



Quantifying the impacts of predation by Great Black-backed Gulls *Larus marinus* on an Atlantic Puffin *Fratercula arctica* population: Implications for conservation management and impact assessments

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ABSTRACT

The management of predator-prey conflicts can be a key aspect of species conservation. For management approaches to be effective, a robust understanding of the predator-prey relationship is needed, particularly when both predator and prey are species of conservation concern. On the Isle of May, Firth of Forth, Scotland, numbers of breeding Great Black-backed Gulls *Larus marinus*, a generalist predator, have been increasing since the 1980s, which has led to increasing numbers of sympatrically breeding Atlantic Puffins *Fratercula arctica* being predated during the breeding season. This may have consequences for species management on the Isle of May and impact assessments of offshore windfarms in the wider Firth of Forth area. We used population viability analysis to quantify under what predation pressure the Atlantic Puffin population may decline and become locally extinct over a three-generation period. The predation level empirically estimated in 2017 (1120 Puffins per year) was not sufficient to drive a decline in the Puffin population. Rather, an increase to approximately 3000 Puffins per year would be required to cause a population decline, and >4000 to drive the population to quasi-extinction within 66 years. We discuss the likelihood of such a scenario being reached on the Isle of May, and we recommend that where predator-prey conflicts occur, predation-driven mortality should be regularly quantified to inform conservation management and population viability analyses associated with impact assessments.

1. Introduction

Predators may exert top down control on prey abundance and thereby shape food-web structure (Berger et al., 2001; Crooks and Soulé 1999; Johnson et al., 2007). However, expanding human activities and environmental change across terrestrial and marine ecosystems have led to drastic changes in habitat quality and availability, altering the communities that inhabit them, including the structure of trophic interactions within and between levels and their influence on ecosystem dynamics (Sinclair and Byrom 2006). Species that are intrinsically more adaptable to change, i.e. generalists, may then gain a competitive advantage over less adaptable species, i.e. specialists (Peery and Henry 2010), leading to potential wildlife conflicts (Garrott et al., 1993).

Predation pressure by native or non-native predators can be responsible for population declines and extinctions of prey species, and the management of such predator-prey conflicts is a key aspect of species conservation in some contexts (Doherty and Ritchie 2017; Engeman et al., 2005). Typically, the primary aim of management strategies is the reduction of predation pressure through lethal (i.e. culling of predators) or non-lethal methods (e.g. diversionary feeding, fisheries management) (Furness 2021; Russell et al., 2016). For such approaches to be effective, a robust understanding of the predator-prey relationship and the life histories of the species involved is essential (Bowen and Lidgard 2013). The removal of or reduction in predation pressure will only result in the recovery of the prey population when conditions meet the “additive hypothesis” described by Valkama et al. (2005), where predation causes

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excess mortality compared to a scenario where the predator was not present. Additionally, the severity by which prey population growth rate is impacted by predation (and the expected recovery if predation is removed/reduced) depends on which individuals are predated within the population and the life history of the species. Short-lived species with high reproductive outputs experience greater declines in population growth rate when individuals that have not reached breeding age (juveniles and immatures) are removed from the population (Sæther and Bakke 2000). Conversely, in long-lived species with low reproductive outputs, the removal of individuals of breeding age (adults) causes the greatest reduction in population growth (Sæther and Bakke 2000).

As well as prey-focused ecological considerations, activities that result in the lethal management of predators must also consider the conservation status of the predator species. In the case of invasive predators, lethal removal of individuals is justified because the predator population is rarely of concern and native species benefit from their removal (Crowley et al., 2017). However, conflicts involving native predators can be more complex, particularly when predators are also of conservation concern, and conservation managers must select management strategies that ensure the continued viability of both predator and prey populations (Waite and Phillips, 1994).

Where estimates of additive prey mortality are available, Population Viability Analysis (PVA) can be conducted to investigate the impacts of predation and potential management strategies upon prey populations of interest. PVAs require accurate demographic and life-history parameters (including survival, breeding success, age of first breeding, age structure, and an initial population size) which are available in many species from field studies (Beissinger and McCullough 2002). PVA models are then used in this context to project future population sizes under varying predation pressures and to identify predator management interventions that achieve desired conservation goals. As such, they have been used on a number of occasions to inform the management of predator-prey conflicts (Elliott 1996; Peery and Henry 2010; Whitehead et al., 2010).

Within seabird communities, generalist, predatory species from the genera *Larus* (large gulls), *Stercorarius* (skuas), and *Macronectes* (giant petrels) have been identified as potential threats to the viability of populations of other seabird species at local and regional scales due to predation during the breeding season (Bicknell et al., 2013). These generalist predators feed on marine and terrestrial invertebrates, fish that are naturally scavenged or obtained from fishing vessels, small mammals, and seabird eggs, chicks and adults, and switch between them according to their abundance (Gulka et al., 2017). Large numbers of seabirds can be predated by these species every year, which may be of particular conservation concern when adult seabirds are predated due to the low reproductive output of seabird species (Sæther and Bakke 2000). Great Skuas (*Stercorarius skua*) have been estimated to predate over 12,500 seabirds in a single breeding season in the Shetland colony of Hermaness, Scotland (Votier et al., 2004a) and over 21,000 Leach's Storm Petrels (*Oceanodroma leucorhoa*) per year on St Kilda, Scotland (Miles 2010). Giant petrels and skuas were identified as the largest cause of breeding failure in King Penguins (*Aptenodytes patagonicus*) breeding in the Crozet Archipelago in the Indian Ocean (Descamps et al., 2005), and large gulls of several species have been recorded regularly taking eggs, chicks, and adults of other seabirds (Finney 2002; Veitch et al., 2016; Westerberg et al., 2019). Most of these scenarios partially meet the "additive hypothesis" described above because predators likely remove individuals that would have died of other causes (e.g., poor health or disease (Tucker et al., 2016); but also remove individuals that would have otherwise survived. Indeed, population-level consequences of predation have been found in some populations (Heubeck et al., 1999; Oro and Furness 2002). Understanding the dynamics of such seabird-seabird relationships and quantifying the impact of predators on prey populations is therefore key to ensure appropriate management strategies are adopted.

The Great Black-backed Gull (*Larus marinus*) is widespread

throughout North Atlantic coasts and is generally found nesting sympatrically with other seabirds. Great Black-backed Gulls have been recorded to predate the eggs, chicks, and adults of several seabird species, including those of conservation concern such as the Atlantic Puffin (*Fratercula arctica*; hereafter Puffin) and Leach's Storm Petrel, leading to potential wildlife conflicts (Buckley 1990; Harris 1980; Stenhouse and Montevecchi 1999; Westerberg et al., 2019). Similar to other *Larus* gulls, the global population of Great Black-backed Gulls has fluctuated throughout the 20th century (Anderson et al., 2016). The global population size of Great Black-backed Gulls peaked in the latter part of the 20th century but then declined by 48% globally between 1985 and 2021, from approximately 320,000 to 166,000 pairs (Langlois Lopez et al., 2022). Although currently classed as "Least concern" on the IUCN Red List of Species, Langlois Lopez et al. (2022) recommended Great Black-backed Gulls be reclassified as "Vulnerable", increasing the complexity of the management of potential wildlife conflicts in which it is involved.

The Isle of May National Nature Reserve (NNR), Firth of Forth, Scotland, is home to an increasing population of Great Black-backed Gulls, with 120 nesting pairs censused in 2021 (Langlois Lopez S. unpublished data). The island also has an internationally important population of Puffins, with an estimated 39,200 pairs in 2017 (Newell et al., 2017), comprising an important qualifying feature of the Forth Islands Special Protection Area (<https://jncc.gov.uk/jncc-assets/SP-A-N2K/UK9004171.pdf>). Puffins are currently classed as "Vulnerable" on the IUCN Red List of Species and are also included in the United Kingdom Birds of Conservation Concern (Birdlife International 2023; Stanbury et al., 2021). The colonisation of the Isle of May by Great Black-backed Gulls in the 1980s and their subsequent increase in numbers led to larger numbers of Puffins being predated (Harris et al., 2000). In 2001, 27 pairs of Great Black-backed Gulls predated an estimated 191 fully grown Puffins (adults and immatures; juveniles were not counted) (Finney 2002). Bennett (2017) further investigated this relationship when the Great Black-backed Gull population had increased to 87 pairs in 2017, and recorded 1120 Puffin remains, of which 577 were fully grown (i.e. not juveniles). With increasing numbers of breeding Great Black-backed Gulls and potential associated increases in Puffin predation, modelling future Puffin population trends is necessary to inform the management of both predator and prey populations. Additionally, such information is of relevance to impact assessments (Environmental Impact Assessments (EIAs) and Habitats Regulations Assessments (HRAs)) of offshore renewable energy developments in the Firth of Forth area that are predicted to potentially impact the Puffin population of the Isle of May. This is because Puffin predation is not homogeneous across the colony, with some areas experiencing higher predation than others, likely due to the heterogeneous distribution of nesting Great Black-backed Gulls. The sub-colony where adult Puffin survival data is collected on the Isle of May experiences negligible levels of predation. As such, the use of these demographic data in population viability analyses associated with impact assessments will likely overestimate population growth if population-level predation is not accounted for.

In this study, we developed PVAs using long-term data on the demography of Puffins from the Isle of May to model current and future Puffin population growth rates based on different levels of predation from Great Black-backed Gulls. Our aims were to 1) quantify the current impact of Great Black-backed Gull predation on Puffin population growth rate, 2) investigate the potential future effects of different levels of predation on Puffin population growth rate and identify decline and quasi-extinction thresholds; and 3) assess how reductions in Puffin predation as part of management strategies affect Puffin population growth rates.

2. Methods

2.1. Population viability analysis (PVA)

2.1.1. Model structure

Analyses were performed in R version 4.1.2 (R Core Team, 2021) using the “nepva” R package (version 4.13), developed by Butler et al. (2021). A stage-based Leslie matrix model (Fig. 1) was parameterised with demographic rates (survival, breeding success, and age of first breeding) and an initial population size of the target population (Puffin). We used deterministic PVAs, where input parameters were fixed and variance in such parameters was not included, to estimate differences in intrinsic population growth rate (λ) of the Puffin population under varying predation pressure. Additionally, we used stochastic PVAs, where random changes in demographic parameters were included based on probability distributions defined from empirical data, to quantify the probability of population decline and quasi-extinction because they offered a more biologically realistic model that incorporated environmental stochasticity. Both deterministic and stochastic approaches were based on breeding pairs with population counts obtained at the start of the breeding season, and assumed an equal sex-ratio, closed population, and no density dependence.

Breeding success was defined as the mean number of offspring produced per pair annually, and survival was defined as the probability of surviving from one stage class to the next. It was assumed no birds of breeding age skipped breeding, i.e., where birds may choose not to breed on a particular year, because the Puffin population from the Isle of May was considered to be below carrying capacity (see section 2.1.5 in the methods). A schematic representation of the Puffin population dynamics can be found in Fig. 2.

To generate population projections, the initial population vector ($N_1 - N_8$; Fig. 1) was used in combination with the Leslie matrix in the following form:

$$N_{(t+1)} = LN_{(t)}$$

where $N_{(t+1)}$ represented the population size (N) at time $t+1$, L was the Leslie matrix, and $N_{(t)}$ was the population size at time t . The stable age structure of the population was needed to generate the initial population vector. This was provided by the right eigenvector of the Leslie matrix and was obtained using the “popbio” R package (Stubben and Milligan 2007). Additionally, the net rate of population change (λ) was obtained from the dominant eigenvalue of the Leslie matrix.

For the stochastic PVAs, a further step was taken to introduce environmental stochasticity. This was done using the long-term mean and standard deviation of adult Puffin survival and breeding success calculated from empirical studies. For each stochastic PVA, a beta distribution was defined from the survival parameters and a gamma distribution was

$$L = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & m \\ s_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_3 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_4 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_5 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_6 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & s_7 & s_8 \end{bmatrix} \begin{pmatrix} N1 \\ N2 \\ N3 \\ N4 \\ N5 \\ N6 \\ N7 \\ N8 \end{pmatrix}$$

Fig. 1. Leslie matrix representing the dynamics of an Atlantic Puffin population. L is the Leslie matrix. Parameter “ S_a ” reflects the survival of each stage class (i.e., survival per year). Parameter “ m ” reflects the breeding success of breeding birds. Because Atlantic Puffins do not breed before aged seven, the breeding success of birds younger than seven was assumed to be zero. States N_1 to N_8 form the population vector and represent the number of birds in each of the eight stage classes.

defined from the breeding success parameters. These distributions were chosen because survival and breeding success can only be a value between zero and one in Puffins. Random values were sampled from each distribution (representing survival and breeding success, respectively) for each year of the PVA, which were then multiplied by the population vector from the previous year to project the population into the future.

The probabilities of population decline and reaching quasi-extinction were calculated from 10,000 iterations. The probabilities of population decline was defined as the proportion of 10,000 iterations that were $<100\%$ of the initial population size and the probabilities of reaching quasi-extinction as the proportion of 10,000 iterations that declined to $\leq 10\%$ of the initial population size at the end of the period of interest.

2.1.2. Initial population size

The latest available population count from the Isle of May Puffin population was used as the initial population size in all PVAs (39,200 breeding pairs in 2017; Newell et al., 2017). Additionally, PVAs were also run using the lower and upper 95% CIs of this estimate (32,000; 46,333) to account for uncertainty in initial population size.

2.1.3. Assessment period

To assess the effects of varying levels of Great Black-backed Gull predation on the viability of the Puffin population, we ran PVAs over a three-generation period as per the International Union for Conservation of Nature (IUCN Standards and Petitions Committee, 2022) guidance for long-lived species, and as previously done by Anderson et al. (2018) with Northern Fulmars (*Fulmarus glacialis*) to frame population trajectories in a conservation context. One generation length is defined as the average age of breeding birds in a cohort, which for Puffins is 21.6 years (rounded to 22 in this study; Bird et al., 2020). We therefore ran PVAs for a period of 66 years. Additionally, we also presented the results from conservation management scenarios after a period of 30 years since this is the typical lifespan of an offshore windfarm and the time associated compensatory measures would be implemented for (see section 2.2 in the methods).

2.1.4. Puffin demographic parameters

We modelled the mark-resighting history of Puffins breeding on the Isle of May to estimate apparent adult survival over the period 1973–2020. We used a CJS survival state space model to model the true state of individual i at time t ($z_{i,t}$) with an apparent survival probability, $\phi_{i,t}$.

$$z_{i,t+1} | z_{i,t} \sim \text{Bernoulli}(z_{i,t} \phi_{i,t})$$

assuming an observation process for whether individual i at time t was observed ($y_{i,t}$) with detection probability, p , where the detection probability was assumed to be constant across years.

$$y_{i,t} | z_{i,t} \sim \text{Bernoulli}(z_{i,t} p)$$

To assess yearly variation in survival, $\phi_{i,t}$, we assumed survival is a realisation of a random process described by a normal distribution with mean μ and variance σ^2 .

$$\text{logit}(\phi_{i,t}) = \mu + \varepsilon_t$$

$$\varepsilon_t \sim \text{Normal}(0, \sigma^2)$$

where ε_t is the deviation from the overall mean survival probability, μ .

Long-term breeding success (mean number of chicks produced per pair) was collected annually on the Isle of May between 1976 and 2019 from a sample of 200 burrows (Table A1). This was a figure between 0 and 1 because Puffins only lay one egg. Lastly, median age of first breeding (seven years old) was obtained from Isle of May past studies (Harris and Wanless 2011) (Table A1).

There are few estimates of the annual survival of juvenile (birds $<$

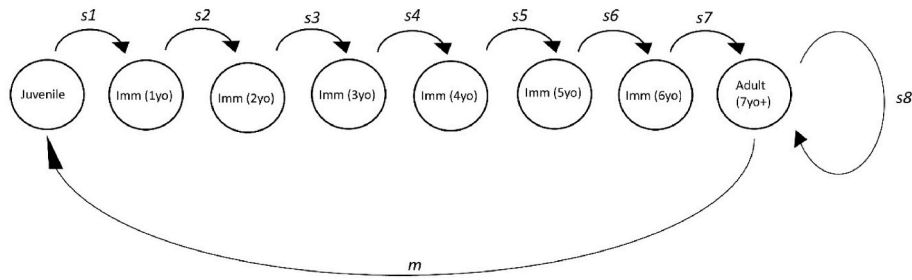


Fig. 2. Flowchart of the dynamics of the Atlantic Puffin population. Parameter “m” represents the breeding success of breeding birds (those seven years old or older), and parameter “s” represents the survival of each age class (i.e., the probability of surviving from one age class to the next). After birds reach breeding age, their breeding success and survival are assumed to remain constant until death. Birds older than seven years were therefore placed in the same stage class (i.e., 7yo+).

one year old) and immatures (birds aged one to seven years old), in published literature and no recent empirical data exist from the Isle of May. This is due to the behaviour of these non-breeding age classes, which do not reliably return to predictable areas in colonies (Harris and Wanless 2011), making capture-mark-recapture studies challenging. Thus, we compared two sources of juvenile and immature survival from past Isle of May studies, which were validated against empirical population counts. Firstly, we used estimates from Harris and Wanless (2011), who suggested juvenile and immature survival between 1973 and 1979 on the Isle of May was extremely high, virtually equal to adult birds, despite the general finding in many species that birds of pre-breeding age experience greater mortality rates than adults (e.g. Common Guillemot *Uria aalge*; Lahoz-Monfort et al., 2017). However, similarly high survival of pre-breeding age Puffins has been found in other colonies (Sandvik et al. 2008). Secondly, we used estimates presented in Harris (1983), who between 1973 and 1983, a slightly longer period, calculated apparent annual immature survival (emigration not included) to be 0.786 on the Isle of May for birds aged 0–5 years old. This equates to an annual survival rate of 0.856 (89% of the adult survival estimated in the same study: 0.96) when accounting for a juvenile emigration rate of 17% (average between 11% and 23% estimated by Harris and Wanless (2011) and Harris (1983), respectively). Thus, the two scenarios considered during parameter validation assumed that either 1) juvenile and immature survival were equal to adult survival, or 2) juvenile and immature survival were 89% of adult survival until aged five, and equal to adults thereafter (Table A1).

2.1.5. Parameter selection and validation

Due to the uncertainty surrounding survival estimates of juvenile and immature Puffins, stochastic PVAs using the two sources of juvenile and immature survival parameters described in section 2.1.4 of the Methods were run and contrasted against existing Puffin population counts from the Isle of May. The source that best reflected the observed Isle of May Puffin population trend was selected to ensure the greatest accuracy when modelling the impacts of Great Black-backed Gull predation.

Because no standard deviations were available for juvenile and immature survival figures, we assumed they were equal to adult standard deviations.

Ten Puffin burrow counts (assumed to represent population size i.e., breeding pairs) were available from the Isle of May between 1975 and 2017 from field studies. Between 1975 and 2003, the population increased from approximately 3000 to 70,000 breeding pairs. However, the population declined to 43,000 in 2008 and then remained relatively stable (panel B in Fig. 3; Newell et al., 2017). This major decline in the early 2000s was attributed to low overwinter survival of adults over two years (0.732 and 0.705 compared to the long-term average of 0.921) rather than to any density dependence or carrying capacity mechanisms at the breeding colony. In fact, Harris et al. (2003) estimated the Isle of May could hold 250,000 Puffin burrows at carrying capacity.

Because the Puffin population fluctuated in size in the early 2000s, we validated stochastic PVAs against two time periods: one including all available population estimates (1975–2017), during which the population expanded and receded, and another, more recent period when the population remained relatively stable (2008–2017). Initial population sizes used in the validation PVAs were 3064 pairs (count from 1975) for those covering 1975–2017, and 42,294 pairs (count from 2008) for those covering 2008–2017. We used the mean adult survival and breeding success from each respective period (Table A1).

Long-term adult Puffin survival data from the Isle of May were collected at a single site within the colony. The site had no breeding Great Black-backed Gulls present, and virtually no predation of adult colour-marked Puffins (i.e., the individuals used to estimate survival) was observed over many years of observations, so we assumed that the demographic parameters used in this study represented a “no Great-black backed Gull predation” scenario within the colony.

Additionally, once the final set of demographic parameters were identified, we ran individual Beta regression models to test for any significant temporal trends in survival or breeding success over the selected validation period since these could potentially bias PVA outputs (Horswill et al., 2022). In these models, adult survival or breeding

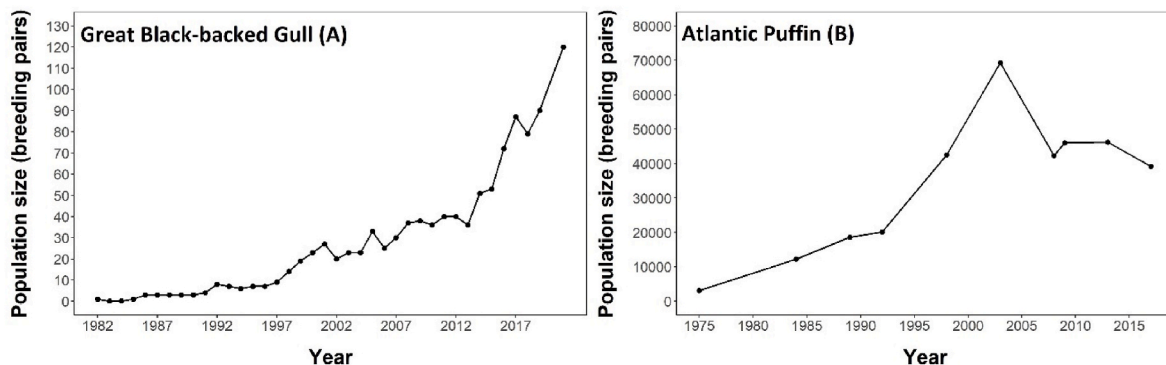


Fig. 3. Empirical population counts of breeding Great Black-backed Gulls (A) and Atlantic Puffins (B) on the Isle of May.

success were the response variables and year was the explanatory variable.

2.2. Impact scenarios

Two past studies have estimated Puffin predation by Great Black-backed Gulls on the Isle of May (Bennett 2017; Finney 2002). Annual predation of full-grown Puffins (adults and immatures) increased from 191 to 577 individuals between 2001 and 2017, a total increase of 302% or a yearly increase of 18.8% (Bennett 2017). Over the same period, the number of breeding Great Black-backed Gull pairs increased from 27 to 87 (panel A in Fig. 3), a change of 322% or a yearly increase of 20.1% (Bennett 2017). This strikingly similar increase between the number of Puffins predated and the number of Great Black-backed Gull pairs suggested that perhaps predation rate per gull has remained consistent between years, which allowed us to extrapolate from Puffin predation figures to Great Black-backed Gull population size when interpreting PVA outputs.

The methodology used by both Finney (2002) and Bennett (2017) to estimate total Puffin mortality on the Isle of May were regular surveys through the Great Black-backed Gull colony and main foraging areas during the 2017 breeding season. Bennett (2017) collected data between the 17th of April and the 25th of July to provide the most recent estimate from 2017. All Puffin carcasses were removed from gull territories and aged as either adult, immature, or juvenile based on bill characteristics and plumage following Harris (2014). It is likely this methodology underestimated total Puffin mortality since some carcasses would have inevitably been missed, but it served as a starting point for our modelling, and it was the only empirical estimate of Puffin predation in recent years.

To investigate the effects of higher levels of Puffin predation, our models used the predation values recorded by Bennett (2017) in 2017 (1120 Puffins) as a starting point (Table A2). Following such initial scenario, we then ran additional scenarios (i.e., separate PVAs) in which predation was 10% higher than in the previous one until the population reached extinction. Predation remained static (i.e., the absolute number of Puffins predated per year stayed constant) throughout the 66 years of each scenario. Additionally, we also included a “no Great Black-backed Gull predation” scenario.

Because wind energy developers or conservation managers may seek to improve Puffin demographic parameters as part of compensatory measures or conservation management, we ran additional PVAs where Puffin predation was reduced by 100 and 550 individuals per year in a scenario where 1120 Puffins were predated per year (i.e., the 2017 predation level estimated by Bennett 2017). These figures were chosen because 100 individuals is a representative example of the direct mortality caused by an anthropogenic development such as an offshore windfarm, and therefore, might be a value set for an associated compensatory measure involving predator control (e.g., Appropriate Assessment of the Beatrice Offshore Windfarm Limited development in the Outer Moray Firth; Marine Scotland 2004). Additionally, 550 individuals was the estimated number of Puffins predated by specialist Great Black-backed Gull pairs in 2017 (Bennett 2017), and exemplified a scenario with a more severe control of predation.

We encountered two limitations when incorporating predation in the PVAs. Firstly, the “nepva” R package did not allow us to independently manipulate the relative predation of juveniles and each immature age class (e.g., we could not specify that one year-old birds were predated in higher numbers than three year-old birds), but it did allow us to differentiate between adults and immatures/juveniles. Secondly, immature Puffins (birds between one and seven years old) cannot be assigned to a specific age class beyond “immature” based on their bill or plumage characteristics, so it was not known whether immatures of different ages were predated in different proportions in Bennett’s (2017) data. It was known that 40.3% of Puffins predated on the Isle of May in 2017 were adults, and that the remaining 59.7% were juveniles and

immatures (Bennett 2017). We thus summed the number of predated juvenile and immature individuals and divided them equally between each immature and juvenile age class in all PVA predation scenarios to mitigate these limitations (Table A2). The same approach was taken in the conservation management scenarios.

3. Results

3.1. Parameter selection and validation

Overall, outputs from validation PVAs covering years 1975–2017 fitted empirical Puffin counts poorly, with virtually all empirical counts outside the models’ 95% CIs (Fig. 4). PVAs generally underestimated population growth between 1975 and 2000, even in scenario A1 which assumed juvenile and immature survival to be equal to adults, which suggests there were additional factors, such as immigration, affecting population growth between 1973 and 2003. PVA outputs for 2008–2017 fitted Puffin counts more accurately. Scenario A2 overestimated population growth, with two of three counts within the 95% CIs. However, Scenario B2, which assumed juvenile and immature survival to be 89% of adult survival until aged five, showed a better fit with all population counts within the 95% CIs of the projected population size (Fig. 4). Demographic parameters from Scenario B2 were therefore considered to best reflect the dynamics of the Isle of May Puffin population in recent years and were used to model the effects of predation by Great Black-backed Gulls (Table 1).

There were no significant temporal trends between 2008 and 2017 in adult survival (estimate = 0.007, (SE = 0.037), z-value = 0.203, p-value = 0.839) or breeding success (estimate = 0.051 (SE = 0.035), z-value = 1.433, p-value = 0.152). We were therefore confident the static parameters used in this study (Table 1) were representative of the population.

3.2. Deterministic PVAs

The mean Puffin population growth rate (λ) over 66 years was >1 for all three initial population sizes under the predation level estimated on the Isle of May in 2017 of 1120 Puffins. However, λ was lower compared to a no-predation scenario. Using an initial population size of 39,200 breeding pairs, the forecast end population would be 34% ($\lambda = 1.0170$) larger after a projected 66 years if there was no predation compared to a population where 1120 Puffins are predated per year ($\lambda = 1.0125$).

Differences in initial population size resulted in λ falling below the threshold of a stable population (i.e., 1) at different predation levels. For the smallest population size of 32,000 (lower 95% CI) the population declined ($\lambda < 1$) when predation >2500 Puffins per year (over two times the predation level estimated in 2017). Assuming a consistent predation rate per gull irrespective of Great Black-backed Gull population size, this level of predation would require 194 pairs of Great Black-backed Gulls. The threshold increased to >3000 (233 Great Black-backed Gull pairs) and >3400 (264 Great Black-backed Gull pairs) Puffins per year for initial population sizes of 39,200 (mean) and 46,333 (upper 95% CI), respectively (top panel in Fig. 5).

At a mean yearly increase in Puffin predation of 18.8% (as recorded between 2001 and 2017), the predation threshold needed to induce a decline in a Puffin population of 39,200 breeding pairs (>3000 Puffins per year) would be reached in six years from 2017 (i.e., 2023).

3.3. Stochastic PVAs

The probability of remaining above the initial population size, a useful measure of the probability of decline, declined with increasing Puffin predation over 66 years (bottom panel in Fig. 5). At predation levels measured on the Isle of May in 2017 (1120 Puffins), the probability of remaining above the initial population size after 66 years was $>95\%$ for all three initial population sizes (i.e., the probability of decline

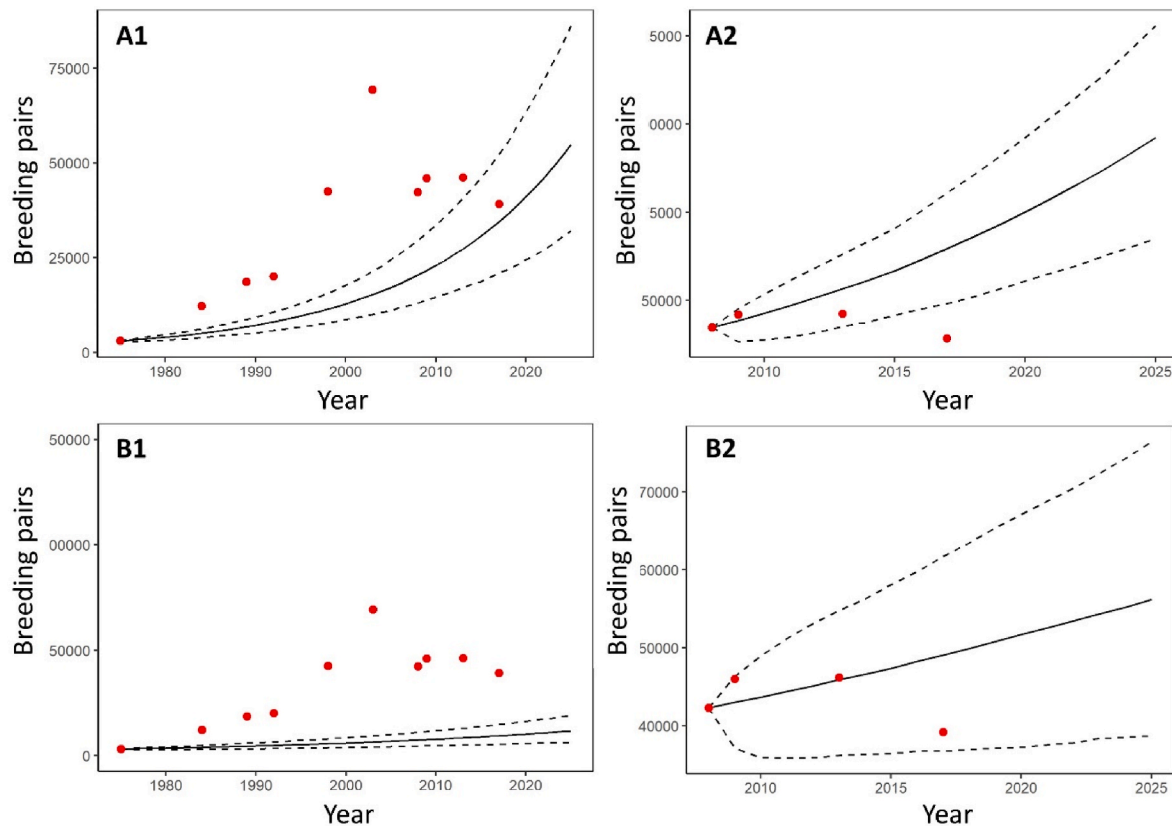


Fig. 4. Stochastic PVA outputs comparing two sources of Atlantic Puffin juvenile and immature survival over two periods. Panels containing the letter “A” used juvenile and immature survival rates that were equal to adults, whereas panels containing the letter “B” used juvenile and immature survival that were 89% of adult survival until aged five, and equal to adults after then. PVAs were run over two periods; 1975–2017 (reflected by the number 1), and 2008–2017 (reflected by the number 2). Lastly, points represent empirical estimates of breeding pairs of Atlantic Puffin on the Isle of May.

Table 1

Atlantic Puffin demographic parameters that best fit empirical population estimates from the Isle of May between 2008 and 2017 identified through stochastic Population Viability Analyses.

Parameter	Mean	SD
Juvenile survival (0–1 years)	0.811	0.057
Immature survival (1–2 years)	0.811	0.057
Immature survival (2–3 years)	0.811	0.057
Immature survival (3–4 years)	0.811	0.057
Immature survival (4–5 years)	0.912	0.057
Immature survival (5–6 years)	0.912	0.057
Immature survival (6–7 years)	0.912	0.057
Adult survival (7+ years)	0.912	0.057
Breeding success	0.71	0.10
Age of first breeding (median)	7	–

was <5% after 66 years). This probability decreased to 50% after 66 projected years when approximately 3000 Puffins were predated per year in a population of 39,200 pairs.

The probability of quasi-extinction (i.e., the probability of the population reaching $\leq 10\%$ of its initial size) after 66 projected years increased with increasing predation (Fig. 6). Under the 2017 predation level (1120 Puffins per year), the probability of quasi-extinction was 0% for all three populations. Quasi-extinction probability then increased with increasing predation and was influenced by initial population size. For an initial population of 32,000 breeding pairs, quasi-extinction probability reached >90% when predation was >4000 Puffins per year. This same quasi-extinction probability was reached when predation increased to >5600 and > 6100 Puffins per year for initial population sizes of 39,200 and 46,333 breeding pairs, respectively.

3.4. Conservation management scenarios

Deterministic PVAs showed management scenarios increased mean Puffin population growth rate (λ). Assuming a predation rate of 1120 Puffins per year, reductions in predation by 100 and 550 individuals per year resulted in final Puffin population sizes 1.6% and 8.7%, and 3% and 16% larger after a period of 30 and 66 years, respectively, than if predation had not been reduced (Table 2).

4. Discussion

In this study we quantified the impacts of predation by Great Black-backed Gulls on a Puffin population using Population Viability Analysis. To inform conservation management, we estimated predation thresholds above which the decline and quasi-extinction of the Isle of May Puffin population would be expected, and we demonstrate the importance of accounting for such predator-prey relationships in Environmental Impact Assessments and Habitats Regulations Assessments of marine anthropogenic developments.

4.1. Predation impacts

Deterministic PVAs showed Puffin predation levels estimated on the Isle of May in 2017 limited Puffin population growth compared to a no-predation scenario but were not severe enough to induce a population decline. Predation would need to increase almost three-fold to >3000 Puffins per year to cause a decline in a population of 39,200 breeding pairs. This was further supported by stochastic PVAs, which estimated there was a 0% probability of population quasi-extinction and <5% probability of decline within 66 projected years under the predation

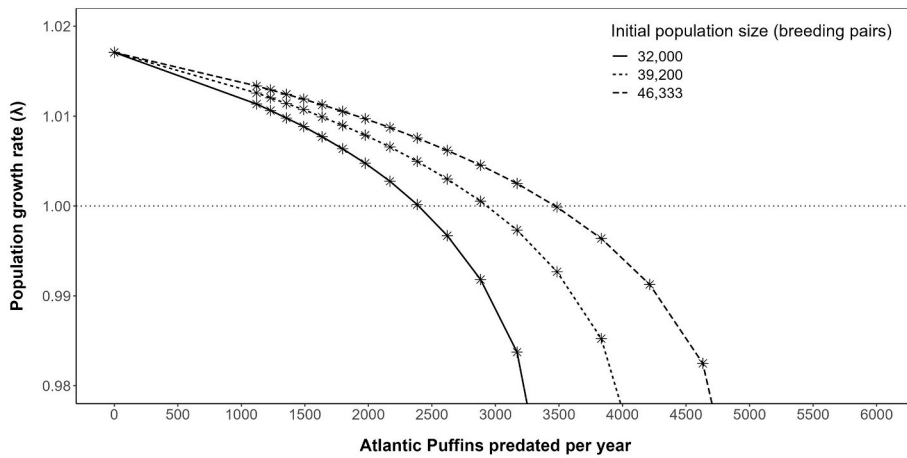


Fig. 5. Top panel – deterministic PVA output showing the mean population growth rate (λ) over 66 years as a function of Atlantic Puffin predation for a combination of three different initial population sizes. Predation was 10% higher in each scenario (asterisks), commencing at 1120 birds. A point representing a no-predation scenario is also included. Additionally, the threshold for a stable population ($\lambda = 1$) is marked by a horizontal, dotted line. Bottom panel – stochastic PVA output showing the probability of the Atlantic Puffin population remaining above the initial population size after a period of 66 years as a function predation. Predation was 10% higher in each scenario (asterisks), commencing at 1120 birds, which was marked by a vertical, dotted line. A scenario of no-predation is also included.

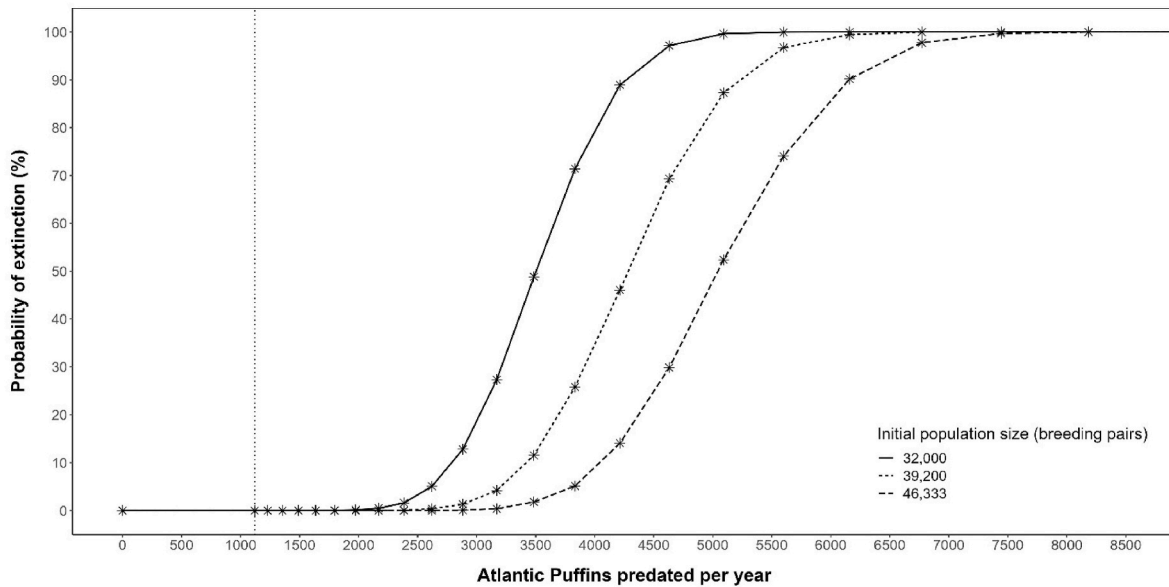
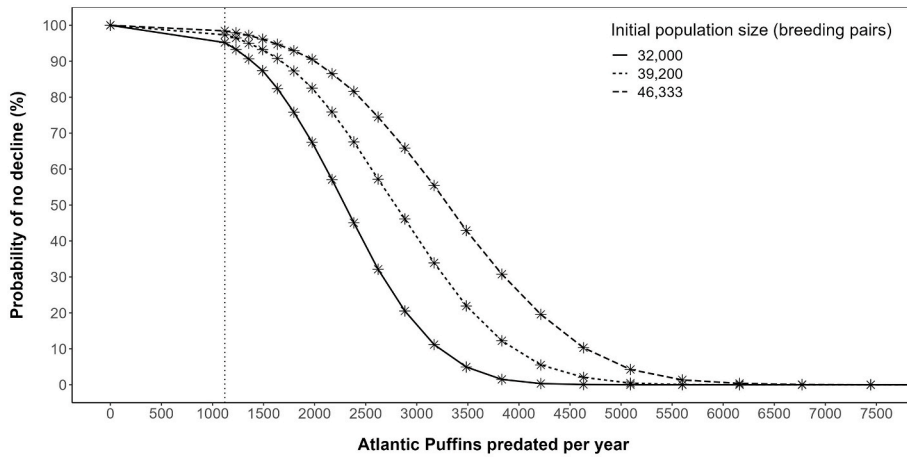


Fig. 6. Probability of the Atlantic Puffin population reaching quasi-extinction (i.e., probability reaching $\leq 10\%$ of its initial population size) after 66 years as a function of predation. Predation was increased in 10% steps (asterisks), commencing at 1120 birds (vertical, dotted line), which was the estimated predation level on the Isle of May in 2017. A scenario of no-predation is also included.

level recorded in 2017. The probability of population decline increased to 50% (equivalent to $\lambda = 1$) when predation increased to approximately 3000 Puffins per year, and the quasi-extinction probability reached 90% when >4000 Puffins were predated per year in a population of 39,200

breeding pairs, showing agreement between the deterministic and stochastic models.

Between 2001 and 2017, Puffin predation increased at a yearly rate of 18.8%, very similar to the increase in Great Black-backed Gull

Table 2

Comparison of estimated Atlantic Puffin population growth rate (λ) and proportional difference in population size after a period of 30 and 66 years between a scenario where 1120 Puffins are predated per year, and scenarios where Atlantic Puffin predation was reduced by 100 and 550 individuals per year. Values were obtained from deterministic PVAs using the Atlantic Puffin population estimate from the Isle of May in 2017 (39,200 breeding pairs) as the initial population size.

Scenario	Mean λ (30 years)	Mean λ (66 years)	30-year pop. size (%)	66-year pop. size (%)
2017 predation	1.0115	1.0125	100.0	100.0
Atlantic Puffin predation reduction by 100 individuals	1.0120	1.0130	101.6	103.2
Atlantic Puffin predation reduction by 550 individuals	1.0143	1.0149	108.7	116.5

breeding pairs of 20.1% per year. Assuming predation has continued to increase at such a rate since 2017, predation would reach the unsustainable figure of 3000 Puffins imminently in the 2023 breeding season, leading to a population decline from that season. Furthermore, given that Bennett's (2017) figure of 1120 Puffins per year was most likely an underestimation of Puffin mortality, 3000 Puffins per year could have been reached already. Assuming a constant predation rate per gull regardless of gull population size, 233 pairs of gulls would be required to kill 3000 Puffins per year. However, such a population size is unlikely to be reached by 2023, with only 120 pairs censused in 2021, equivalent to a 9.1% annual increase between 2017 and 2021, showing population growth has slowed down in recent years (Langlois Lopez et al., 2022. Unpublished data; Outram and Steel 2018). Ultimately, it is unknown whether the Great Black-backed Gull population could reach 233 breeding pairs. The species has declined by 48% globally in the last 36 years and declines are still ongoing (Langlois Lopez et al., 2022). More specifically, the breeding population in Scotland was estimated to be 69% smaller in 2018 than in 1986, and some of the largest colonies such as those in Orkney, Shetland, and the Outer Hebrides have experienced even larger declines, from hundreds or thousands of breeding pairs down to single figures (JNCC 2021). With decreasing populations elsewhere in Scotland, the Isle of May is perhaps acting as a sink population, receiving individuals from decreasing populations. Based on the current nesting density and distribution of breeding Great Black-backed Gulls on the Isle of May, the carrying capacity of the island likely exceeds the number of pairs required to induce a decline in the Puffin population. Whether the figure of 233 breeding pairs is reached will likely depend on immigration rates and the population's dynamics.

The critical threshold of 3000 Puffins killed per year could also be reached through changes in gull diet rather than changes in population size. Smaller Great Black-backed Gull populations have been recorded predated greater numbers of seabirds than what is currently predated on the Isle of May. For example, over 2600 fully-grown Puffins were predated by 40 Great Black-backed Gull pairs in a single breeding season on St Kilda (Harris 1980), and in some colonies seabirds make up most of the gull population's diet during the breeding season (Westerberg et al., 2019). Through the predation surveys carried out by Bennett (2017) on the Isle of May, it was apparent some pairs of Great Black-backed Gulls were Puffin specialists, whose diet was over 50% Puffin during the breeding season. Specialists predated an estimated 546 fully-grown and juvenile Puffins (approximately 49% of total predation). The figure of 3000 Puffins predated per year is thus within reach at the current gull population size of 120 breeding pairs if the number of specialist pairs increased, or if there was a general increase in Puffin predation across the population. The likelihood of this occurring is unknown. However, there is evidence of increased seabird predation by Great Skuas when the availability of other marine resources such as fish discards and shoaling

fish decreased (Oro and Furness 2002; Votier et al., 2004b). The facultative nature of Great Black-backed Gulls means they likely respond to the same mechanisms and Puffin predation could increase if the availability of other marine and terrestrial food sources decreases during the breeding season.

4.2. Conservation management and impact assessments

Seabirds are exposed to several cumulative threats that act simultaneously upon their populations such as invasive species, bycatch from fisheries, climate change, wildlife conflicts, and anthropogenic developments (Crocoll et al., 2012; Dias et al., 2019). This means that populations where predator-prey conflicts take place are not exempt from further potential anthropogenic impacts.

The Firth of Forth, Scotland, is an area undergoing rapid expansion of offshore wind energy developments, several of which are in the vicinity of the Isle of May seabird populations and could potentially impact them (The Crown Estate, 2021). Wind energy developers are required to carry out impact assessments, where impacts on population growth rates are generally quantified using PVAs, and, for any negative effects that are considered unacceptably high by regulators, must propose compensatory measures if mitigation options are not sufficient. We therefore included two scenarios of conservation management in our analysis of interest to offshore wind developers and conservation managers. We showed reductions in predation of 100 and 550 Puffins per year successfully yielded populations 1.6% and 8.7% larger after a period of 30 projected years, which is the average lifespan of a windfarm and the period over which compensatory measures would be active, assuming a predation level equivalent to the one estimated on the Isle of May in 2017. Additionally, populations 3.2% and 16.5% larger could be achieved if such reductions in predation were applied over 66 years.

4.3. Implications of this study and recommendations

Predation levels on the Isle of May in 2017 were not sufficient to result in a decline in the Puffin population and predation would have to increase to 3000 Puffins per year to induce a decline within 66 years. Two possible mechanisms could lead to such a figure being reached: increases in Great Black-backed Gull population size or changes in diet preferences, or a combination of both. Gull population counts are undertaken annually on the Isle of May, as well as capture-mark-recapture studies to estimate Puffin annual survival. However, additive mortality (i.e., the increased mortality of puffins that would have otherwise survived the breeding season had they not been predated) is rarely estimated. These data can singlehandedly inform whether predation approaches unsustainable levels and whether per capita Puffin predation changes over time. Thus, we recommend regular surveys (as described by Bennett (2017)) are incorporated into standard monitoring on the Isle of May to estimate annual Puffin mortality during the breeding season in addition to population counts. Within these surveys, the ageing of Puffin carcasses into juveniles, immatures, and adults, following Harris (2014), is also highly recommended to improve the accuracy of predation impact modelling as part of conservation management decisions and impact assessments.

Conservation management scenarios showed that reasonable increases in the Puffin population size and growth rate of between 1.6% and 8.7% after 30 years could theoretically be achieved through reductions in predation of between 100 and 550 Puffins per year. Such reductions in seabird predation by *Larus* gull species have been typically achieved through lethal control of the predator (Oro and Martínez-Abraín 2007). However, Great Black-backed Gulls have recently been identified as a species of conservation concern. They are on the Amber Birds of Conservation Concern list in the United Kingdom (Stanbury et al., 2021), and it is recommended their IUCN Red List status is changed from "Least Concern" to "Vulnerable" as a result of recent declines in population size (Langlois Lopez et al., 2022). The use of lethal

control on Great Black-backed Gulls to reduce Puffin predation, as a conservation measure or as a compensatory measure for negative effects of renewable energy developments on Puffins, is therefore unlikely to be considered appropriate. Therefore, any management decisions where the predation of other seabird species by Great Black-backed Gulls is of conservation concern should look to employ non-lethal methods to achieve such goals, such as fisheries management, diversionary feeding of predators, or the removal of invasive mammalian predators to improve seabird demographic parameters elsewhere (Furness 2021).

Offshore wind developers are required to carry out impact assessments during consenting phases where expected seabird mortality is modelled and PVAs are used to estimate impacts on population growth (Cook and Robinson 2017; Jitlal et al., 2017). Seabird predation that occurs at the scale recorded on the Isle of May or other colonies with a large presence of seabird predators may have consequences on the population dynamics of the prey species. However, this additive mortality may not be captured by mark-capture-recapture studies if, within a colony, demographic data is collected at sites where no predation takes place. More importantly, impact assessments often extrapolate demographic data from other populations when no data exists from the population of interest (Beissinger and Westphal, 1998; Horswill et al., 2022). Seabird predation can vary significantly between populations even at local scales (Anker-Nilssen et al., 2023), which may lead to PVAs overestimating population growth if demographic data from a predation-free population are used to represent the dynamics of a predation-impacted population.

The validation of PVA outputs against empirical population counts is an essential step to ensure appropriate demographic parameters are selected and minimise bias (Searle et al., 2020; Horswill et al., 2022). During model validation we encountered two limitations. Firstly, none of our stochastic PVAs were able to recreate the observed rapid increase in the Puffin population in the late 20th century and subsequent decline in the early 2000s (panel B in Fig. 3). This was partly due to the nature of PVAs, which use static demographic parameters to recreate population dynamics and do not cope well with fluctuating populations. Past studies that used integrated population models, which combine yearly demographic parameters with empirical population counts, were able to recreate the fluctuations of the population (Lahoz-Monfort et al., 2017). Additionally, other mechanisms for which no empirical data was available, such as immigration, had been demonstrated during the time when the Isle of May Puffin population was increasing rapidly (Harris 1977). We were able to overcome this by validating stochastic PVA outputs against a more recent period (2008–2017) once the Puffin population had stabilised. Over this period our models were able to accurately reflect the dynamics of the Isle of May population with all empirical counts within 95% CIs. Secondly, survival data from juvenile and immature long-lived, pelagic seabirds such as Puffins generally represent a knowledge gap because these age groups do not reliably return to predictable areas within breeding colonies where they can be resighted, making capture-mark-recapture studies challenging (Harris and Wanless 2011). These data were only available over very few, early years of the validation periods of 1975–2017 and 2008–2017 on the Isle of May. We therefore considered two sources of juvenile and immature survival estimates, with values from Harris (1983) producing the best fit in validation PVAs. Overall, this validation procedure highlighted some aspects of seabird population dynamics which are still poorly understood and require further work, in particular net movements between populations of all age classes and survival rates of juvenile and immature seabirds, both of which require labour-intensive, multi-colony fieldwork to gather the necessary data.

When accurate demographic parameters are used and PVAs are validated against empirical counts, this approach provides a useful tool for informing the management of predator-prey conflicts. The robust applicability of such an approach with site-specific data and model validation, however, requires the establishment of multi-year work, particularly if a large enough sample size of population counts for

validating PVAs is needed. We therefore highlight the importance of long-term studies and the need to establish monitoring prior to the management of predator-prey conflicts so demographic data that appropriately reflects the dynamics of the populations of interest are collected and avoid data extrapolation from populations with potentially different predation dynamics.

4.4. Conclusion

Predator-prey conflicts are widespread across the world's oceans and their management has become a key aspect of species conservation. Conservation managers are often faced with challenges regarding the implementation of predator management strategies due to a lack of comprehensive mechanistic understanding and quantification of predation pressure. When demographic data and population counts are available, Population Viability Analysis is a valuable tool to quantify predation. We demonstrated how empirical estimates of predation can be incorporated into PVAs to assess predation impacts on a population, establish predation thresholds that lead to decline and quasi-extinction, and inform impact assessments of anthropogenic developments, including the effectiveness of compensatory measures and improved accuracy of population viability analyses.

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Author statement

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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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2023.105994>.

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