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Using population viability analysis to examine the potential long-term impact of fisheries bycatch on protected species

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ABSTRACT

Fisheries bycatch is recognised as the dominant anthropogenic threat facing many protected species globally. Estimates of total bycatch are often associated with wide confidence intervals as a result of limited coverage by on-board observers. This makes it difficult for managers to assess risk and design effective management plans. Here, we present a case study of grey seal (*Halichoerus grypus*) bycatch in static net fisheries across Irish waters, where potentially unsustainable bycatch levels have been reported with typically wide confidence intervals. We used Population Viability Analysis (PVA) to explore potential bycatch scenarios at a national level in order to inform future monitoring and management efforts; including (i) a baseline scenario where the probability of seals becoming bycaught was independent of age and sex; (ii) probability was biased towards juvenile, male, or female seals; (iii) there was net immigration of seals from outside of the national population; and (iv) colony-specific bycatch rates were applied to assess the relative vulnerability of the major grey seal breeding colonies to bycatch mortality. Results demonstrated that (i) higher levels of bycatch reduced population growth, with bycatch of 800 seals per year reducing the national population by 99% over 100 years; (ii) population viability was most sensitive to bycatch mortality of female seals, and more robust to juvenile or male mortality; (iii) recruitment of 500 seals per year prevented population decline despite a worst-case bycatch scenario of 800 seals bycaught per year; (iv) colonies in the south and southwest were the first to show signs of decline under increasing bycatch pressure. PVA provides a clear justification for improved monitoring of seal bycatch to obtain more precise bycatch estimates, and highlights the need for future studies to identify appropriate grey seal management units.

1. Introduction

Fisheries bycatch represents the dominant anthropogenic threat facing many protected marine species (Avila, Kaschner, & Dormann, 2018; Dias et al., 2019; Gray & Kennelly, 2018; Wallace et al., 2010). However, assessing the population-level impact of bycatch remains challenging, especially for protected, endangered, and threatened (PET) species (Taylor, Wade, De Master, & Barlow, 2000; Wakefield et al., 2018). For PET species populations, bycatch may represent a rarely observed but significant event, requiring extremely high observer coverage to monitor effectively (Wakefield et al., 2018). However, such high levels of observer coverage are rarely met, resulting in a high degree of uncertainty around bycatch rates, and extremely wide confidence intervals around estimates of total bycatch (Barlow & Berkson, 2012; Wakefield et al., 2018). Bycatch estimates such as these may include a range of scenarios ranging from negligible numbers of animals being removed from a population, to unsustainable levels of bycatch, severely limiting the ability of policy makers to make informed management decisions.

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 over the long term (Chaudhary & Oli, 2020; Radchuk, Oppel, Groeneveld, Grimm, & Schtickzelle, 2016; Reed et al., 2002). 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

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viability (Lacy, 2019; Morris, Bloch, Hudgens, Moyle, & Stinchcombe, 2002; Reed et al., 2002). 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 (Howell et al., 2020; Pe'er et al., 2013). 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). In this study, we demonstrate the applicability of PVA in exploring a range of scenarios to examine the potential impact of bycatch on a protected species, and how these simulations can identify priorities for improved monitoring and management of PET species bycatch.

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). Seals fitted with GPS tags at 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). While grey seals exhibit a high degree of breeding-site fidelity once recruited into a breeding population (Langley et al., 2020; Pomeroy, Twiss, & Redman, 2000), 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). 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 grey seal breeding population, based on a multiplier of 3.5–4.5 of total pup production estimates, representing the ratio of newborn pups to the all-age population (Harwood & Prime 1978), grew from an all-age population of 5509–7083 seals in 2005 to 7284–9365 seals in 2012 (Ó Cadhla, Keena, Strong, Duck, & Hiby, 2013; Ó Cadhla et al., 2007), and while more recent breeding population estimates are unavailable, summer counts suggest that the number of seals attending haulouts has continued to increase (Morris & Duck, 2019).

Static net fisheries involve setting nets, such as gillnets or tangle nets, in the water to soak for hours or days at a time. Recent studies have highlighted the risk of grey seals becoming entangled in static net fisheries (Cosgrove et al., 2016; Luck, Cronin, et al., 2020; Luck, Jessopp, et al., 2020), with potentially hundreds of seals caught in Irish waters each year (Luck, Jessopp, et al., 2020). Because of limited scientific observer programmes and data gaps regarding the distribution of fishing effort, confidence intervals around best estimates of annual seal bycatch are wide, ranging from near zero to beyond sustainable limits. 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.

In this study, we construct a population-based model of grey seals in Ireland to explore the effects of bycatch mortality at the population level. First, we explore the full range of confidence intervals around estimates of annual bycatch mortality, as calculated by (Luck, Jessopp, et al., 2020), independent of immigration of seals from outside of Ireland. Second, we test how higher levels of bycatch amongst juvenile, female, or male seals might alter the effect of bycatch on population viability. We examine the potential effect of immigration of seals from outside of Ireland in mitigating the effect of bycatch mortality on the Irish population. Management units for grey seals in NW Europe have yet to be delineated; in this final scenario the national population is treated as a *meta*-population comprised of individual colonies, and colony-specific bycatch levels are approximated based on colony size and estimated bycatch rates in adjacent waters (Luck, Jessopp, et al., 2020), to explore which colonies may be more susceptible to decline caused by bycatch mortality.

2. Methodology

2.1. 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. Inbreeding depression has the potential to affect lifetime breeding success of inbred individuals and this can become more prevalent in reduced populations (Huisman et al. 2016; Ballou 1997). Therefore we included inbreeding depression as a reduced first-year survival of inbred individuals resulting from recessive lethal alleles (Lacy & Pollak 2017). Table 1 outlines the input demographic parameters used to construct the baseline model. Demographic parameters including birth rates, death rates, population sex ratio, and individual probabilities of birth and death occurring included a degree of annual random variation following a binomial distribution (Lacy et al. 2017). *VORTEX* can also model annual fluctuations in birth and death rates that might result from environmental variation (EV). To model environmental variation, each demographic parameter is assigned a distribution with a mean and standard deviation that is specified by the user. Annual fluctuations in probabilities of reproduction and mortality are modelled as binomial distributions (Lacy et al., 2017).

Multiple subsequent scenarios were constructed to explore the range

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

Parameter	Value	Reference
Inbreeding depression – lethal equivalent% due to lethal equivalents	6.2950%	Default value – O'Grady et al., 2006
Reproductive system	Polygynous	
Age of first offspring – females (years)	6	Harwood & Prime, 1978
Age of first offspring – males (years)	10	Harwood & Prime, 1978
Max. # of progeny/ brood	1	
Max. # of broods/year	1	
Sex ratio at birth	1:1	
Density dependant reproduction	Not included	
Maximum lifespan & maximum age of reprod (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 for both sexes (SD due to environmental variation)		
- Age 0–1	0.52 (0.09)	Thomas et al. 2019
- Age 1+	0.05 (0.01)	Thomas et al. 2019
Initial population size (*N*)	7200	Ó Cadhla et al., 2013
Catastrophe effects	Not included	
Dispersing sex	Both	
Dispersing age class (years)	0–6	
Survival during dispersal	100%	
Dispersal rate	10%	
Carrying capacity (*K*)	Unknown. Assumed K ~ 2 N	NA
SD in K due to environmental variation	0	

of potential effects of bycatch mortality on the viability of the Irish grey seal population. Model assumptions are outlined in supplementary material.

2.2. Bycatch mortality

Bycatch mortality was incorporated into the baseline scenario as a pre-determined number of seals removed from the population each year. A pre-defined bycatch rate was applied to the population, and unless otherwise specified, the same bycatch rate was applied to each age and sex class. Luck, Jessopp, et al. (2020) 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 initially ranging from 0 to 800 seals (equivalent to 0.0–11.1% of the initial population size), in increments of 100. As bycatch rates may be influenced by the frequency of seal-net encounters, total annual bycatch was scaled by population size. If the population grew or declined by X% between one year and the next, the number of animals removed as bycatch also increased or decreased by X%. In this way, while the total number of seals bycaught each year changed, the proportion of seals removed from the population remained constant. We considered this would allow for more realistic rates of population decline and growth than by applying fixed, constant bycatch removals each year. However, results should be interpreted with an abundance of caution as under these conditions fishing effort is assumed to remain constant and extinctions are unlikely to occur, as diminished populations will be exposed to reduced bycatch removals. Therefore we will focus our discussion on the rate of population decline rather than the possibility of extinction, defined in Vortex as only one sex remaining in the population. See also “Model assumptions” in supplementary material for a detailed explanation of this approach.

2.3. Age/sex-structured bias in bycatch probability

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 (Bjorge, Oien, Hartvedt, Bothun, & Bekkby, 2002; Burns, 1999). 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 bycatch probability was highest during a seal’s first year, then declined by approximately half in year 2, and again in year 3, before declining gradually thereafter so that older seals were less likely to become bycaught (figure S2).

Observations of bycatch on-board static net fishing vessels in Irish waters have suggested a potential sex bias as approximately 50% more males were recorded as bycatch than females (Cosgrove et al., 2016; Luck, Cronin, et al., 2020). A scenario was therefore constructed in which the probability of bycatch for males was 1.5 times that of females. Alternatively, female grey seals typically forage closer to shore than males (Beck, Bowen, Mcmillan, & Iverson, 2003; Breed, Jonsen, Myers, Don Bowen, & Leonard, 2009) where they may potentially interact with inshore static net fisheries. Currently, fishing vessels smaller than 12 m 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 <12 m fishing vessel activity is extremely limited (Rogan, Read, & Berggren, 2021). 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 bycatch probability for females was 1.5 times that of males.

2.4. Immigration from outside Ireland

To understand how immigration of seals from outside of Ireland might offset the effect of bycatch mortality, we ran multiple simulations including varying levels of bycatch and immigration from outside of the Irish population. Again, bycatch initially ranged from 0 to 800 seals per year (evenly distributed between sex and age classes, scaling with population size), and immigration ranged from 0 to 500 seals per year (independent of population size, with the exception of populations at carrying capacity (*K*), to which no additional seals were added). 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 (Langley et al., 2020; Pomeroy et al., 2000; Thomas, Buckland, Newman, & Harwood, 2005). 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.

2.5. Colony-specific bycatch effects

To explore the potential effect of bycatch mortality at the colony level, we defined the national population as a *meta*-population made up of seven major colonies within the Republic of Ireland, at the key breeding sites, comprising 84% of the national breeding population (Fig. 1; Ó Cadhla et al., 2013). *K* was assumed to be double the present population at each colony, as surveys have been too infrequent to determine if any colonies are approaching or at *K*. Colony-specific bycatch rates were approximated based on initial population size and total bycatch estimates from adjacent waters (Table 2; Luck, Jessopp, et al., 2020). As before, annual bycatch scaled linearly with population growth or decline. Scenarios allowed for an approximation of density-dependent inter-colony dispersal, so that if a given colony was at *K*, 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, with the number of seals to be removed from each colony scaling with population growth or decline, independent of other colonies or the larger *meta*-population. 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.

3. Results

3.1. Effect of bycatch on baseline model

The baseline model, with zero bycatch mortality, resulted in continuous population growth with population size reaching 90% of *K* after 9 years (Fig. 2). As the number of seals bycaught annually increased, so too did the time to reach *K* as the growth rate slowed (table S1). With annual bycatch of 400 seals, the population grew to 90% of *K* after 55 years. With bycatch of 500 seals per year, the population gradually declined, resulting in a depleted population of fewer than 6000 seals. Annual bycatch of 600 seals resulted in an extremely depleted population of approximately 1200, and bycatch of 800 seals per year resulted in rapid decline and an extant population of approximately 50 individuals after 100 years (Fig. 2).

With annual bycatch levels initially set to between 100 and 200 seals per year, population growth was in line with the population trends observed between the most recent population surveys in 2005 and 2009–2012 (Fig. 3).

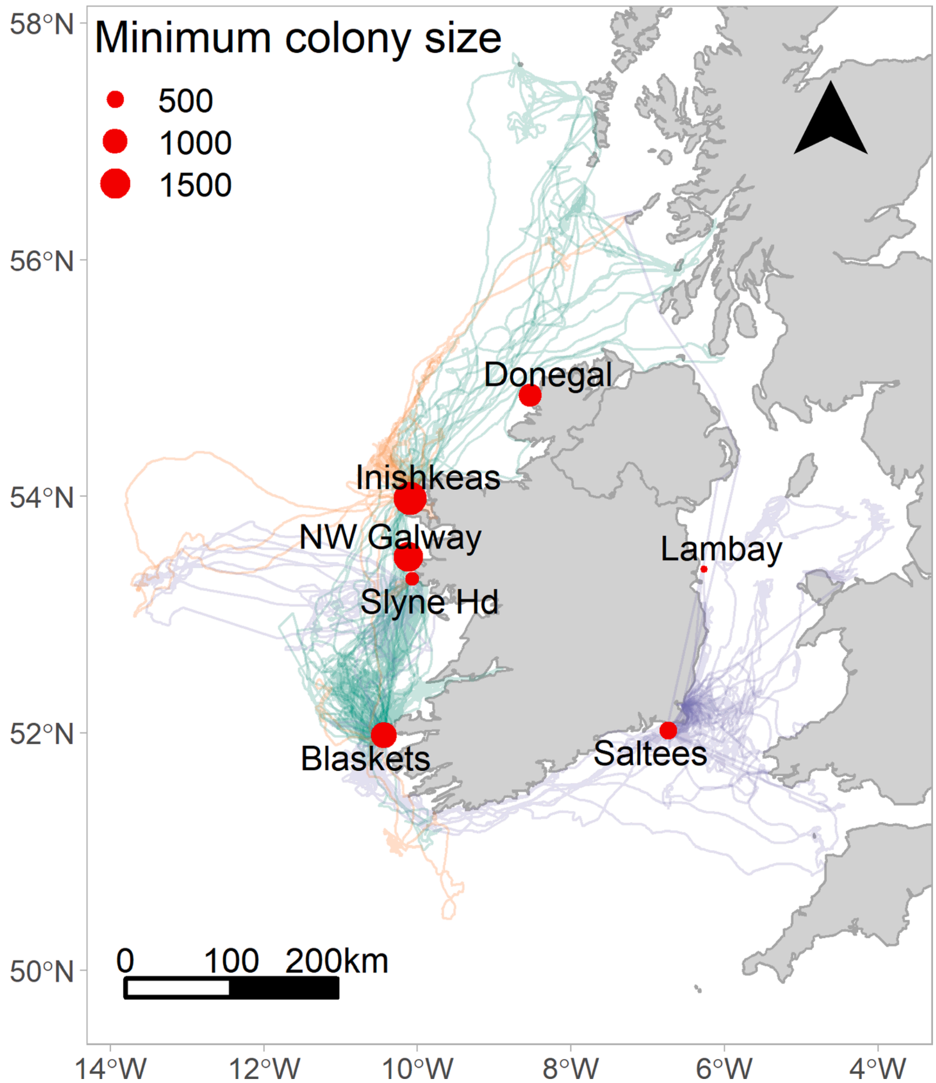

Fig. 1. Map of major breeding colonies of grey seals in the Republic of Ireland. Colony size according to population survey by Ó Cadhla et al. (2013). Coloured lines indicate movements of grey seals fitted with GPS tags at the Inishkeas (orange), Blasket Islands (green), and Wexford Harbour (purple). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Colony size, and proportion of total bycatch mortality at each colony. The proportion of total population at each colony was increased or decreased, based on the Luck, Jessopp, et al. (2020), 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(Luck, Jessopp, et al., 2020)	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

3.2. 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 500 seals per year, bycatch mortality evenly distributed between all sex and age groups led to a gradual population decline to 42% of K over 100 years. Where bycatch was highest among pups and juveniles, populations gradually increased (Fig. 4). Increasing the number of males bycaught to 1.5 times that of females resulted in a greater rate of population growth, and a population that reached 90% of *K* within 44 years (Fig. 4). An equivalent bias towards female seals resulted in accelerated population decline and total extirpation within 90 years (table S2; Fig. 4).

3.3. Immigration from outside of national population

Fig. 5 shows the simulated population size over 100 years, given predetermined levels of bycatch mortality and immigration of seals from outside of the Irish population. In all scenarios, higher levels of immigration resulted in faster growth rates (table S1) and larger extant populations after 100 years. Net immigration of 500 seals per year (approximately 0.3% of the UK population) allowed for population persistence at all simulated levels of bycatch mortality, and resulted in a modest population increase over 100 years, even with bycatch of 800 seals per year (table S2; Fig. 5).

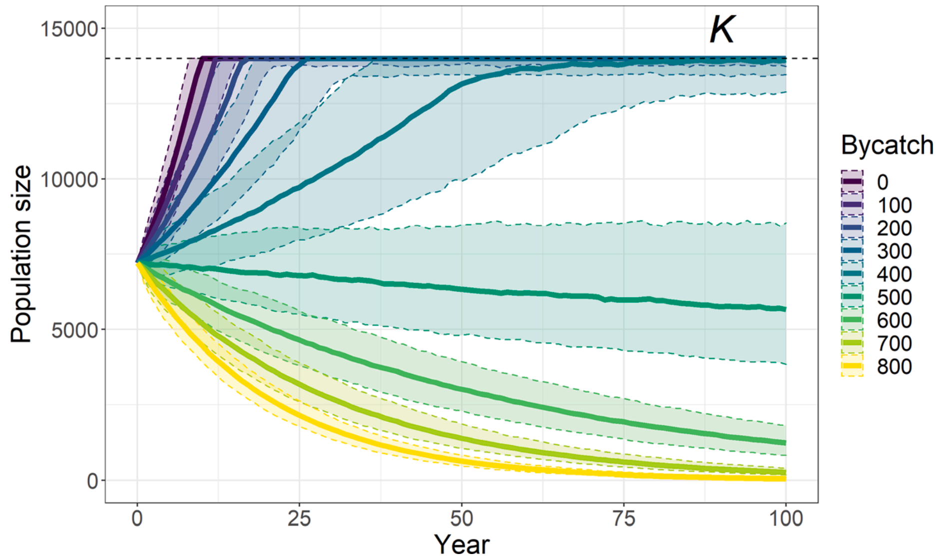

Fig. 2. Simulated population trends of the national grey seal population over 100 years, including varying levels of annual bycatch mortality. Solid lines represent 50% quantile values across 1000 iterations and shaded areas represent 5% to 95% inter-quantile ranges. *K* represents the assumed carrying capacity of the national population.

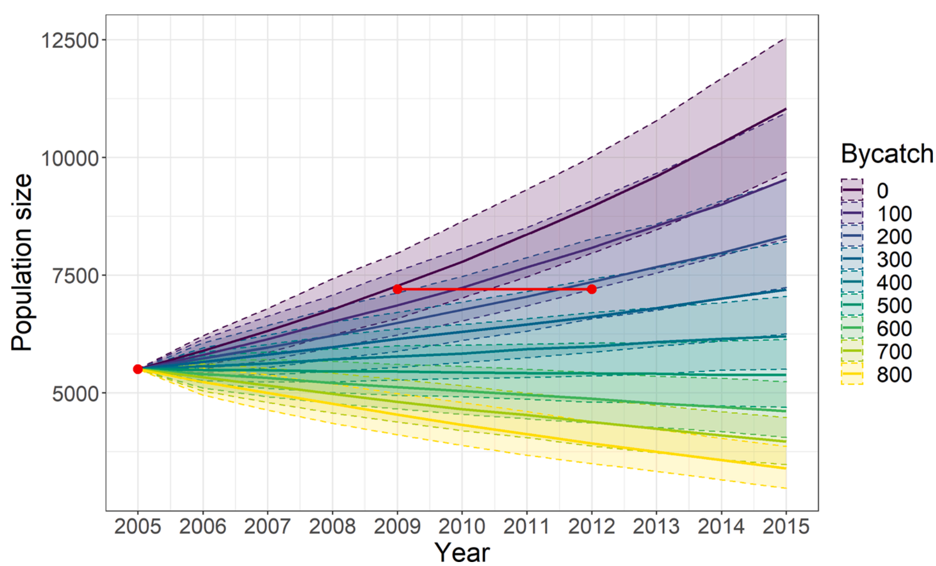

Fig. 3. Simulated population trends of the national grey seal population between 2005 and 2015. Solid lines represent 50% quantile values across 1000 iterations and shaded areas represent 5–95% inter-quantile ranges. Red circles and lines indicate the timing of the most recent surveys of the grey seal population and the minimum estimated population sizes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. Colony-specific bycatch mortality

At the colony level, increasing levels of annual bycatch mortality resulted in lower growth rates (table S1), 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 (Fig. 6).

4. Discussion

4.1. Impact of bycatch on Irish 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, often reflecting the limitations of onboard observer programmes. Notwithstanding such limitations, PVA allows us to clearly 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 population. These simulations provide important insights into the potential long-term impact of bycatch, and allow for more informed management decisions and improvements to future monitoring and research.

Luck, Jessopp, et al. (2020) provided the first estimates of annual

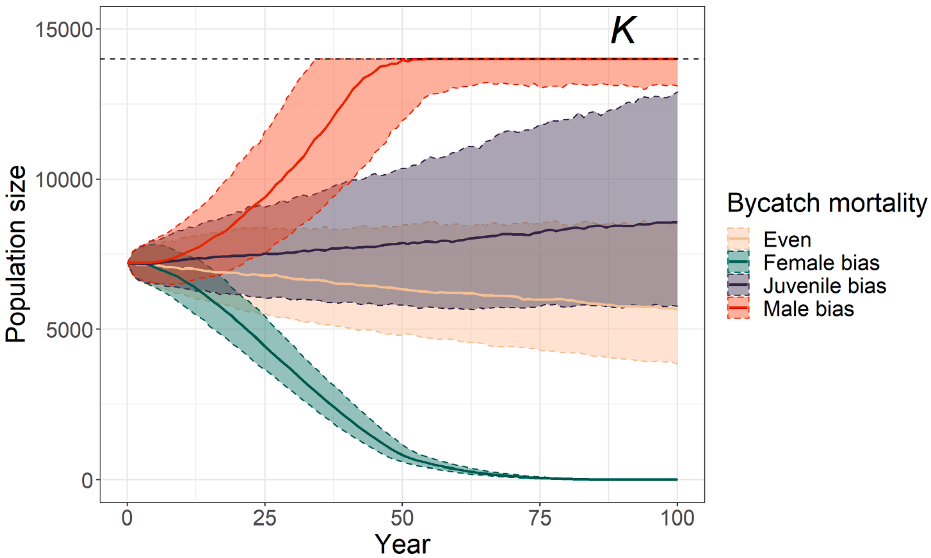

Fig. 4. Simulated trends of the national population with annual bycatch mortality of 500 seals simulated over 100 years. Scenarios include an even distribution of bycatch mortality among age and sex classes ("Even"), scenarios in which the rate of bycatch is 1.5 times as high for females ("Female bias") or males ("Male bias"), and a scenario in which the bycatch rates decrease with age ("Juvenile bias"). Solid lines represent 50% quantile values across 1000 iterations and shaded areas represent 5% to 95% inter-quantile ranges. *K* represents the assumed carrying capacity of the national population.

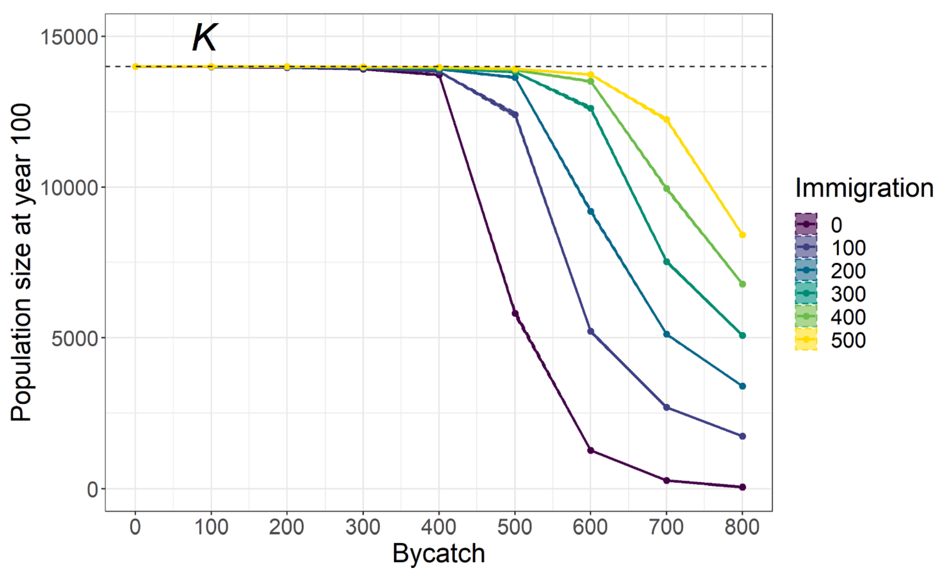

Fig. 5. Simulated grey seal population size after 100 years of annual bycatch mortality, offset by annual immigration of 0 to 500 seals from outside of Ireland.

grey seal bycatch in Irish waters. In that study, estimates were compared to a sustainable threshold value calculated as Potential Biological Removal (PBR). PBR, calculated as the product of the minimum population estimate (7284; Ó Cadhla et al., 2013), half of the intrinsic growth rate (0.12 for pinnipeds (Wade, 1998), and a recovery statistic F_r (set to between 0.1 and 1.0), is designed to allow a population to maintain at least half of the estimated maximum population size, given no human-caused mortality (Taylor et al., 2000; Wade, 1998). Comparing the bycatch thresholds derived from estimates of PBR (ranging from 218 to 437 seals per year; Luck, Jessopp, et al., 2020) with the results from this study suggest that keeping bycatch within even the least conservative levels of PBR would indeed allow the population to reach more than half of *K* within 100 years. However, at the upper limit of PBR estimates, 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 (Punt, Moreno, Brandon, & Mathews, 2018; Punt et al., 2020; Wade, 1998). 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 current bycatch estimates are mortality levels that could drive the population to near-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. Fig. 3 suggests that bycatch levels of 100 to 200 seals per year is consistent with the growth rate seen in the breeding population of grey seals in Ireland between 2005 and 2009–2012. However, it has been ten years since the most recent population survey and we cannot assume that this trend has continued. In fact, a recent study highlighted extremely high levels of bycatch in the southwest of Ireland, 193 seals caught between 2017 and 2020 (Tully & Palma Pedraza 2022), suggesting that it is biologically implausible that the local breeding population (on the Blasket Islands) has sustained this level of bycatch without supplementation from other colonies. Therefore, as long as bycatch estimates include potentially unsustainable levels of mortality, a precautionary approach to fisheries management requires us to account for this

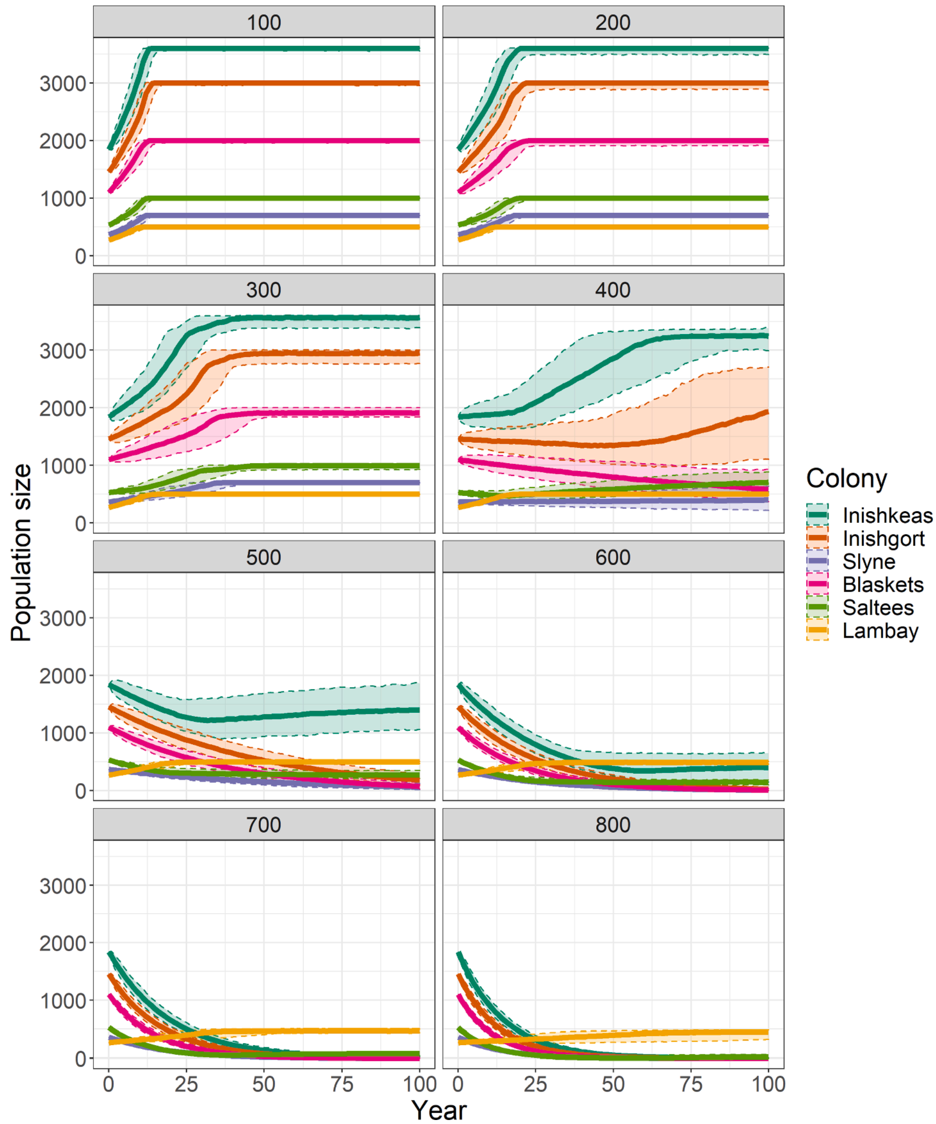

Fig. 6. Simulated population trends at each of the major grey seal colonies simulated over 100 years with annual bycatch mortality (in grey) ranging from 100 to 800 seals per year. Solid lines represent 50% quantile values across 1000 iterations and shaded areas represent 5% to 95% inter-quantile ranges.

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 simulations demonstrated, a bias towards male or female bycatch has a much stronger potential impact on population viability than age-based bias in mortality.

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). 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 grey seal population in the Netherlands 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, Kingston, & Thomas, 2017). It is therefore possible that either bycatch in Irish waters includes a number of 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 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 (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 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. Our simulations assumed a constant rate of recruitment, however, in reality this recruitment is likely to vary with density-dependence in UK colonies. In this way, the status of Irish grey seal colonies may be intrinsically linked to the status of colonies in the UK; further highlighting the importance of establishing appropriate management units for the species in Western Europe.

For the successful conservation of any mobile species, it is critical to identify demographically independent management units within a species range, and manage each unit independently (Curtis et al., 2015; Taylor, 1997). 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 that have been separated over a long time period (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 (Carter et al., 2020; Jessopp, Cronin, & Hart, 2013; Vincent et al., 2017), and one seal tagged in Ireland was observed breeding in Wales (unpublished data), suggesting a lack of demographic isolation. In the absence of evidence of such, 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. Luck, Cronin, et al. (2020) identified environmental drivers of bycatch, including water turbidity, which will likely affect the rate of bycatch experienced in 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 (Luck, Jessopp, et al., 2020). 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 50 km of the coast (Cronin, Pomeroy, & Jessopp, 2013; Jones et al., 2015), it may be these vessels that seals in Ireland interact with the most. This is not unique to Ireland, small-scale fisheries are poorly monitored globally, despite potentially experiencing higher levels of protected species bycatch than larger fisheries (Alfaro-Shigueto et al., 2011; Lewison et al., 2014; Peckham et al., 2007; Rogan et al., 2021).

In Ireland, the highest levels of seal bycatch potentially occur off the southwest and south coasts (Luck, Jessopp, et al., 2020), 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 (Luck, Jessopp, et al., 2020). 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.

4.2. Conclusion and recommendations

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. 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 these 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 and wildlife management to effectively conserve the grey seal population in Western Europe.

These findings also provide a framework for future studies and monitoring efforts to reduce the uncertainty around potential impacts 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 significantly narrow confidence intervals around total bycatch estimates. Collection of simple biometric data, including length and sex of bycaught seals 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 (Benoît & Allard, 2009; Gilman, Brothers, & Kobayashi, 2005).
- 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.
- In Ireland, comprehensive surveys of the grey seal breeding population have only occurred twice in the past 15 years (Ó Cadhla et al., 2013, 2007), 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.
- New methodologies are consistently being developed to effectively assess and manage marine mammal bycatch in data-poor environments (e.g. Brandon et al., 2017; Punt, Sepúlveda, et al., 2021; Punt, Siple, et al., 2021), many of which could be applicable to grey seal bycatch in the Northeast Atlantic.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2022.126157. See supplementary material for a detailed discussion of the assumptions and limitations of the PVA models presented in this study, and graphical representation of the binomial distribution used to apply an age-based distribution of bycatch mortality.

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