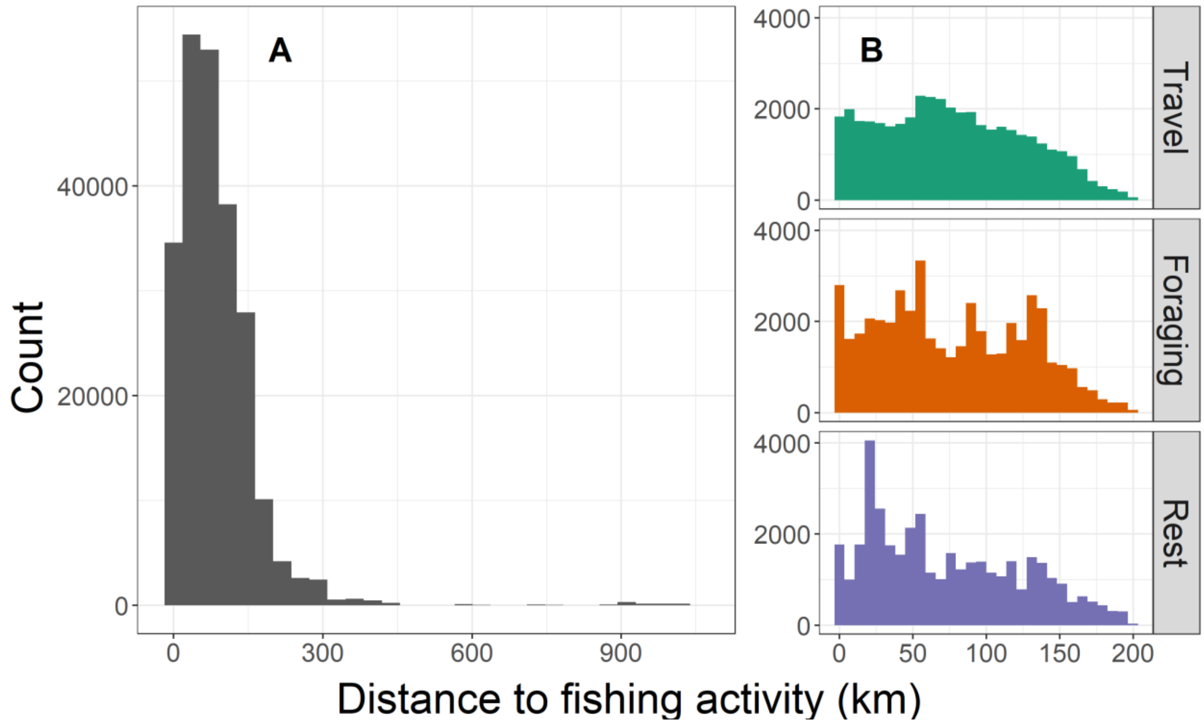

Figure 3: Histograms of distance to nearest static net fishing activity for all interpolated grey seal positions (A) and only positions included in the HMM analysis, coloured by behavioural states assigned using the Viterbi algorithm based on the BIC-favoured model (B).

According to the BIC-selected model, which included only distance to net as a covariate effect on state transition probabilities, seals were more likely to switch from inferred traveling to foraging states when they were close to fishing nets. This effect size was greatest within 1km and diminished with increasing distance to net (figure 5). In the AIC-selected model, a similar pattern was evident for female seals in the Atlantic and both males and females in the North Sea regions, with the likelihood of switching to foraging increasing closer to fishing nets. There were no clear differences in state transition probabilities for male seals in the Atlantic or male and female seals in the Irish and Celtic Seas (figure 6).

Using a computer with a 2.3 GHz Intel i5 processor and 8.00 GB of RAM, total computation time to fit the six HMMs with the AIC-selected model structure at each distance threshold was 13 hours and 10 minutes compared to 1 hour and 43 minutes to fit the equivalent six models with the BIC-selected model structure.

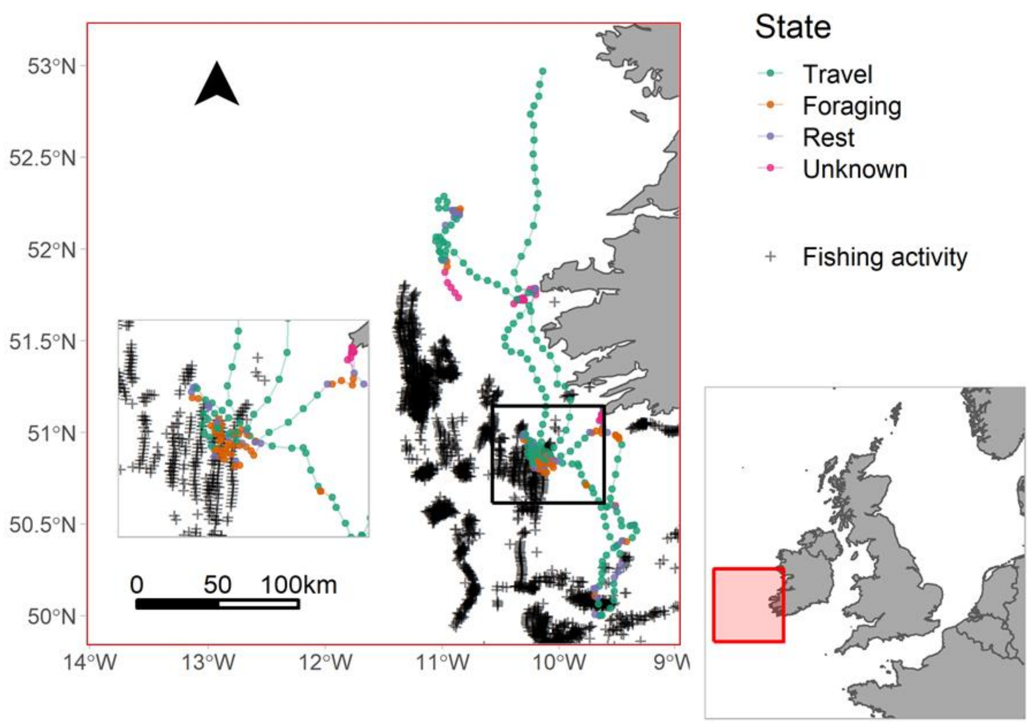

Figure 4: Movement track of a grey seal tagged in the west of Ireland, over a 27-day period and likely locations of static net fishing activity during that time. Behavioural states were predicted from the AIC-selected model using the Viterbi algorithm.

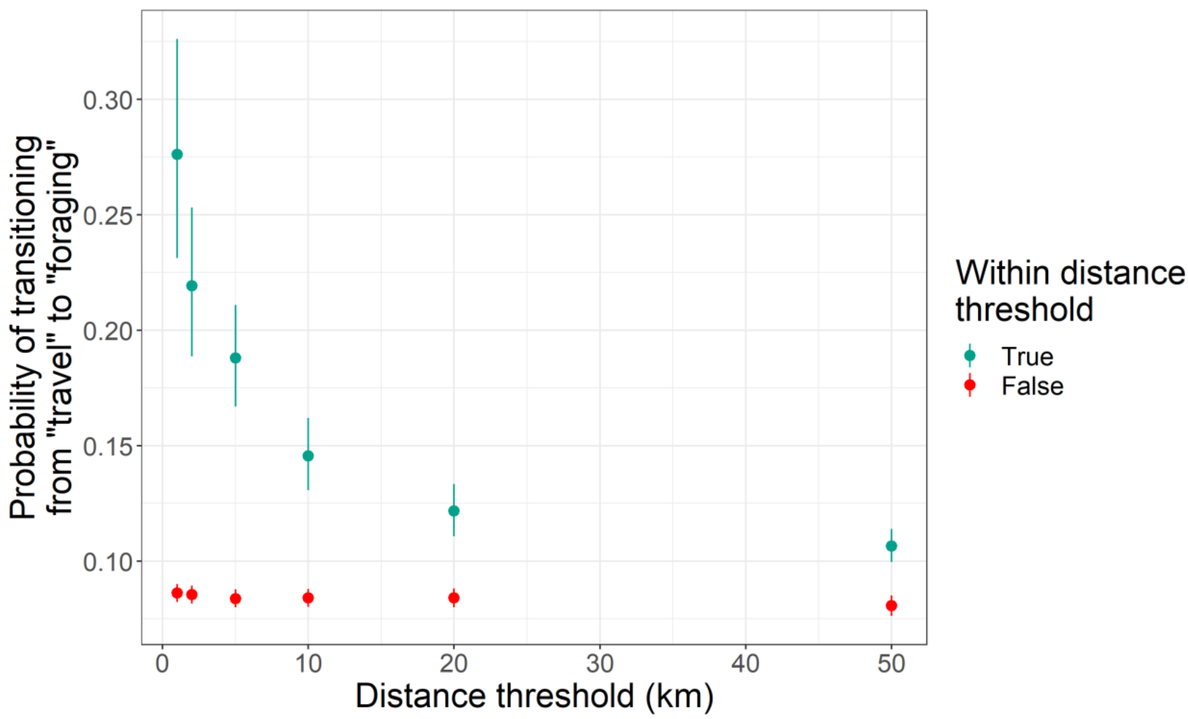

Figure 5: The probabilities of seals transitioning from "travel" to "foraging" behaviour within and beyond a given distance (1km, 2km, 5km, 10km, 20km, 50km), based on models including distance to fishing activity as the only covariate effect on transition probabilities.

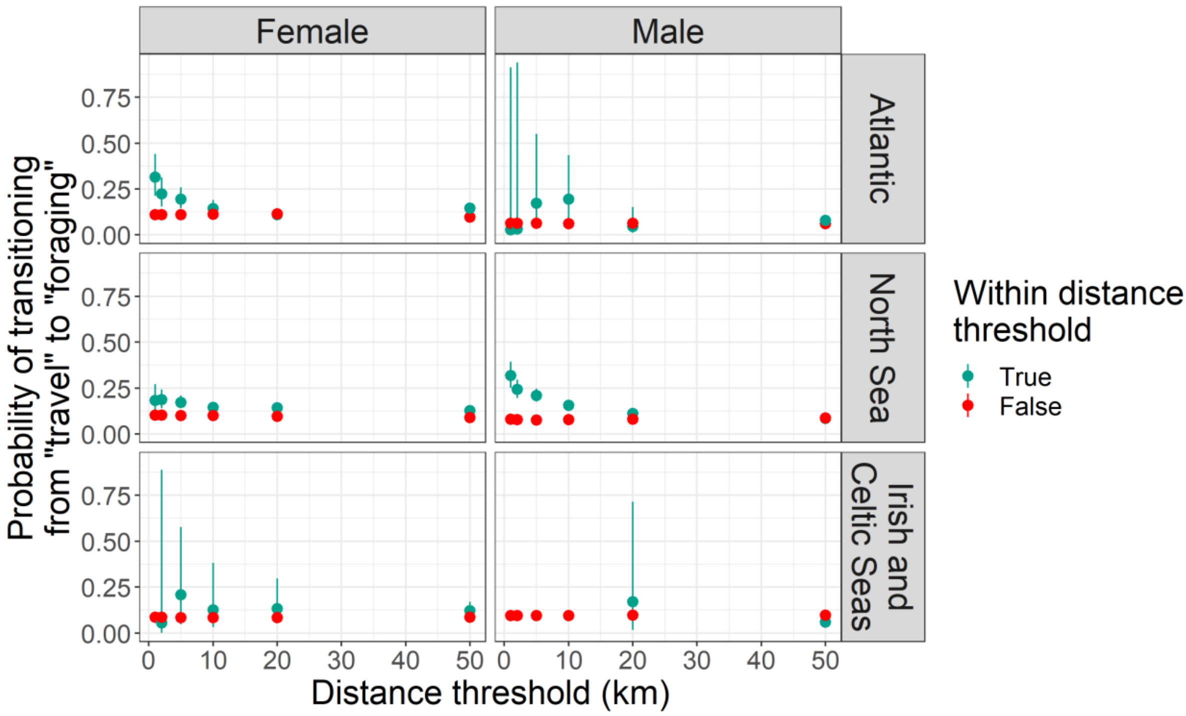

Figure 6: The probabilities of seals transitioning from "travel" to "foraging" behaviour within and beyond a given distance (1km, 2km, 5km, 10km, 20km, 50km), based on models including a three-way interaction effect between distance to fishing activity, sex, and region as covariate effects on transition probabilities.

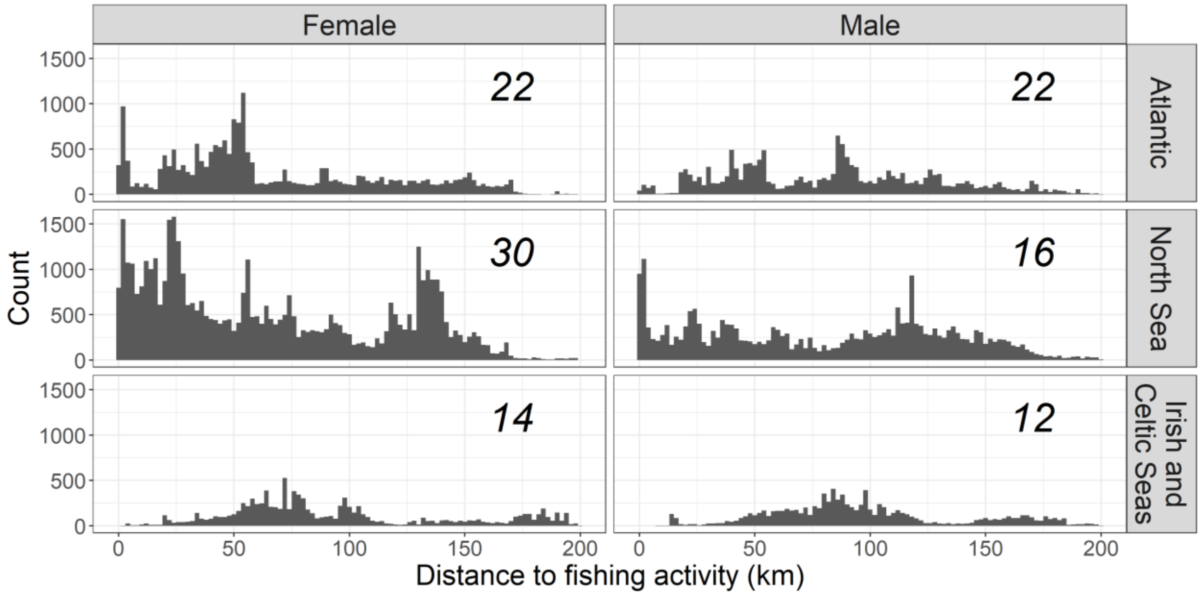

Figure 7: Histograms of distance to nearest static net fishing activity (limited to 200km) data, per sex and region, included in HMMs. Italicised numbers indicate the number of individual seals included in each dataset.

4.5 Discussion

4.5.1 Seal foraging and static net activity

Based on the available data and model outputs, there was a clear relationship between the probability of grey seals switching from travel to foraging behaviour and proximity to concurrent static net fishing activity. While the BIC-selected model suggests that grey seals are more likely to forage close to static nets, the AIC-selected model shows that this may vary with sex and region.

Firstly, it is important to clarify that while these results suggest a relationship between grey seal foraging behaviour and fishing activity, they do not necessarily suggest causation. Seabirds are known to associate with fishing vessels and exhibit clear behavioural responses to vessels (Votier et al. 2010; Tew Kai et al. 2013; Bodey et al. 2014). Bodey et al. (2014) found that Northern gannets (*Morus bassanus*) could respond to fishing vessels up to 11km away, and were more likely to transition to foraging behaviour closer to the vessel. This behaviour was further influenced by the vessel type and activity, suggesting that gannets were responding to increased availability of discards or lost catch during hauling or processing, and the attraction may have been enhanced by the presence of other gannets. Seals on the other hand may be attracted by fishing activity from a distance (Hamer & Goldsworthy 2006; Lyle et al. 2016), but they are unlikely to detect a static net during the soak period, when there may be no fishing vessel nearby to provide a foraging cue (Martin & Crawford 2015; Chapter 2). Therefore, I suggest that the observed changes in foraging behaviour in relation to fishing activity may represent a behavioural response to the presence of fishing nets or more simply that seals and fisheries have targeted similar prey assemblages or areas for foraging and fishing.

Adult grey seals are sexually dimorphic and exhibit sex-specific differences in diet (Beck et al. 2007), dive behaviour (Beck et al. 2003), activity budgets (Russell et al. 2015), and early-life ontogeny (Carter et al. 2017, 2020). Male grey seals typically forage further from shore and dive to deeper depths than females, which on average dive more frequently, to shallower depths, and closer to shore (Beck et al. 2003; Breed et al. 2009). This is possibly driven by sexual dimorphism and differential energetic demands of reproduction (Beck et al. 2003; Kelso et al. 2012). These contrasting foraging strategies may result in male and female grey seals encountering static nets at different rates in different locations, depending on the distribution of fishing effort within their foraging range. Carter et al. (2020) analysed the at-sea movements of grey seal pups in two geographically distinct regions and similarly found region and sex to have an interacting effect on behaviour, suggesting that local environmental conditions may influence sex-specific foraging strategies. Indeed a range of environmental covariates including bathymetry, sea surface temperature, salinity, and bottom sediment type have been shown to affect foraging behaviour and diet in grey seals (Jessopp et al. 2013; Gosch et al. 2019; van Beest et al. 2019), which may lead to region-specific foraging strategies and rates of fishery interaction. Therefore, the probability of seal foraging and fishing activity co-occurring is likely influenced by both intrinsic (sex) and extrinsic (distribution of local fishing effort) factors and may explain the observed sex and region effects on state transition probabilities in this study.

Previous studies of overlap between grey seals and fisheries in Western Europe have highlighted varying degrees of interaction. Cronin et al. (2012) found that female seals foraging in southwest Ireland did not significantly overlap with active fishing gears which were the predominant gear-type used at the time. However, a later study found significant overlap between seals and passive fishing gears in the Irish and Celtic Seas (Cronin et al. 2016). In the Iroise Sea, northwest France, tagged grey seals overlapped with fisheries to the greatest extent close to the colony at which they were tagged (Vincent et al. 2016).

Readers are cautioned against over-interpretation of regional differences in the co-occurrence of seal foraging and fishing activity. The regions defined in this study are broad with varying degrees of habitat heterogeneity, and though the sex ratio of tagged animals was approximately even within each region, with the exception of the North Sea (figure 7), this was not true of each set of tag deployments. Male seals tagged in the Atlantic region, and male and female seals tagged in the Irish and Celtic Seas did not generally come as close to static net fishing activity or as often as other sex-region groups (figure 7), which likely affected the models' ability to detect a covariate effect of distance to net on foraging behaviour. Thus, though the model failed to detect a relationship between seal foraging and fishing activity within these sex-region groups, this does not necessarily suggest that the likelihood of interaction is low or that sub-areas within each region do not experience high levels of seal-fishery overlap. For example, high levels of interaction between seals and static net fisheries have been observed in inshore waters along the west and south coast of Ireland (Cosgrove et al. 2015, 2016; Chapter 2), and around the southwest of England (Northridge et al. 2017b).

Finally, we consider the potential significance of the co-occurrence of foraging and fishing activity for depredation and seal bycatch. Grey seals are generalist feeders, consuming a wide variety of prey (Ridoux et al. 2007; Beck et al. 2007; Gosch et al. 2019). Grey seals forage predominantly at or near the benthos and foraging generally involves spending increased time at the seafloor (McConnell et al. 1999; Austin et al. 2006; Jessopp et al. 2013). Presumably, this increases the likelihood of seals encountering a bottom-set net. Furthermore, foraging behaviour involves more tortuous, exploratory movement, and increased time spent in an area (Carter et al. 2016; Bennison et al. 2017; Planque et al. 2020), increasing the likelihood of encountering nearby nets. In the Baltic Sea, individual seals have been observed repeatedly depredating from fishing gear (Königson et al. 2013; Kauhala et al. 2015), although this degree of specialisation has not been observed in Western Europe (Northridge et al. 2013). This suggests that the rate of depredation may be affected by the behaviour of individual seals in addition to encounter rates between seals and nets. In chapter 2, results showed that the rate of seal bycatch observed on static net fishing vessels increased closer to major grey seal colonies, suggesting that higher encounter rates between seals and nets led to higher rates of bycatch. Additional factors known to affect seal bycatch rates include net mesh size, target species, depth in certain regions, and water turbidity (Cosgrove et al. 2016; Northridge et al. 2017a; Chapter 2). Martin & Crawford (2015) applied a sensory ecology perspective to literature on protected species bycatch and surmised that animals became entangled when they failed to detect a net, suggesting that the rate of seal bycatch may be a product of the encounter rates between seals and nets and the net's detectability in the environment.

4.5.2 Data limitations

While recent developments in satellite technologies have made data on the at-sea distribution of fishing activity increasingly available (Rô Me Guietid et al. 2019; Park et al. 2020), certain key information are still lacking. The vessel location data used in this study was derived from AIS data. In Europe, AIS is mandatory on fishing vessels larger than 15m, although smaller vessels may opt to use it as a safety measure. A similar Vessel Monitoring System is mandatory on all European fishing vessels larger than 12m, providing finer-resolution locations of fishing vessels. However, these data are considered commercially sensitive, and are generally less available to researchers studying fisheries that cross national jurisdictions. What both technologies fail to capture is the distribution of small-scale inshore fishing vessels. This is a critical data gap, as smaller vessels are typically restricted to inshore waters, with potentially high levels of depredation and bycatch, even in excess of larger fisheries (Peckham et al. 2007; Alfaro-Shigueto et al. 2011; Cronin et al. 2014). Considering that 18% and 24% of seal foraging intervals occurred within 5km and 10km of the coast respectively, it is likely that these results considerably underestimate the potential for interactions between seals and static net fisheries in inshore waters.

The tracking dataset used in this study comprised predominantly adult seals. While depredation is often carried out by adult grey seals (Königson et al. 2013; Kauhala et al. 2015), the risk of bycatch may be highest among pups and juveniles. Bjorge et al. (2002) tagged 3571 grey seal pups along the Norwegian coast over 23 years with mark-recapture tags, and based on 259 tag recoveries, found that bycatch in bottom-set nets accounted for 79% of recorded mortalities. Seals were most likely to become bycaught during the first three months post-birth, and the risk of bycatch remained high for the first eight to ten months (Bjorge et al. 2002). The authors suggest this may be a consequence of inexperience foraging near nets, or less well-developed diving responses relative to adult seals (Burns 1999; Bjorge et al. 2002). Future tracking studies targeting pups and juveniles would allow us to explore how fishery interactions might vary with age, using generalised HMMs to account for changes in movement behaviour of developing pups (Carter et al. 2020). Understanding the bycatch risk of grey seals throughout their life history is important for understanding the potential impact of bycatch on population viability, as age and sex-specific mortality levels may have varying effects (Harwood & Prime 1978; Goldsworthy & Page 2007).

4.5.3 Methodological considerations

HMMs are increasingly used in ecology to infer behaviour from patterns in animal movement (Carter et al. 2016; Bennison et al. 2017; Patterson et al. 2017). When considering such inferences, it is important to remember that this is a data-driven analysis. The states identified by the model are but a proxy for the underlying behaviours and should be interpreted with caution (Leos-Barajas et al. 2017). It is equally important that models be carefully constructed *a priori* to maintain biological realism. Therefore, we must carefully consider if the temporal resolution of movement will allow us to identify discrete behaviours, how best to account for individual or group-level variation, and balancing biological realism against model complexity and computation time (Pohle et al. 2017). Firstly, HMMs require locations to be at regular time-intervals. For many animal movement datasets (especially marine animals which surface intermittently), location data are irregularly spaced in time due to patchy location acquisition opportunities. In this case, locations must be interpolated to a regular interval, and the temporal resolution of this interpolation can affect the model's ability to detect fine-scale behaviours (Pinaud 2008; Carter et al. 2016). The time interval of 2 hours was considered an appropriate temporal resolution for this analysis. Similar studies have inferred behaviours from grey seal movement data using 2 hour time intervals (Russell et al. 2015; Carter et al. 2017, 2020), and grey seal dive data suggests that they typically exhibit bouts of consistent behaviour for 3.4 ± 0.5 hours (Austin et al. 2006). Nonetheless, it is important to acknowledge that seals may occasionally exhibit multiple behaviours within a 2-hour interval, or forage during straight-line travel (Thompson et al. 1991; McConnell et al. 2002; Kuhn et al. 2009), which may not be detected by a HMM (Carter et al. 2016).

There is currently no consensus on how best to account for individual variation in HMM analysis. Some studies have included covariates as discrete random effects on state transition probabilities (DeRuiter et al. 2017; Isojunno et al. 2017). This comes, however, at great computational cost, requires a large sample size, and has little effect on state assignment (McClintock 2020). Instead, models accounted for group-level variation by including sex and region as covariate effects on state transition probabilities (known as 'partial pooling'; Zucchini et al. 2016). Regions were delineated over broad geographical scales to maintain a balanced sample size of male and female seals within each region. Exploring the environmental drivers of inter-regional variation was beyond the scope of this study but including such drivers as state-dependent parameters could potentially account for inter-regional variation as an alternative to including region as a covariate effect.

Adding additional covariate effects and behavioural states can improve biological realism but comes at a cost of increased model complexity and computation time (Pohle et al. 2017). While neither of the AIC or BIC-selected models required prohibitively long computation times, the more complex model included two additional covariates and a three-way interaction, requiring the estimation of 60 additional regression coefficients for covariate effects on transition probabilities and a more than 700% increase in computation time. The information-criterion approach to multi-modal inference recognises that, given the limitations of the data available, there may not be one model that best fits the data, but multiple models that are similarly close to the *true* model and offer comparable explanatory power (Burnham et al. 1998, 2011). For this reason, it is not suggested that one of the two model structures selected by AIC or BIC are correct, but that distance to net was retained in both models suggests that there is a robust relationship between seal foraging and static net fishing activity.

4.5.4 Conclusion

Overall, this study demonstrates that seals are likely to forage close to static nets, and the degree of interaction is dependent on the sex of the seal, behavioural responses to local environmental conditions, and the distribution of fisheries in the area. Exploring the relationship between environmental covariates and the co-occurrence of seal foraging and fishing activity will allow us to better identify areas or seasons where seal-fishery interactions may be most prevalent. This will enable future policy makers to develop targeted mitigation strategies where necessary, ensure the conservation of a protected species, and facilitate an ecosystem-based approach to fisheries management.

4.6 Supplementary material

Table S1: The number of grey seals tagged per location throughout Ireland, the UK, and northern France between 2012 and 2019.

Year	Location	Seals (F/M)
2012	BDS, France	11 (0/11)
2012	Blaskets, Ireland	3 (0/3)
2012	MOL, France	2 (0/2)
2013	Abertay, UK	4 (2/2)
2013	MOL, France	6 (1/5)
2013	Tentsmuir, UK	1 (0/1)
2013	Wexford, Ireland	3 (0/3)
2014	Isle of May, UK	8 (4/4)
2014	Wexford, Ireland	9 (3/6)
2015	Blakeney, UK	10 (5/5)
2015	Donna Nook, UK	11 (8/3)
2015	Tentsmuir, UK	2 (2/0)
2016	Tentsmuir, UK	2 (1/1)
2017	Burray, UK	2 (2/0)
2017	Colonsay, UK	3 (1/2)
2017	Flotta, UK	1 (1/0)
2017	Monach Isles, UK	13 (6/7)
2017	Nave Island, UK	4 (4/0)
2017	Oronsay, UK	3 (2/1)
2017	River Dee, UK	11 (6/5)
2017	Stroma, UK	2 (0/2)
2018	Ardersier, UK	1 (1/0)
2018	Bardsey, UK	9 (6/3)
2018	Dornoch Firth, UK	8 (7/1)
2018	Findhorn, UK	1 (0/1)
2018	Stroma, UK	5 (2/3)

2019	Colonsay, UK	1 (0/1)
2019	Inishkeas, Ireland	8 (2/6)
2019	Monach Isles, UK	10 (5/5)
2019	Nave Island, UK	1 (1/0)
2019	Oronsay, UK	4 (3/1)
2019	Ramsey, UK	4 (2/2)
2019	Skomer, UK	1 (0/1)

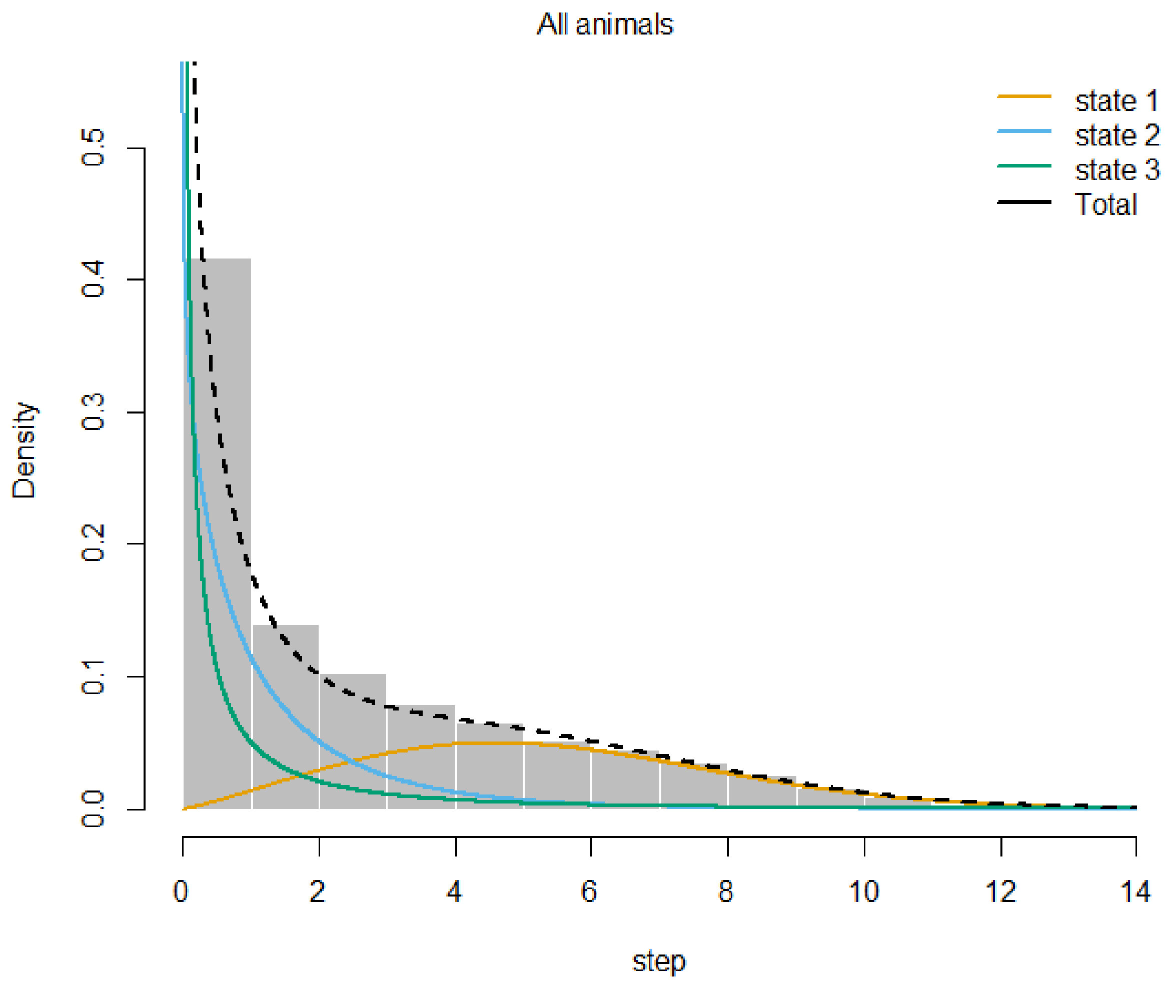

Figure S2: Step lengths overlaid with the state-dependent distributions as estimated by the BIC-selected model, including distance to fishing activity as the only covariate effect on state transition probabilities.

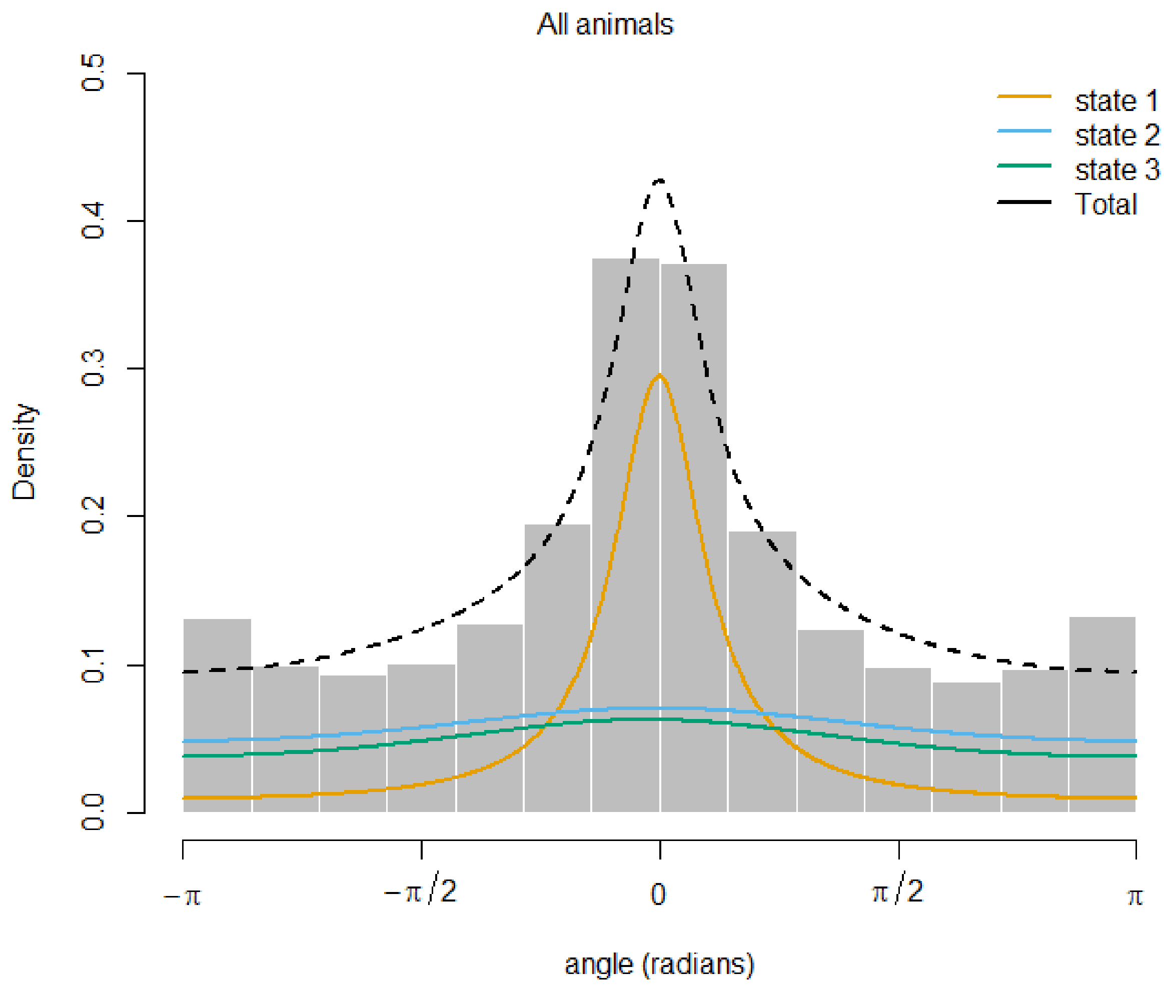

Figure S3: Turning angles overlaid with the state-dependent distributions as estimated by the BIC-selected model, including distance to fishing activity as the only covariate effect on state transition probabilities.

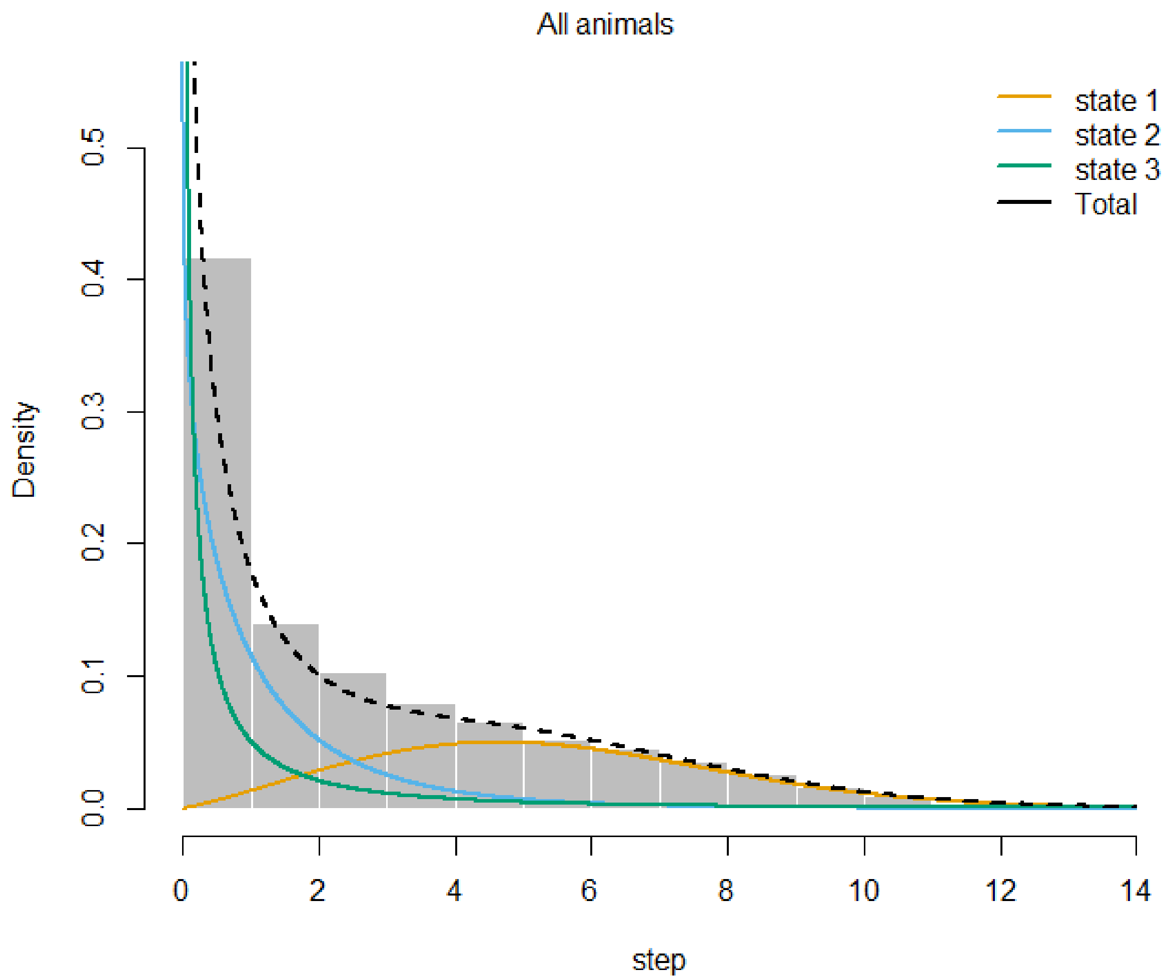

Figure S4: Step lengths overlaid with the state-dependent distributions as estimated by the AIC-selected model, including an interaction between distance to fishing activity, sex, and region as only covariate effects on state transition probabilities.

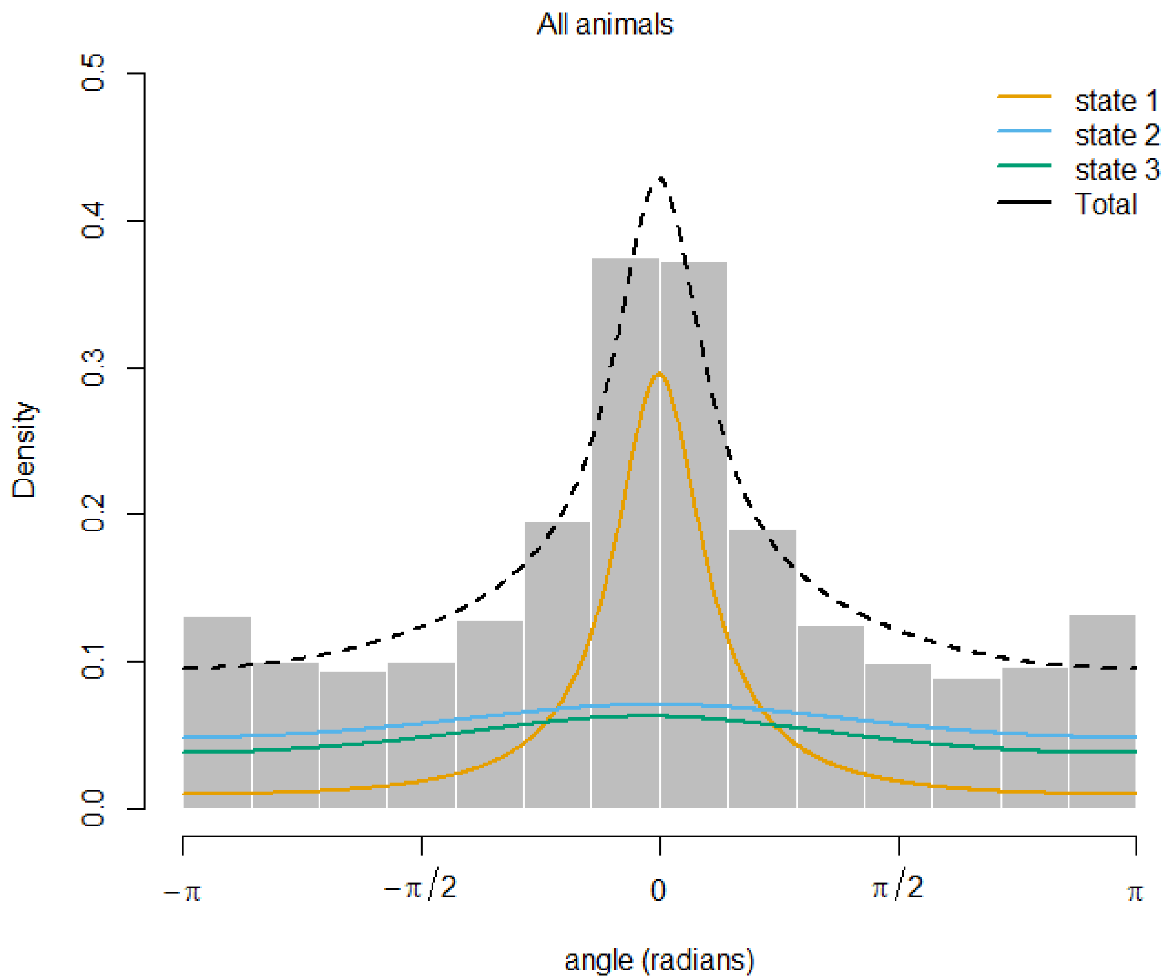

Figure S5: Turning angles overlaid with the state-dependent distributions as estimated by the AIC-selected model, including an interaction between distance to fishing activity, sex, and region as only covariate effects on state transition probabilities.

Chapter 5: Population viability analysis of grey seals (*Halichoerus grypus*) under a range of bycatch scenarios

Target journal for publication: Biological Conservation

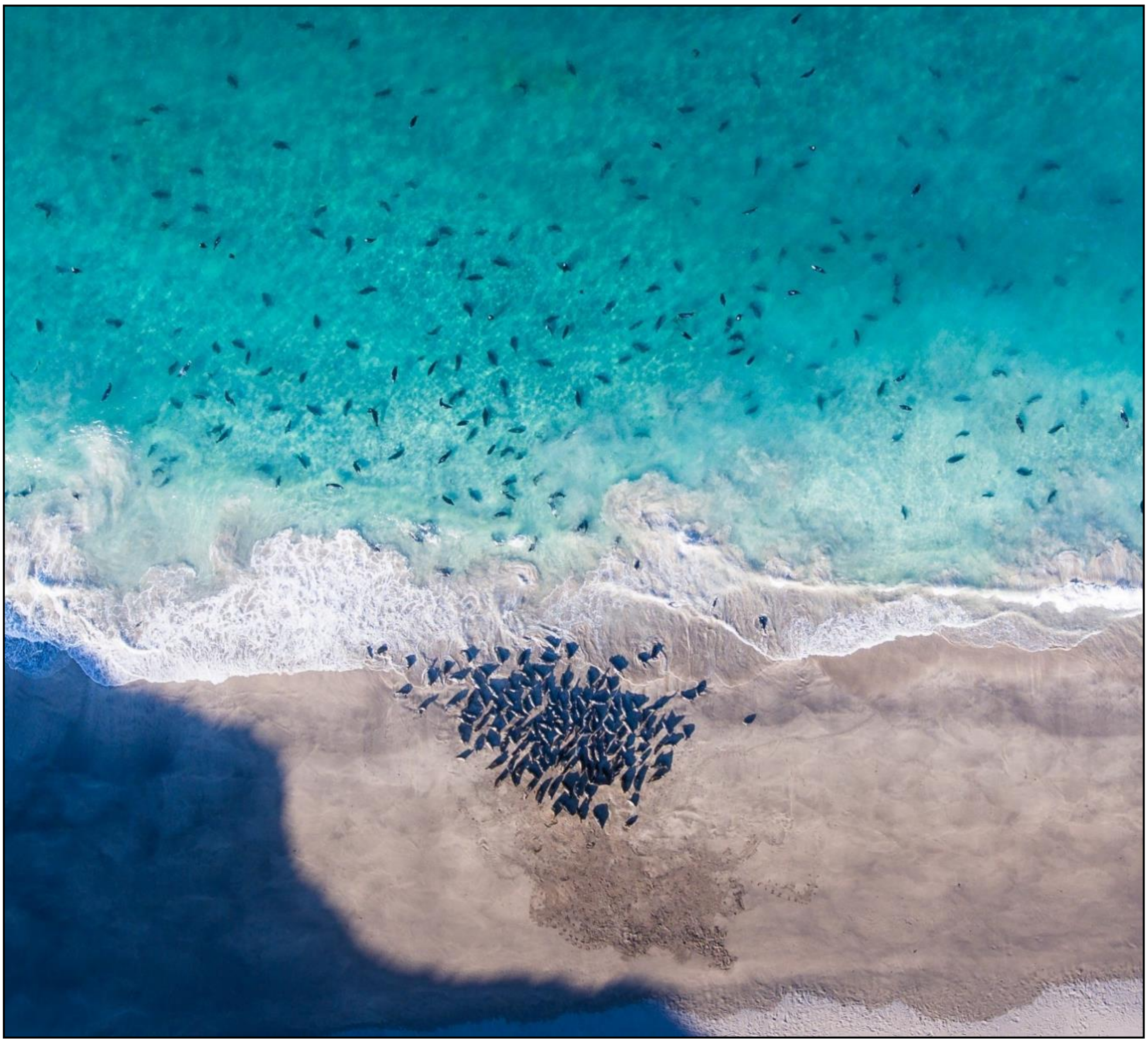

Image: Aerial photograph of grey seals at Blasket Islands, Co Kerry. Photo by Jolene Cronin.

5.1 Abstract

Recent studies have highlighted potentially unsustainable levels of bycatch of grey seals (*Halichoerus grypus*) in static net fisheries operating in Irish waters. Confidence intervals surrounding these bycatch estimates are wide; a reflection of uncertainties and gaps in the underlying data. Because of this uncertainty, a full range of plausible bycatch scenarios and the potential effects on viability of breeding population of grey seals should be considered. In this study Population Viability Analysis (PVA) was used to construct a range of plausible scenarios, exploring the full range of bycatch mortalities within the 90% confidence interval of recent bycatch estimates. Scenarios included exploring the effect of bycatch (i) assuming an even distribution of bycatch mortality across age and sex classes, independent of immigration of seals from outside of Ireland; (ii) assuming a distribution of bycatch mortality biased towards juvenile, male, or female seals; (iii) allowing immigration of seals from outside of the national population; and (iv) exploring colony-specific bycatch levels to assess relative vulnerability of the major grey seal breeding colonies to bycatch mortality. Under the different scenarios (i) higher levels of bycatch reduced population growth, and bycatch in excess of 700 seals per year lead to extirpation within 25 years; (ii) population viability was most sensitive to mortality of female seals, and more robust to juvenile or male mortality; (iii) recruitment of 400 seals per year allowed the national population to persist despite the worst-case bycatch scenario of 800 seals caught per year; (iv) colonies in the south and southwest were the first to show signs of decline under increasing bycatch pressure. These findings provide a clear justification for improved monitoring of seal bycatch to obtain more precise bycatch estimates, and highlight the need for future studies to delineate appropriate management units for grey seals in Western Europe, allowing for effective management of a wide-ranging protected species.

5.2 Introduction

Grey seals (*Halichoerus grypus*) are top marine predators, distributed across the North Atlantic with three recognised population centres in the Northwest and Northeast Atlantic and Baltic Sea. In Europe, grey seals are protected as an Annex II species under the EU Habitats Directive (92/43/EEC), which obliges member states to ensure populations are maintained at “favourable conservation status”. The Republic of Ireland is home to approximately 6% of the breeding population in Western Europe, while the UK is home to a much larger population including approximately 38% of grey seals worldwide (Russell et al. 2019). In Western Europe, pup production has generally increased over the past 20 years, leading to overall population growth (OSPAR Commission 2017; Russell et al. 2019). In Ireland, the most recent population surveys indicate that the grey seal breeding population grew from an all-age population of 5509-7083 seals in 2005 to 7284-9365 seals in 2012 (Ó Cadhla et al. 2007, 2013). Seals fitted with GPS tags in Irish, UK, and French colonies have regularly moved between the three countries, yet the degree to which breeding populations mix is unknown (Jones et al. 2015).

Recent studies have highlighted the risk of grey seals becoming entangled in static net fisheries (Cosgrove et al. 2016; Chapter 2-3), with potentially hundreds of seals caught in Irish waters each year (Chapter 3). Because of limited scientific observer programmes and data gaps in the distribution of fishing effort, confidence intervals around best estimates of annual seal bycatch are wide, ranging from near zero to beyond sustainable thresholds. Given the lack of certainty around the level of annual bycatch mortality, it is important to explore all plausible bycatch scenarios and the potential long-term impacts of each scenario on the Irish grey seal population.

Population Viability Analysis (PVA) provides a useful analytical tool for assessing the long-term viability of populations, the potential impact of anthropogenic threats at the population level, and the potential efficacy of management strategies (Reed et al. 2002; Radchuk et al. 2016; Chaudhary & Oli 2020). PVA is a broad term that encompasses many types of nuanced analysis, but generally uses simulation models to project population trajectories, simulating scenarios to explore the potential effects of conservation pressures and/or management strategies on population viability (Reed et al. 2002; Morris et al. 2002; Lacy 2019). In this study, a population-based model of the Irish grey seal population is constructed to explore the effects of bycatch mortality at the population level.

Firstly, I explore the full range of the confidence intervals around estimates of annual bycatch mortality, as calculated Chapter 3, independent of immigration of seals from outside of Ireland. Secondly, I test how higher levels of bycatch amongst juvenile, female, or male seals might alter the effect of bycatch on population viability. While grey seals exhibit a high degree of breeding-site fidelity once recruited into a breeding population (Pomeroy et al. 2000; Langley et al. 2020), there is evidence for some degree of migration between populations, especially from larger populations within the UK to smaller populations within the UK and mainland Europe (Brasseur et al. 2015; Thomas et al. 2019). I examine the potential effect of immigration of seals from outside of Ireland in mitigating the effect of bycatch mortality in the Irish population. Lastly, there is still a need to delineate appropriate assessment units for management of grey seals in Western Europe (OSPAR Commission 2017). Without this key information, there remains a risk if management actions are taken at too large a scale that overall population growth may mask local extinctions (Taylor 1997; Curtis et al. 2015). In this scenario, the Irish population is treated as a meta-population comprised of individual colonies, and colony-specific bycatch levels are estimated based on colony size and the estimated bycatch levels in adjacent waters (Chapter 3), to explore which colonies may be more susceptible to decline caused by bycatch mortality.

5.3 Methodology

5.3.1 Baseline demographics

A baseline population-based model of the grey seal breeding population within the Republic of Ireland, was constructed using the software *Vortex* (version 10.0.7.9; Lacy & Pollak 2017). *Vortex* allows for the simulation of deterministic and stochastic effects on wildlife populations. Each scenario was simulated 1000 times, over 100 years, with a one-year time step, to explore long-term population trends and allow for multi-generational effects to be observed. Population extinction was defined as occurring when only one sex remained. Table 1 outlines the input demographic parameters used to construct the baseline model. Multiple subsequent scenarios were constructed to explore the range of potential effects of bycatch mortality on the viability of the Irish grey seal population.

Table 1: Demographic parameters used in baseline grey seal population model.

Parameter	Value	Reference
Inbreeding depression – lethal equivalent	6.29	Default value – O'Grady et al. 2006
Reproductive system	Polygynous	
Age of first offspring – females (years)	6	Harwood and Prime 1978
Age of first offspring – males (years)	10	Harwood and Prime 1978
Maximum lifespan (years)	46	Bonner 1971
Proportion of adult females breeding (SD due to environmental variation)	0.90 (0.06)	Thomas et al. 2019
Age-specific mortality		
- Age 0-1	0.52	Thomas et al. 2019
- Age 1+	0.09	Thomas et al. 2019
Initial population size (*N*)	7200	O'Cadhla et al. 2013
Carrying capacity (*K*)	Unknown. Assumed K ~ 2N	NA

5.3.2 Bycatch mortality

Bycatch mortality was incorporated into the baseline scenario as a fixed number of seals removed from the population each year. The number of seals removed was constant between years and divided evenly between all age and sex classes. Chapter 3 provided estimates of annual bycatch of grey seals in Irish waters between 2011 and 2016. The highest of these bycatch estimates occurred in 2011, with an estimate of 349 seals and a 90% confidence interval ranging from 6 to 833 seals. Based on this, multiple simulations were run with annual bycatch ranging from 0 to 800 in increments of 100.

5.3.3 Bias in bycatch mortality

Additional scenarios included the same range of total bycatch mortality, while exploring the effect of a skewed distribution of mortality across age and sex classes. Some studies have suggested that pups and juvenile grey seals are more susceptible to bycatch than adults (Burns 1999; Bjorge et al. 2002). To test the effect of higher bycatch mortality among pups and juveniles the rate of bycatch with age was assumed to follow a simulated negative binomial distribution, so that pups experienced the highest rate of bycatch (figure S1).

Observations of bycatch on-board static net fishing vessels in Irish waters have suggested a potential bias towards males over females, as approximately 50% more males were recorded as bycatch than females (Cosgrove et al. 2016; Chapter 2). A scenario was therefore constructed in which total bycatch of males was 1.5 times that of females. Alternatively, female grey seals typically forage closer to shore than males (Beck et al. 2003; Breed et al. 2009) where they may potentially interact with inshore static net fisheries. Currently, fishing vessels smaller than 12m in length are not mandated to carry Vessel Monitoring System (VMS) or Automatic Identification System (AIS) technology. As a result, our knowledge of the distribution of <12m fishing vessel activity is extremely limited. Considering this data gap, and the potential for female seals to encounter inshore fishing vessels more frequently than males, an additional scenario was constructed in which total bycatch of females was 1.5 times that of males.

5.3.4 Immigration from outside Ireland

To understand how immigration of seals from outside of Ireland might offset the effect of bycatch mortality, multiple simulations were run including varying levels of bycatch and immigration from outside of the Irish population. Again, bycatch ranged from 0 to 800 seals per year (evenly distributed between sex and age classes), and immigration ranged from 0 to 400 seals per year. Adult seals show strong breeding site fidelity once recruited into a breeding population, and dispersal between colonies is most likely to occur when young seals recruit into a breeding population (Pomeroy et al. 2000; Thomas et al. 2005; Langley et al. 2020). In these simulations immigrating seals included only pups and juveniles younger than the age of first breeding and an even proportion of males and females.

Table 2: Colony size, and proportion of total bycatch mortality at each colony. The proportion of the total population at each colony was increased or decreased, based on the results of chapter 3 of this thesis, to provide an approximation of the expected distribution of bycatch mortality across each colony.

Colony	Initial population size	Proportion of initial meta-population	Bycatch rate multiplier (based on Chapter 3)	Proportion of total annual bycatch per colony
Donegal	844	0.13	0.8	0.104
Inishkeas	1841	0.29	1.2	0.348
Inishgort	1456	0.23	0.8	0.184
Slyne	364	0.06	0.8	0.048
Blaskets	1099	0.17	1.2	0.204
Saltees	529	0.08	1	0.08
Lambay	270	0.04	0.8	0.032

5.3.5 Colony-specific bycatch effects

To explore the potential effect of bycatch mortality at the colony level, the national population was defined as a meta-population made up of seven major colonies within the Republic of Ireland. These colonies make up 84% of the national breeding population (O'Cadhla et al 2013). Carrying capacity was assumed to be double the present population at each colony, as surveys have been too infrequent to allow us to identify any colonies approaching carrying capacity. Colony-specific bycatch rates were approximated based on initial population size and total bycatch estimates from adjacent waters (table 2; Chapter 3). Scenarios allowed for density-dependent inter-colony dispersal, so that if a given colony was at carrying capacity, 5% of seals (males and females of pre-breeding age) dispersed to the next adjacent colony each year, in both directions along the coast of Ireland, with the exception of Donegal and Lambay colonies which dispersed to only one colony each, because of their relative isolation from the other colonies. In these scenarios total bycatch was set as an initial value that was distributed each year amongst all seven colonies and the number of seals to be removed from each colony remained constant between years. In this way, if one colony was so reduced that the number of seals became less than the specified number of seals to be removed as bycatch, or if a colony became extinct, the remainder of the total bycatch was not redistributed between the other colonies.

5.4 Results

5.4.1 Effect of bycatch on baseline model

The baseline model, with zero bycatch mortality, resulted in continuous population growth with population size reaching 99% of *K* after 11 years (figure 1). As the number of seals bycaught annually increased, so too did the time to reach *K*. With annual bycatch of 400 seals, the population grew to 99% of *K* after 37 years. With bycatch of 500 seals per year, the population failed to reach *K* but plateaued at approximately 10,000 seals. Annual bycatch of 600 seals resulted in an extremely depleted population of less than 200 and bycatch in excess of 600 seals per year resulted in extirpation in as few as 23 years (Figures 1). The probability of the population still being extant after 100 years was 1.0 with the annual number of seals removed between 0 and 400. At 500 seals bycaught per year the probability of remaining extant began to decline and at 700-800 seals per year extirpation at 100 years was a certainty in these simulations (figure 2).

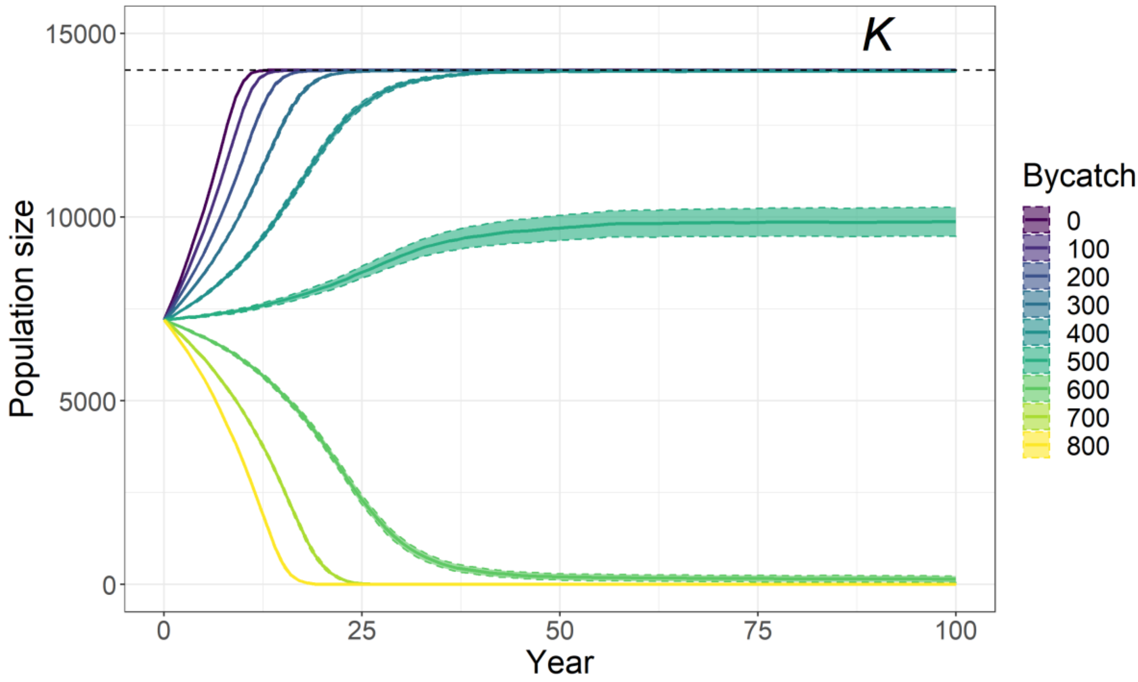

Figure 1: Simulated population trends of the national grey seal population over 100 years, including varying levels of annual bycatch mortality. Solid lines represent mean values across 1000 iterations and shaded areas represent 95% confidence intervals around mean values.

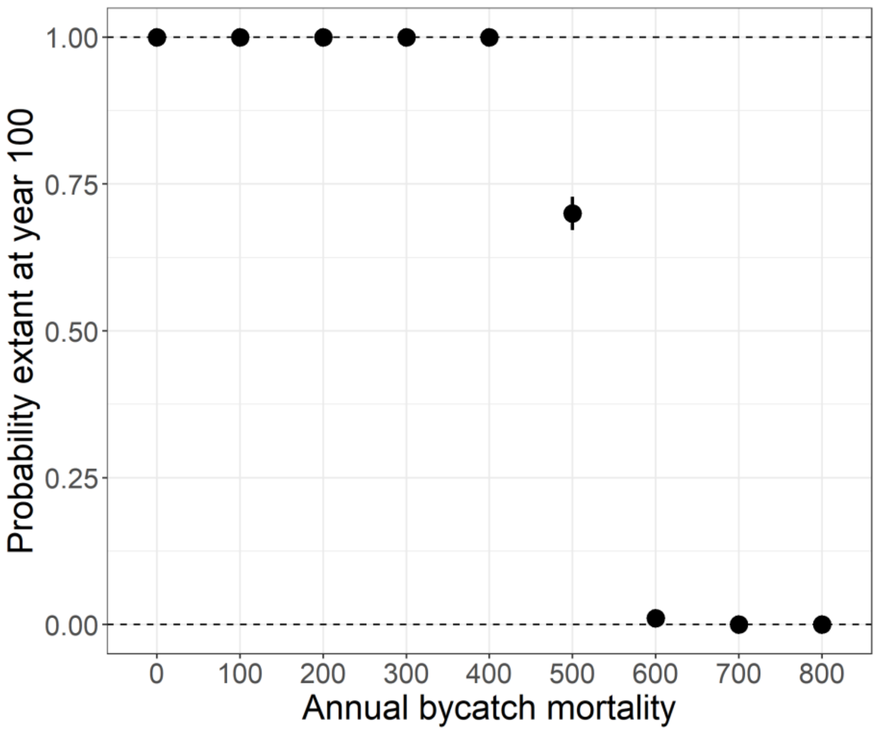

Figure 2: The probability of the national population being extant after 100 years of annual bycatch mortality, independent of immigration.

5.4.2 Distribution of bycatch mortality among sex-age classes

At all levels of bycatch mortality, increased juvenile and male bycatch lessened the impact of bycatch on population growth, whereas increased bycatch of female seals led to accelerated population decline. For example, with annual bycatch fixed at 600 seals per year, an even distribution of bycatch mortality between all sex and age groups resulted in a severely depleted but extant population after 100 years. Where bycatch was highest among pups and juveniles, the rate of population decrease was lower resulting in a slightly less diminished population after 100 years (figure 3). Increasing the number of females bycaught to 1.5 times that of males resulted in a higher rate of population decline and extinction after 26 years (figure 3). An equivalent bias towards bycatch of male seals allowed for population growth which plateaued at approximately 10,000 seals (figure 3).

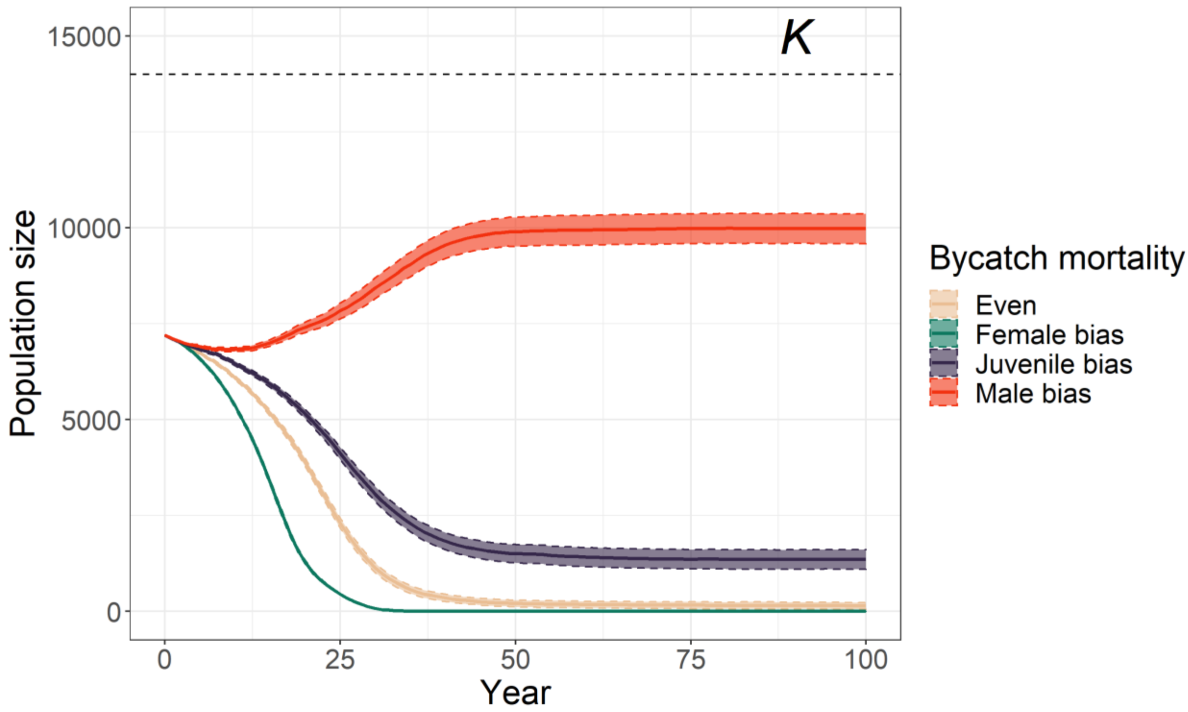

Figure 3: Simulated trends of the national population with annual bycatch mortality of 600 seals simulated over 100 years. Scenarios include an even distribution of bycatch mortality among age and sex classes (“Even”), scenarios in which the rate of bycatch is 1.5 times as high for females (“Female bias”) or males (“Male bias”), and a scenario in which the bycatch rates decrease with age (“Juvenile bias”). Solid lines

represent mean values across 1000 iterations and shaded areas represent 95% confidence intervals around mean values. *K* represents the assumed carrying capacity of the national population.

5.4.3 Immigration from outside of national population

Immigration of seals generally increased the probability of the national population being extant after 100 years, and net immigration of 400 seals per year (approximately 0.3% of the UK population) allowed for population persistence at all simulated levels of bycatch mortality (figure 5).

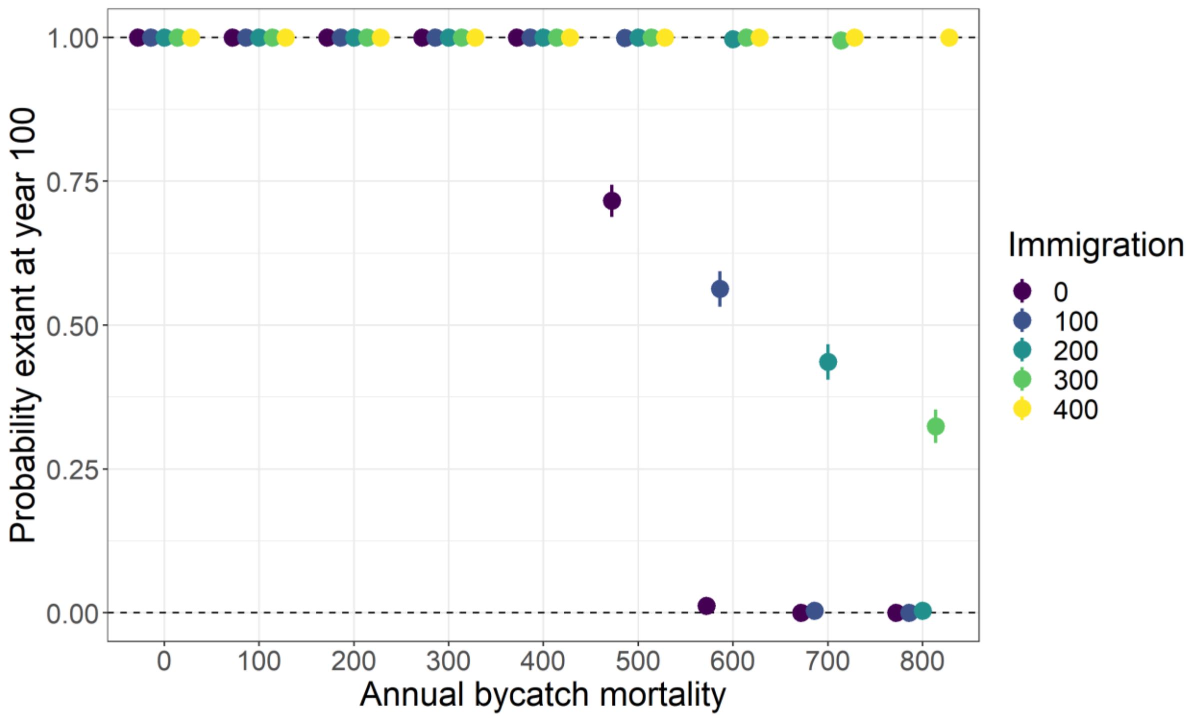

Figure 4: The probability of the national population being extant after 100 years of annual bycatch mortality, offset by immigration of 0 to 400 seals from outside of Ireland.

5.4.4 Colony-specific bycatch mortality

At the colony level, increasing levels of annual bycatch mortality resulted in lower growth rates, and when bycatch reached 400 seals per year, the colony at the Blasket Islands showed a markedly greater decrease in growth than other colonies. With bycatch of 500 seals per year, 5 out of 7 colonies showed severe declines, and at 600 seals per year, these 5 colonies were extirpated within 25 years. With bycatch of 800 seals per year, the colonies at Donegal and Lambay Island were still extant after 100 years, although the colony at Donegal had declined by approximately half (figure 5).

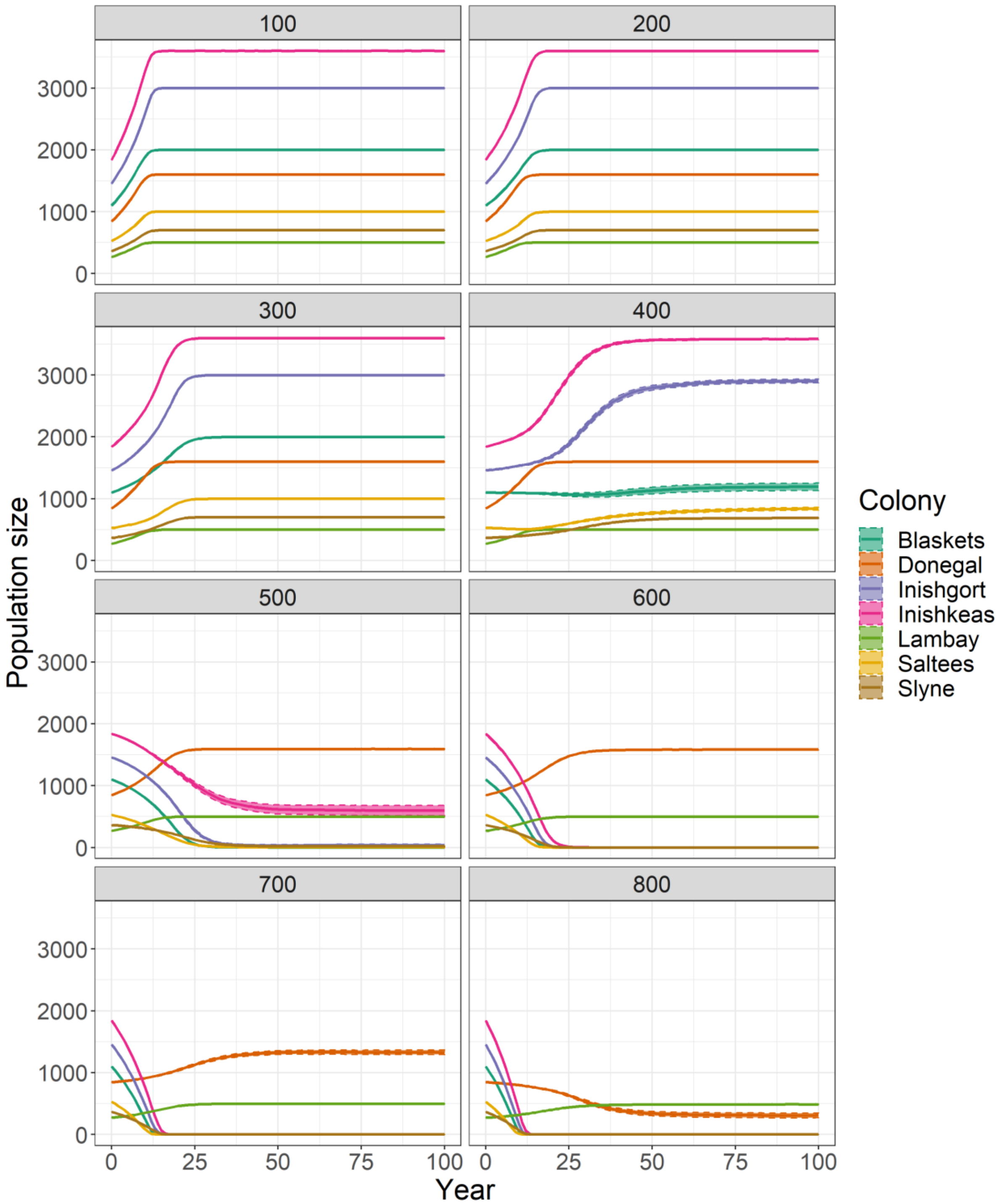

Figure 5: Simulated population trends at each of the major grey seal colonies simulated over 100 years with annual bycatch mortality (in grey) ranging from 100 to 800 seals per year. Colony-specific bycatch rates were estimated based on Chapters

2-3. Solid lines represent mean values across 1000 iterations and shaded areas represent 95% confidence intervals around mean values.

5.5 Discussion

5.5.1 Impact of bycatch on grey seal population

Quantifying the effect of fisheries bycatch on a protected species' population is often challenging because of wide confidence intervals surrounding bycatch estimates, reflecting gaps and uncertainties in the underlying data. Notwithstanding such limitations, these results demonstrate that within the plausible range of annual bycatch mortalities for grey seals breeding in Ireland, there are a number of potential scenarios which could place significant pressure on the national grey seal population.

Results from chapter 3 provided the first estimates of annual grey seal bycatch in Irish waters. In this study, estimates were compared to a sustainable threshold value calculated as Potential Biological Removal (PBR), which is designed to allow a population to maintain at least half of the estimated maximum population size, given no human-caused mortality (Wade 1998; Taylor et al. 2000). PBR is calculated as the product of the minimum population estimate ($N_{min} = 7284$), half of the maximum growth rate (0.12 is the default value for pinnipeds), and a recovery statistic (F_r) which ranges from 0.1 to 1.0, depending on the conservation status of the population, the degree of certainty surrounding the conservation status, and the management goals for the population. In chapter 3, I compared bycatch estimates to the full range of PBR values, with F_r ranging from 0.1 to 1.0, and found that estimates fell between the default (218 seals per year; $F_r = 0.5$) and least conservative values for PBR (437 seals per year; $F_r = 1.0$). In this case, keeping bycatch within even the least conservative levels of PBR would indeed allow the population to reach more than half of carrying capacity within 100 years, however, at the upper limit of PBR, the growth rate is much reduced. Importantly, the scenarios presented here ignore uncertainty in the underlying data that lower values of F_r allow for (Wade 1998; Punt et al. 2018, 2020). Punt et al. (2020) demonstrated that the precision of abundance estimates had a strong effect on conservation performance of PBR management, especially for pinniped species, and given that only two extensive surveys of grey seal breeding population have been carried out in the past 20 years, the default value of F_r (0.5) remains the most appropriate value in calculating PBR for the grey seal population.

These results demonstrate that within the 90% confidence interval of bycatch estimates, presented in chapter 3, are mortality levels that would drive the population to extinction, without immigration of sub-adult seals from populations outside of Ireland. This highlights the importance of increased monitoring effort of seal bycatch to calculate more refined estimates of total bycatch, with narrower confidence intervals. Otherwise, as long as bycatch estimates include potentially unsustainable levels of mortality, a precautionary approach to fisheries management requires us to account for this possibility in management decision-making (Garcia 1994; Gonzaíez-Laxe 2005).

Similar to Brandon et al. (2017), results suggested that the grey seal population was more robust to bycatch when mortality was biased towards males or juveniles, and more vulnerable when biased towards females. This trend has been recognised before, for example, catch limits defined by the International Whaling Commission are reduced if females are more susceptible to capture than males (IWC 2012), and Brandon et al. (2017) suggested that default PBR thresholds were overly conservative when bycatch disproportionately affected males. Considering this, future monitoring strategies would benefit from training observers to identify the sex of bycaught seals and maximising the use of dedicated bycatch observers. As demonstrated in this study, a bias towards male or female bycatch has a much stronger potential impact on population viability than age-based bias in mortality (Brandon et al. 2017).

The potential effect of immigration of seals from UK colonies in mitigating the effect of bycatch mortality highlights the need for trans-boundary management of this wide-ranging species. There is little understanding of the degree of connectivity between grey seal colonies in Ireland, the UK, and France, but evidence suggests that some recruitment of seals born in other colonies does occur. Gaggiotti et al. (2002) found evidence of density-dependent dispersal between grey seal colonies in the Orkneys, UK, with those for which pup production had reached an asymptote contributing more recruits to newly established colonies. Furthermore, substantial inter-colony dispersal would be required to explain trends in local pup production at some UK colonies (Russell et al. 2019). Brasseur et al. (2015) constructed a Bayesian demographic model to identify the parameters driving the growth of the Dutch grey seal population and concluded that immigration of sub-adult seals, most likely from the UK, could account for approximately 35% of population growth. In the southwest of the UK, annual bycatch estimates have regularly exceeded PBR for the region, but local colonies have continued to grow (Northridge et al. 2017b). The most likely explanation is either that bycatch in Irish waters includes seals that breed elsewhere or that mortality of seals breeding in Ireland is being offset by movement of seals from larger colonies in the UK, particularly in Scotland. In the UK, the majority of colonies grew continuously from the beginning of regular surveys in 1984 until the mid-1990s, when pup production and population growth began to slow (Thomas et al. 2019; Russell et al. 2019). Now, colonies in the North Sea region continue to grow, while those in the Inner Hebrides, Outer Hebrides, and Orkney regions appear to have reached carrying capacity (Thomas et al. 2019). It is possible that in reaching carrying capacity, density dependence at these colonies has led to dispersal of recruiting seals to other colonies, and conversely, declines in these populations may result in lower dispersal rates. In this way, the status of Irish grey seal colonies may be intrinsically linked to the status of colonies in the UK.

Outside of the breeding season, grey seals may range widely, moving between coastal waters and distinct foraging areas offshore, with some movement between colonies and countries (Jones et al. 2015). Consequently, the total number of seals caught in Irish waters, likely includes a combination of seals that breed at Irish colonies and seals that breed in the UK. Similarly, seals from Irish colonies may become bycaught in UK waters. This highlights the need for identifying appropriate management units for grey seals in Western Europe. For the successful conservation of any wide-ranging species, it is critical to identify demographically independent management units within a species range, and manage each unit independently (Taylor 1997; Curtis et al. 2015). If a management unit contains multiple discrete populations, then local depletions may be masked by overall population growth. Genetic analysis is the most reliable method for delineating populations (DeYoung &

Honeycutt 2005), however, to date this has not been applied to grey seals throughout Western Europe. Biotelemetry can provide some, albeit limited, information on population structure. Grey seals tagged in Ireland, the UK, and France have regularly moved between countries (Jessopp et al. 2013; Vincent et al. 2017; Carter et al. 2020), and one seal tagged in Ireland was observed breeding in Wales (unpublished data), providing no clear evidence of demographic isolation. In the absence of such information, the OSPAR Commission define an Assessment Unit for grey seals in Western Europe that extends from the Atlantic margin to the greater North Sea area, inclusive of Irish waters (OSPAR COMMISSION, 2017). Future studies on the genetic structure of grey seals in Western Europe will be critical in determining if more appropriate management units exist.

Without a comprehensive understanding of population structure it is impossible to reliably estimate colony-specific impacts of bycatch mortality, but it is nonetheless likely that some colonies will be more heavily impacted than others. In chapter 2, I identified environmental drivers of bycatch, including water turbidity, which will likely affect the rate of bycatch experienced by static net fisheries operating close to major colonies, but the most important predictor of total bycatch will be the total sum of fishing effort in a given area (Chapter 3). This highlights, once more, the most critical data gap in estimating the impact of grey seal bycatch; the distribution of the inshore fishing fleet. While the total fishing effort of small-scale fishing vessels is dwarfed by that of larger vessels, these smaller vessels fish exclusively in inshore waters, throughout the year, and given that grey seals may spend close to 90% of their time within 50km of the coast (Cronin et al. 2013; Jones et al. 2015), it may be these vessels that seals in Ireland interact with the most. This is not unique to Ireland, as small-scale fisheries are poorly monitored globally, despite potentially experiencing higher levels of protected species bycatch than larger fisheries (Peckham et al. 2007; Alfaro-Shigueto et al. 2011; Lewison et al. 2014). Based on the findings from Chapter 3, the highest levels of bycatch potentially occur off the southwest and south coasts of Ireland, suggesting that colonies such as the Blasket Islands and Saltees may be more heavily impacted by bycatch mortality than others. The Blaskets are also furthest removed from potential source populations in the UK of immigrating seals. Both of these breeding colonies are within designated Special Areas of Conservation (SAC) for grey seals. Targeting increased monitoring effort by scientific observers on board fishing vessels operating within or near these SACs would increase our understanding of potentially high-risk fisheries for seal bycatch.

5.5.2 Model assumptions

PVA is an umbrella term used to describe a suite of methodologies varying in complexity and the type of data used (Morris et al. 2002). In designing a model for PVA it is important to ensure that complexity corresponds appropriately to data availability (Ralls et al. 2002). Model complexity is largely determined by the life history of the species in question, the research objectives, and the quality and availability of demographic data (Radchuk et al. 2016). Over the past three decades, the number of published PVA studies has increased, at least partly due to the development and availability of software packages, including *Vortex* (Chaudhary & Oli 2020). As computational capacity and statistical analyses have advanced, increasingly complex models have been developed to carry out PVA (Pe'er et al. 2013; Howell et al. 2020). Despite these advances, the majority of published studies continue to use relatively simple model structures, primarily due to the paucity of demographic, dispersal, and spatial data regarding the species in question (Pe'er et al. 2013; Radchuk et al. 2016). This study relies on demographic data collected from colonies throughout the species range. Thomas et al. (2019) constructed a Bayesian age-structured model of UK grey seal population dynamics using informative priors of demographic data from studies of grey seal colonies in the UK, Canada, and Baltic Sea. These demographic data are challenging to collect, and in the past have often relied on costly long-term monitoring programmes (e.g. den Heyer et al. 2013) or culls (e.g. Harwood & Prime 1978). There are no equivalent data available from the Irish population of grey seals and the posterior distributions from the analysis by Thomas et al. (2019) provide the most informative demographic data available for our models.

Another important consideration is whether the duration of simulations is appropriate for the life history of the study species. When designing a model for PVA, simulations should be run for a long enough duration so that, accounting for the generation time of the species, long-term population trends can be detected and transient dynamics due to initial simulation conditions can be avoided (Pe'er et al. 2013). Given the maximum lifespan and age at first breeding of grey seals, 100 year simulations were considered sufficient to detect multi-generational effects while allowing for the reporting of a widely-used standard in conservation; the probability of extinction after 100 years (IUCN 2010).

Without historical data and regular population surveys it is difficult to infer the population carrying capacity. In this case, assuming a large carrying capacity of double the current population size allows us to identify bycatch pressures resulting in a limited population size that would have been masked if the assumed carrying capacity was too small.

5.5.3 Recommendations for improved monitoring and future studies

These findings provide a framework for designing future studies and monitoring efforts to reduce the uncertainty around the potential impact of bycatch mortality on grey seal populations. To summarise:

- An improved and expanded monitoring effort by dedicated observers on-board static net fishing vessels could narrow confidence intervals around total bycatch estimates. Collection of simple biometric data, including length and most importantly sex of bycaught seals, when possible, would provide a better understanding of population-level impacts and inform appropriate bycatch limits. Observers should ideally collect bycatch data as a priority, as many studies have shown that non-dedicated observers are less likely to notice and record incidences of bycatch (Gilman et al. 2005; Benoît & Allard 2009).
- Identifying demographically distinct management units of grey seals (if more than one exists) in Western Europe should be a priority to allow for management decisions to be made at the appropriate scale to ensure population conservation without risking depletions of smaller sub-

populations. This will likely require a collaborative genetic analysis of tissue samples collected from breeding colonies in Ireland, the UK, and mainland Europe.

- Improved monitoring of fishing activity by small-scale fishing vessels is urgently needed to fully understand the potential impact of bycatch on grey seal populations. Until this data gap can be addressed, we can only hope to understand the effect of a proportion of total bycatch.

5.5.4 Conclusion

In conclusion, this study explores a range of plausible bycatch scenarios for the Irish grey seal population and shows that, considering the data available, we cannot exclude the possibility that bycatch mortality represents a significant anthropogenic pressure on the population. As demonstrated, bycatch has the potential to slow population growth, limit population size, and in extreme cases, cause significant population decline. These findings provide clear incentive for improving data collection and prioritising future studies to identify appropriate grey seal management units. Density-dependent recruitment of seals from source populations in the UK has the potential to offset some of the effects of bycatch mortality, and the conservation status of the two populations may be intrinsically linked. Given the uncertain future of shared legislation between the European Union and the UK, there is a clear need for international cooperation in fisheries management to effectively conserve the grey seal population in Western Europe.

5.6 Supplementary material

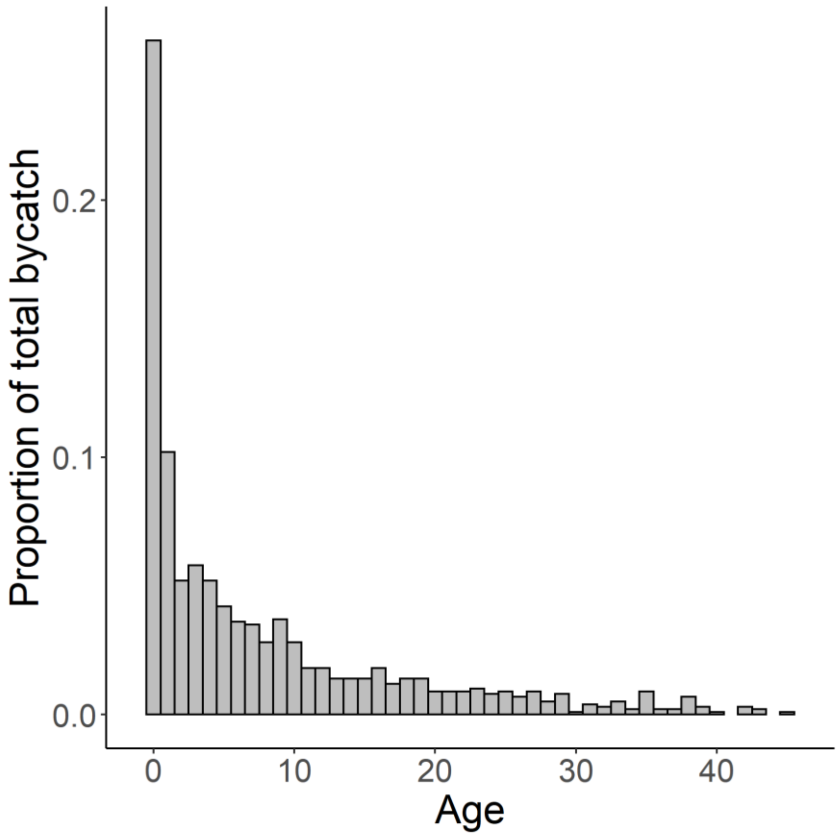

Figure S1: Simulated negative binomial distribution of bycatch mortality among age classes of grey seals in the scenario in which bycatch mortality was biased towards pups and juveniles (“juvenile bias”).

Chapter 6: General Discussion

Image: An inshore fishing vessel, moored at a secluded berth in Co Cork.

6.1 Key findings

“A central conundrum of applied ecology, and the cause of many anthropogenic ecological disasters, is that exploitation of the natural world has always progressed faster than our understanding of it” (Matthiopoulos et al. 2008). Bycatch of marine megafauna is typically an infrequent but significant event, and although from the perspective of one fisher, may seldom occur, the cumulative effect of bycatch can significantly affect the conservation of protected species.

This thesis aimed to address critical gaps in our understanding of grey seal bycatch in static net fisheries. In chapter 2, I compiled the largest dataset of seal bycatch observations collected in Irish waters, and provided clear evidence for two newly identified drivers of grey seal bycatch. These were the distance between the net and the nearest major grey seal colony and the first evidence for the role of water turbidity in bycatch of any species. In chapter 3, I applied the explanatory model constructed in chapter 2 as a predictive model to logbook data to provide the first estimates of total seal bycatch in static net fisheries in Irish waters. This required extensive data quality control and expertise to address missing information in reported fishing effort and outlined a method for estimating bycatch in other fisheries with comparable observer effort. In chapter 4, I examined how grey seal foraging behaviour was influenced by proximity to static nets. This analysis showed that where seals and static net fisheries co-occurred in time and space, seals were more likely to switch from travel to foraging behaviour, possibly increasing the probability of direct interaction. Finally, in chapter 5, the full range of impacts that bycatch could plausibly have on the Irish grey seal breeding population was explored, using Population Viability Analysis (PVA) to construct a number of bycatch scenarios based on the findings of the previous three chapters. Results showed that confidence intervals around current bycatch estimates included levels of bycatch mortality that could place significant pressure on the grey seal population and that the status of the Irish breeding population may be intrinsically linked to the status of the population in the UK.

These findings have implications for (i) identifying high risk fisheries and directing future monitoring efforts accordingly, (ii) designing effective mitigation strategies, and (iii) the conservation management of the grey seal population.

6.2 Improving bycatch monitoring

The infrequent nature of bycatch makes designing effective monitoring programmes challenging, as observers can spend considerable effort at sea without observing any bycatch events. Observations often come from finite research projects with logistical and financial restraints on observer effort (Wakefield et al. 2018). If an observer programme can only include a small proportion of the fleet, then a non-targeted distribution of observer effort could result in overly zero-inflated bycatch data, potentially making analysis of small datasets infeasible. Two important predictors of seal bycatch rates were identified in chapter 2, namely the turbidity of the water and the distance between the net and the closest major grey seal colony. This will enable identification of areas and seasons where the rate of bycatch would be expected to be high, and where targeted observer effort may have an increased probability of observing bycatch. For research of bycatch drivers or trials of potential mitigation strategies, this offers a means of maximising limited observer resources.

Alternatively, if the aim instead is to extrapolate the observed levels of bycatch to include the effort of the wider fleet, then a more stratified distribution of observer effort across predicted high and low risk fisheries may be more appropriate. Annual estimates of total seal bycatch presented in chapter 3 included extremely wide confidence intervals, spanning a range between almost zero and over 800 seals caught per year, far in excess of sustainable thresholds, as demonstrated in chapter 5. Increasing observer effort across a wider range of fisheries could allow for a more refined estimate of total bycatch with narrower confidence intervals. Bycatch data used in this thesis was collected from 14 fishing vessels, all but 3 of which were smaller than 12m in length, and all operated exclusively off the west and south coasts of Ireland. While these data represent important vessel size classes and areas for static net fishing activity, the study could have been improved with data collected from a broader sample of the total fleet effort. However, widespread data collection by observers is challenging, especially in a fleet including large numbers of small vessels with limited space to accommodate observers (Salas et al. 2007; Alfaro-Shigueto et al. 2011; Cardiec et al. 2020). An alternative to on-board observers is the installation of Remote Electronic Monitoring (REM) systems. REM offers a cheaper alternative to on-board observers (Ames et al. 2005), and can prove effective at detecting incidences of bycatch (Wakefield et al. 2018; Bartholomew et al. 2018; Glemarec et al. 2020), although efficacy may vary with species, and initial trials should include concurrent effort by on-board observers (Bartholomew et al. 2018).

The results presented in chapter 4 demonstrated that grey seals are likely to forage in areas also targeted by static net fisheries. Analysis of biotelemetry data from tagged seals have identified some key foraging areas to which seals repeatedly travel (Matthiopoulos et al. 2004; McClintock et al. 2012; Jones et al. 2015). Species distribution modelling of grey seal tracking data could identify key foraging areas for grey seals in Irish waters, allowing for any fishing vessels operating in such areas to be prioritised for monitoring/mitigation.

Finally, the results of PVA in chapter 5 suggested that some colonies are potentially more susceptible to bycatch pressure than others, due to high levels of static net fishing in adjacent waters and being further removed from potential source populations in the UK. Crucially for future monitoring, this study highlighted the importance of sex-specific impacts of bycatch. Observers should be trained to identify the sex of bycaught seals, as a skewed distribution of bycatch mortality towards females or males was demonstrated to have a significant impact on the sustainability of populations due to bycatch removals.

6.3 Designing effective mitigation

The design of effective bycatch mitigation strategies is dependent on understanding the causal factors of entanglement (Northridge et al. 2017a). The significant effect of water turbidity on the rate of seal bycatch (as demonstrated in chapter 2) suggests that increasing the detectability of nets could significantly reduce the rate of bycatch. Illuminating static nets with light emitting diodes (LEDs) has proven extremely effective in reducing bycatch of seabirds (Mangel et al. 2018), cetaceans (Bielli et al.

2020), and turtles (Wang et al. 2013; Ortiz et al. 2016; Bielli et al. 2020), by up to 85%, 70%, and 74% respectively, with no change in target species catch. Martin & Crawford (2015) caution against the use of light emitting devices and instead suggest adding high contrast wooden panels to nets so as not to affect the dark-adapted underwater vision of predators. Nonetheless, whether using LEDs or wooden panels, increasing the visibility of static nets could significantly reduce the rate of grey seal bycatch in static net fisheries. However, further research is needed to determine the potential effect of making nets more detectable to seals on the rate of depredation.

The results of this thesis also demonstrated the importance of encounter rates between seals and nets in grey seal bycatch. In chapter 2, distance to the nearest major colony was identified as a significant predictor of bycatch rate and chapter 4 showed that when seals and nets co-occurred, seals were likely to switch from traveling to foraging behaviour, potentially increasing the chance of directly interacting with the net. The duration of the soak period in static net fisheries is understood to affect the bycatch rates of marine mammals, turtles, and seabirds (López-Barrera et al. 2012; Žydelis et al. 2013; Northridge et al. 2017a). Shorter soak periods for static nets close to major seal haulouts could significantly reduce the rate of interaction between certain fisheries and seals. Reducing the soak duration can also limit the availability of fish to depredating seals, and many fishers have already adopted shorter soak periods to try to mitigate against depredation (Cronin et al. 2014). Nonetheless, some fisheries, particularly those targeting crustaceans, which are rarely depredated in comparison to fish (personal observation), may still deploy nets for exceedingly long soak durations of two weeks or more. Future studies should explore the relationship between soak time, bycatch, depredation, and target catch, to identify an optimal soak length that would minimise direct interactions with seals while also minimising the potential cost for fishers in lower catch of target species.

Grey seal bycatch and depredation both occur in Irish fisheries, but it is unclear to what extent, if at all, the two events are correlated. An analysis of stomach contents of grey seals bycaught in static nets found few prey remains belonging to the target species of the fishery, providing little evidence that bycaught seals had been attempting to depredate the nets before they became entangled (Gosch, 2017).

Cosgrove et al. (2015) compiled a dataset of observations of grey seal bycatch and depredation on-board three static net fishing vessels, and modelled the rate of seal depredation of three target species separately. In the monkfish depredation model, the rate of seal bycatch was significantly and positively correlated with the rate of depredation. However, similar correlations were not observed in depredation of hake or pollack. Tixier et al. (2020b) found that all 21 species of pinniped known to depredate were caught in the same fisheries in which depredation occurred. Pinniped bycatch was recorded in 88% of depredated trawl fisheries, 67% of seines, and 55% of static nets, suggesting that depredation might increase the risk of bycatch, but the risk seems greater when interacting with active rather than passive gears. This suggests that potential mitigation strategies for reducing seal depredation, including the development of acoustic deterrent devices (Götz & Janik 2013; Gosch et al. 2017), may have some effect in reducing seal bycatch. Furthermore, mitigating depredation is important to appease the concerns of fishers and reduce the incentive for retaliatory actions against seals.

6.4 Implications for management

Thirteen Special Areas of Conservation (SACs) have been designated for grey seals around important breeding colonies in the Republic of Ireland. Large numbers of seals can still be found in many of these areas outside of the breeding season, as evident by thermal-imaging surveys carried out in August (Morris & Duck 2019). Given the importance of distance to colony as a driver of seal bycatch (chapter 2) and the propensity of grey seals to forage close to shore (chapter 4; see also Jones et al. 2015), it is likely that these SACs are well-placed to reduce bycatch, if fishing with high-risk gear were to be restricted within their boundaries. Personal observations of seal bycatch involved large-mesh nets deployed for longer than two weeks, within sight of a haulout of several hundred grey seals, inside of an SAC designated for grey seals. Given the lack of information regarding the distribution of fishing effort by the inshore fleet, it is hard to assume that these observations were unique or anomalous. The enforcement of knowledge-based restrictions, such as time-area closures targeting high risk gears during periods of high bycatch risk within SACs, could significantly reduce the encounter rates between grey seals and high risk fisheries, and presumably overall levels of seal bycatch.

There is currently no evidence of demographic isolation between populations of grey seals in Ireland, the UK, and mainland Europe. Grey seals tagged in Ireland, the UK, and France, regularly move between multiple jurisdictions, as seen in chapter 4, and some degree of density-dependent dispersal of grey seals has likely led to recruitment of seals from source colonies in the UK into breeding colonies in mainland Europe (Brasseur et al. 2015; Russell et al. 2019). As demonstrated in chapter 5, this dispersal has the potential to significantly affect the impact of bycatch mortality on the national grey seal population. Furthermore, fishing vessels from across Europe fish throughout the range of each grey seal population. Seals from Irish breeding colonies are undoubtedly bycaught outside of Irish waters, as seals breeding outside of Ireland are bycaught within Irish waters. In this way, no one state can expect to ensure the "favourable conservation status" of their breeding population in isolation. Managing the impact of bycatch on grey seals throughout Western Europe will require consistent cross-country collaboration. The formal departure of the UK from the EU occurred in January 2020 and, at the time of writing, the ongoing legal and trade negotiations creates a strong need for international collaboration in the management of our shared marine resources and protected populations.

In Ireland, comprehensive surveys of the grey seal breeding population have only occurred twice in the past 15 years (Ó Cadhla et al. 2007, 2013), and the most recent population estimate is now 8-11 years out of date. More frequent surveys are needed to assess population trends and for setting appropriate bycatch threshold limits. Potential Biological Removal (PBR) as a threshold limit is based on the single most recent minimum population estimate (N_{min}), and Brandon et al. (2017) showed that combining multiple recent estimates of N_{min} can result in calculation of more stable PBR values over time and less regulatory uncertainty for fisheries.

6.5 A note about policy

The increasing recognition of bycatch as a major threat to the conservation of marine species has unfortunately not been reflected in Irish or EU policy. The EU Habitats Directive (92/43/EEC) and Common Fisheries Policy (EU1380/2013) both include vague objectives for managing bycatch, but the only policy focused on monitoring and mitigating bycatch is the EU Regulation 812/2004, which has recently been replaced by the Technical Conservations Measures Regulation (2019/1241). Both of these regulations mandate fishing vessels longer than 15m, under the conditions outlined in Annex III, to carry scientific observers for the monitoring of incidental catches of cetaceans, and oblige operators of vessels over 12m in métiers defined in Annex I to use acoustic deterrent devices to mitigate cetacean bycatch. The shortcomings of these regulations, which aim to reduce bycatch of cetaceans only, have been well documented as they fail to target many high risk metiérs (more than 90% of European static net vessels are smaller than 12m) and compliance by Member States has been largely inconsistent (ICES 2020; Rogan et al. in press).

Furthermore, there exists a dichotomy between the strategies typically used for managing fisheries and wildlife populations within the EU. Whereas fisheries are typically subject to legally binding Regulations, wildlife management more often involves Directives, which merely define conservation goals without a clear framework for how to achieve said objectives (Rogan et al. in press). By allowing each EU Member State to independently interpret conservation objectives such as "favourable conservation status" (EU Habitats Directive) or "good environmental status" (Marine Strategy Framework Directive), there is an inevitable incentive for policy makers to develop minimally restrictive management plans, potentially at the cost of effective mitigation.

In contrast, the US National Bycatch Reduction Strategy outlines clear objectives for mitigating bycatch of protected species. The US Marine Mammal Protection Act affords protection to all marine mammals, requires monitoring of bycatch by independent scientific observers, and establishes clear bycatch thresholds which, when exceeded, trigger immediate management action. For example, if the level of bycatch mortality for a marine mammal stock, across all fisheries, exceeds PBR, it is designated a “Strategic Stock”, at which point a Take Reduction Plan must be implemented to reduce bycatch to below PBR within six months (Moore et al. 2008).

There is a clear and present need for more stringent regulation of bycatch in European fisheries. Earlier this year, two reports were submitted to the European Commission by 26 environmental and non-governmental organisations, highlighting unsustainable levels of bycatch of common dolphins in the Bay of Biscay and harbour porpoises in the Baltic Sea, and requesting the implementation of emergency mitigation measures. These reports were reviewed by ICES working groups, which echoed the concerns raised in the reports and suggested modified emergency measures be implemented immediately and monitoring be increased in high risk fisheries. This clearly demonstrates that current EU policies on bycatch have been insufficient to ensure the conservation of protected species, and in order to avoid the need for future emergency measures, new regulations should (i) expand the requirements for bycatch monitoring to include more high risk metiérs, (ii) define quantitative management objectives, (iii) and implement effective mitigation strategies when objectives are not met (Rogan et al. in press).

6.6 Limitations of the study

Ireland is home to two species of phocid seal, grey seals and harbour seals (*Phoca vitulina*). In this thesis, I focused on bycatch of grey seals due to the greater frequency with which they have been recorded as bycatch in Ireland (Cosgrove et al. 2016) and the UK (Northridge et al. 2017b), and the more restricted movement range of harbour seals (Cronin 2011; Jones et al. 2015). Nonetheless, there is a potential that high levels of harbour seal bycatch occur, unobserved in this study, particularly, close to high-usage areas by harbour seals where inshore fisheries are likely to operate, e.g. Bantry Bay, Co Cork (Cronin 2011). Importantly, because of the more limited range of harbour seals, there is a greater likelihood that multiple discrete management units of harbour seals exist in Ireland, which may experience varying levels of bycatch pressure. Summer counts of harbour seals, carried out using thermal imaging aerial surveys, have steadily increased from 2,955 in 2003 (Cronin et al. 2007) to 4,007 in 2017-2018 (Morris & Duck 2019), with the largest numbers occurring off the northwest, west, and southwest coasts. Future observer effort should include fisheries operating in expected high-usage for harbour seals (see Jones et al. 2015).

The lack of information regarding the effort of the inshore fishing fleet has received some attention in preceding chapters but deserves reiteration here as it is the most critical impediment to understanding the potential impact of bycatch on the grey seal population. VMS technology is specifically designed for fisheries management, while AIS is primarily a safety feature which has seen increased use by researchers due its greater accessibility in recent years. On the high seas these technologies can be assumed to capture almost all of the fishing activity taking place, with the exception of vessels that deliberately tamper or deactivate their tracking technology (Witt & Godley 2007; Park et al. 2020). However, in inshore waters, where large numbers of small-scale fishing vessels operate without VMS or AIS, these technologies provide only a partial picture of the distribution of fishing effort. Critically for seals, it is these inshore waters where bycatch may be highest, as observed bycatch rates were highest close to major colonies (chapter 2) and almost a quarter of grey seal foraging behaviour occurred within 10km of shore (chapter 4). In Europe, fishing vessels smaller than 10m in length are not required to submit logbooks of catch and effort. The national registry of fishing vessels in Ireland includes about 2000 fishing vessels, 86% of which are smaller than 12m in length and are not obliged to carry VMS, and 75% of which are under 10m and submit no logbooks. Punt et al. (2020) clearly showed that only managing a part of a fleet undermines the performance of bycatch thresholds and reduces the likelihood of achieving conservation goals. Without knowing the distribution of effort by the inshore fishing fleet we can only hope to quantify the impact of a proportion of total seal bycatch.

6.7 Future research

The information deficit surrounding the catch and effort of the small-scale fishing fleet is not a unique issue to Ireland. Bycatch in small-scale, data-poor fisheries is a major challenge to sustainable fisheries management worldwide (Moore et al. 2010;

Dmitrieva et al. 2013; Vanhatalo et al. 2014; Karamanlidis et al. 2020). Fishers themselves possess vast amounts of tacit knowledge, and interview-based studies have proven effective in filling information gaps surrounding fishing effort (Karamanlidis et al. 2020), target catch (Young et al. 2006), and levels of bycatch (Moore et al. 2010; Dmitrieva et al. 2013). Applying Bayesian analyses to interview responses in Baltic fisheries allowed Vanhatalo et al. (2014) to predict bycatch levels of grey seals beyond areas where interview data were available. Fishers do not possess perfect memory and they are less likely to remember relatively "unimportant" events including non-target catch (Young et al. 2006), and bycatch may be under-reported for fear of negative repercussions (Walsh et al. 2002). Nevertheless, soundly designed interview-surveys, coupled with robust analysis of responses can provide insights into the potential extent of bycatch where widespread observer coverage is not feasible (Moore et al. 2010; Vanhatalo et al. 2014). In the absence of an expanded observer effort or introduction of REM technology on small-scale fishing vessels, a well-designed interview-based study could provide some insight into the distribution of effort by the inshore fleet and allow for a more complete estimation of the level and impact of grey seal bycatch.

Mitigation measures should be evidence-based and no more restrictive to fishers than necessary. Static time-area closures can cause significant economic losses for fishers and do not always optimally protect bycaught species which may move in and out of restricted areas (Dunn et al. 2016; Maxwell et al. 2020). Dynamic management allows for time-area restrictions to change in response to the expected distribution of protected species and can achieve similar levels of protection to static restrictions while displacing a fraction of the same fishing effort (Kraak et al. 2012; Dunn et al. 2016; Hazen et al. 2018; Maxwell et al. 2020). Hazen et al. (2018) demonstrated an effective methodology for using dynamic management to minimise protected species bycatch while maintaining optimal catch of target species for fishers. They created multiple species distribution models for target and non-target species, combining probabilities of occurrence for each species into a single predictive surface, which was then weighted by the conservation concern of each species. This allowed for dynamic time-area restrictions of fishing 2 to 10 times smaller than static closures while still achieving the same degree of bycatch reduction. By combining the known bycatch risk factors for grey seals, identified in chapter 2, with the state-space models of chapter 4 which identified the locations of grey seal foraging behaviour, there is an opportunity to produce a dynamic predictive model of bycatch risk for grey seals. Coupled with species distribution models for common target species this could provide fishers with a tool to maintain or improve target species catch while minimising bycatch of seals and its associated costs, such as damage to gear, or time lost disentangling seals.

6.8 Conclusion

In conclusion, this thesis contributed important new insights into the cause and effect of grey seal bycatch in static net fisheries. Before commencing this study, we had an extremely limited understanding of the drivers of seal bycatch, and no information regarding total bycatch levels in Irish waters or the potential impact of bycatch at the population level. This thesis has addressed these critical knowledge gaps, identified promising new avenues for designing effective mitigation strategies, provided new insight into the behavioural interactions between grey seals and nets at sea, and outlined means of improving future bycatch monitoring. As conflicts between marine predators and fisheries continue around the world, these studies will allow for a more informed management of predator-fishery interactions and place us a few steps closer to achieving an ecosystem approach to fisheries management.

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