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RESEARCH ARTICLE

Building quantitative resources using PVA to assess the responses of UK seabirds to extrinsic threats

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Abstract

1. Seabird populations are exposed to a wide range of threats from anthropogenic activity, and many species are rapidly declining. For decision-makers and practitioners to give advice on the impacts of human activities and design of mitigation or compensation strategies, understanding how impacts to key demographic rates influence population dynamics and trajectories across different species is essential. Importantly, practitioners must do so in the context of the resources and information that are available to them.
2. In this study, we build a quantitative resource using population viability analysis (PVA) that allows comparative assessment of resultant population outcomes following a wide range of impacts to breeding success and survival. We project population responses at different sizes and under varying density-dependent regulation scenarios using a commonly utilised impact assessment tool. We examine positive and negative impact scenarios, with a view to quantifying the effectiveness of theoretical management measures. We use five UK seabird species representing a range of life-history strategies.
3. By running over 100,000 population models testing the responses of five seabird species to a variety of impact scenarios, we present a wide range of population projections in response to impacted seabird demographic rates. Broadly, we find that species differ as expected in sensitivity to changes in breeding success and survival according to their life-history strategies. We demonstrate the importance, within and between species, of including density-dependent regulation in population dynamics, even within a simple comparative resource such as this. Finally, we show population responses to interactions between degree and duration of impact to demographic rates, although we found little interspecific variation here.

4. *Practical implications*. We provide a comprehensive and valuable resource that could help inform decisions around development planning and consenting. This resource allows practitioners and users to readily consider quantitative scales of impact for various 'realistic' scenarios when making preliminary assessments of potential impacts of new developments on seabirds, without necessarily performing detailed quantitative population modelling, while incorporating critical processes such as density dependence. It could also inform the design and evaluation of potential interventions as part of strategic compensation and wider conservation measures to sustain declining populations.

KEYWORDS
breeding success, demography, density dependence, environmental impact assessment, population dynamics, population viability analysis, seabird

1 | INTRODUCTION

Seabirds are a highly threatened group of organisms, with 47% of species declining, and 1 in 3 species considered globally threatened (Phillips et al., 2023). Seabirds are highly mobile species that straddle both terrestrial and marine habitats, as well as utilising large stretches of the globe: This makes them vulnerable to trans-national pressures from both land and sea. These anthropogenic pressures include the removal of food resources by fisheries (Frederiksen et al., 2008), bycatch mortality (Clay et al., 2019), pollution and waste (Roman et al., 2021; Votier et al., 2005), the introduction of non-indigenous species (Oppel et al., 2022), the spread of pathogen-borne diseases (Falchieri et al., 2022), harvesting (Inch et al., 2024) and large-scale disturbance and displacement (BirdLife International, 2022). Seabirds are also likely to be profoundly affected by global climate breakdown, which may affect food availability, increase the frequency of marine heatwaves and storm surges and enhance the spread of pathogen-borne disease (Fuller et al., 2012; Mitchell et al., 2020; Schoen et al., 2022).

The globally vulnerable status of seabirds has driven conservation efforts on regional and local scales, particularly in areas where they are abundant or ecologically and culturally significant (BirdLife International, 2022), and in many regions they fall under legislative protections. In the United Kingdom, which hosts internationally important breeding populations across 25 species (Burnell et al., 2023), varied approaches have been used to evaluate seabird sensitivity to anthropogenic activities, with the aim of effectively targeting conservation efforts and prioritising highly vulnerable species and populations. These include both holistic (Rogerson et al., 2021; Spencer et al., 2022) and trait-based (Furness et al., 2013) species-specific and multi-species assessments, as well as broader ecological component assessments for the marine environment as a whole (Borgwardt et al., 2019). These assessments are derived qualitatively from existing literature and expert elicitation, and assess the vulnerability of UK seabird populations to specific anthropogenic pressures. Such assessments provide invaluable insights into the relative vulnerabilities of different species to activities and pressures, and/or broad-scale challenges that may affect multiple species. However, qualitative assessments cannot be used to establish and/or compare consequences of potential impacts on population dynamics, which requires quantitative estimates of demographic impact. This is especially crucial where the degree and duration of impacts may interact. Quantitative understanding of the ways in which ranges of plausible impacts to demographic rates by combinations of activity and pressure affect seabird populations would facilitate more precise planning and conservation action. This in turn would engender better understanding of priority impacts for specific populations.

In the United Kingdom, new marine developments are required to assess and, where possible, mitigate, their likely impact to local populations of seabird using environmental impact assessments (EIAs) (Green et al., 2016; Horswill et al., 2017). These can vary in complexity from purely qualitative assessments to quantitative predictions of population responses to changes in key demographic processes, such as survival and breeding success. Population viability analysis (PVA) is a commonly used framework for making relative quantitative predictions using a simplified representation of population dynamics (Maclean et al., 2007; Reed et al., 2002). While there is a body of work examining the use of PVA for seabirds and many other groups (Horswill et al., 2021; Jitlal et al., 2017; Miller et al., 2019), high data requirements and uncertainties in input parameters mean that the majority of PVAs used in seabird EIAs do not include processes such as density-dependent regulation of demographic rates (Horswill & Robinson, 2015; Howells et al., 2023). The exclusion of positive density-dependent regulation of breeding success is likely to produce outcomes that underestimate impact on small, declining populations, while omitting negative regulation may produce assessments that are overly precautionary and allow for unrealistic unconstrained population growth (Horswill et al., 2017; Merrall et al., 2024). Evidence is therefore lacking to make effective comparisons of plausible population outcomes resulting from impact on a multi-dimensional scale (i.e. incorporating the interacting effects of different impact degrees and

TABLE 1 Species demographic inputs.

Species	Age at first breeding	Maximum brood size	Breeding success (chicks per nest)	Adult survival	Juvenile survival (0–1)	Immature survival (>1)	Incidence of skipped breeding	Population sizes
Black-legged kittiwake	4	3	0.683	0.803	0.79	0.7965 (1–4)	0.180	100, 1000
Common guillemot	6	1	0.626	0.901	0.56	0.792 0.917 0.938 0.9195 (4–6)	0.079	1000, 10,000
European shag	2	4	1.46	0.800	0.513	0.737	0.42	100, 1000
Northern fulmar	9	1	0.414	0.936	0.845	0.845 (1–9)	0.050	100, 1000
Northern gannet	5	1	0.643	0.935	0.483	0.829 0.891 0.895 0.81	NA	1000, 10,000

Note: Age at first breeding, maximum brood size, breeding success, survival and incidence of skipped breeding, assigned from Tyler et al. (In review, updated from Horswill & Robinson, 2015). Population sizes representing 'small' and 'large' populations are approximated using seabird census 2023 data on breeding populations in the United Kingdom (Burnell et al., 2023).

durations, and varying population dynamics). PVA can be a powerful tool for producing quantitative evidence, but the lack of evidence described above coupled with uncertainty around the precise impacts of anthropogenic activities and pressures, make its effective application challenging.

In this study, we demonstrate how the strengths of population viability analysis (PVA) can be harnessed to develop a quantitative resource that complements existing broad qualitative sensitivity assessments while satisfying some of the more detailed quantitative requirements of certain environmental impact assessments (EIAs). This resource will enable practitioners to rapidly and easily compare the effects of different impact types on key demographic rates, both within and across species. We use a widely used practitioner PVA tool to model the population consequences of 841 scenarios of impact on five UK species of seabird under three formulations of density dependence. We demonstrate responses of theoretical populations under scenarios spanning varying impact magnitudes and acute to chronic impact durations (1, 3, 5, 10 and 25 years). These durations were chosen to reflect the range of duration of anthropogenic activities and environmental pressures, enabling the comparison of:

1. How seabird populations respond to combinations of impacted survival and breeding success, and how response varies between species with contrasting life-history strategies.
2. How population and species responses to combinations of impacted breeding success and survival vary with the addition of positive and negative density-dependent regulation of breeding success.
3. How the degree and duration of impact to demographic rates interact to affect population outcomes in different seabird species.

We model both positive and negative impact on demographic rates to reflect the growing use of compensatory measures employed to reduce existing pressures on seabirds, and offset residual impacts from offshore wind and other marine developments (Furness & Furness, 2025; McGregor et al., 2022). In doing so, we demonstrate how an accessible library of pre-modelled population trajectories can be developed using existing tools and data currently available to practitioners. This resource can be used for a comparative approach to support more informed conservation decision making and streamline marine development consenting processes.

2 | MATERIALS AND METHODS

2.1 | Projecting impact using PVA

We ran PVAs for theoretical populations of five seabird species to examine how a range of demographic impacts would alter their population trajectories. We selected five species: black-legged kittiwake (*Rissa tridactyla*, hereafter kittiwake), common guillemot (*Uria aalge*, hereafter guillemot), European shag (*Gulosus aristotelis*, hereafter shag), northern fulmar (*Fulmaris glacialis*, hereafter fulmar) and northern gannet (*Morus bassanus*, hereafter gannet). We constructed each PVA using the 'nePVA' package (v.4.13, Searle et al., 2019, updated Butler et al., 2020) in Program R (v.4.1.0, R Core Team, 2020). Species-specific age at first breeding, maximum brood size breeding success, age-specific survival and breeding percentage (not available for gannet) were assigned using national estimates from Tyler et al. (In review) (Table 1). These rates are a recent update to the widely used report by Horswill and Robinson (2015), who collated all published demographic rates for UK seabirds, using appropriate proxy species or populations where necessary. The species chosen represent the diversity of UK seabird behavioural attributes and life histories, with broad variation in demographic rates the inevitable consequence of this. For example, they represent the full range of 'age at first breeding' and 'maximum brood size' for UK seabirds included in the nePVA tool. Where immature survival was not available for a given age category, a mean was taken between the adjacent two values (e.g. juvenile and adult survival). The nePVA package uses demographic information and assumes a 1:1 sex ratio in the population to create a Leslie matrix where the dominant eigenvalue is used to estimate the initial stable age structure. Environmental stochasticity was applied to annual survival and breeding success events using logit-normal distributions, and demographic stochasticity was included using binomial distributions on annual survival and breeding success probabilities. These processes were assigned using the underlying functionality of the nePVA package. Each PVA was run for 10,000 simulations.

PVAs were constructed for two generic magnitudes of initial population size per species: small (100 in the case of kittiwake, fulmar and shag, or 1000 for gannet and guillemot) and large (1000 in the case of kittiwake, fulmar and shag, or 10,000 for gannet and guillemot). These were selected for each species using population count ranges reported in the seabird census 2023 on UK seabird breeding populations, while retaining maximum comparability between species (Burnell et al., 2023; Table 1). The generic population sizes are intended to represent plausible population sizes for each species towards the extremes of their population size ranges in order to capture density-dependent processes resulting from species-specific environmental carrying capacities while producing viable population trajectories within the modelled time frames. To reflect population regulation mechanisms identified in UK seabird colonies (Horswill et al., 2017), we ran PVAs under both positive and negative density-dependent regulation of breeding success, as well as a density-independent scenario. We used a log-linear formulation to apply positive density-dependent regulation, and a Weibull formulation to apply negative regulation (Merrall et al., 2024). These formulations are included as options in the nePVA R package (Butler et al., 2020) and are specified using the following equations:

$$\text{Log}-\text{linear}: \lambda = a + b\log_{10}(x) \tag{1}$$

$$\text{Weibull}: \lambda = a + bx^{c} \tag{2}$$

where λ is the transformed species-specific demographic rate (in this case the logit transformation of the ratio of breeding success to maximum brood size), a is equal to the intercept value at population size zero, b is the slope coefficient (i.e. density-dependent regulation), x is population size, and c is the chosen Weibull exponent (Equation 2). We applied an exponent of x^2 for negative regulation (for the shape of these formulations of density dependence, see Merrall et al., 2024). To specify b, we applied a median estimate of the slope coefficients previously reported for eight species of seabird (exempting clear outliers); 1.840 for the log-linear formulation, and -3.52×10^{-9} on the logit scale for the Weibull formulation (Merrall et al., 2024). This approach provides biologically plausible estimates of density-dependent regulation for seabirds. The intercept values representing breeding success at population size zero (a) were therefore calculated by rearranging the equations as follows:

$$\text{Log}-\text{linear}: a = (\lambda) - b\log 10(x) \tag{3}$$

$$\text{Weibull}: a = \lambda - \left(b\left(x^{c}\right)\right) \tag{4}$$

The parameters controlling breeding success at population size zero were selected using a numerical optimisation process involving simulating breeding success 100,000 times for each parameter combination and using numerical optimisation (via the 'optim' function in R) to minimise the sum of squared differences between simulated mean and SD values and values from Tyler et al. (In review). The parameters for survival were also selected via numerical optimisation, but density-dependent regulation of this rate was not considered.

We ran each PVA to assess 841 scenarios with varying degrees of impact (29 scenarios of impact on breeding success and 25 scenarios of impact on survival). In addition, three formulations of density-dependent regulation per species were simulated (Figure S1). We included positive impacts (increases in demographic rates) to investigate conditions under which the trajectories of UK populations could stabilise or grow. Adjustments to demographic rates, that is, degree of impact, were selected to encompass a range of plausible impacts that could result from anthropogenic pressures on international seabird populations (Figure 1; Table S1). This range was established using a coarse search of the literature for examples of reported impact to seabird (and other aquatic bird species) survival and breeding success. Impacts within the nePVA tool are specified as absolute reductions in annual demographic rates. Impacts to absolute breeding success were modelled at intervals of 0.05, spanning a 0.4 increase (an impact of 0.4) to a 1.0 decrease (an impact of -0.1) (Figure S1). Impacts to survival spanned a 0.1 increase to a 0.5 decrease. To provide a realistic examination of small scale and chronic impacts while keeping model load at a manageable size, we modelled impacts to survival greater than 0.1 at increments of 0.1, and impacts less than 0.1 at increments of 0.01 (Figure 1; Figure S1 and Table S1). Not all scenarios are plausible for all species (i.e. some impacts exceed the existing population's breeding success or survival rates), however, to simplify the modelling process, all scenarios were run, but only plausible scenarios are presented in the Results. We explored five durations of impact for all 841 degree of impact scenarios, to match plausible durations of various

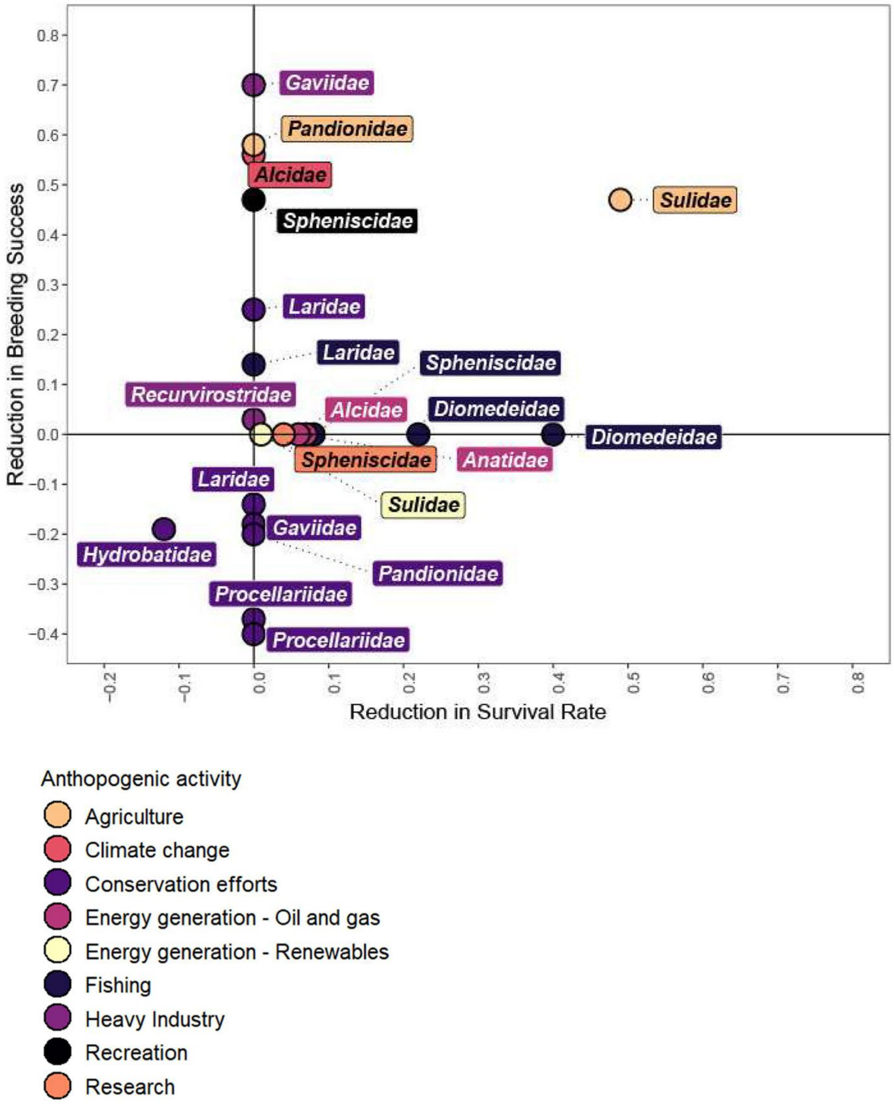

FIGURE 1 Range of quantified impacts on rates of adult survival and breeding success as reported in literature for seabirds (and other aquatic species), and the broad category of causal anthropogenic activity they fall under. Impacts are recorded as reductions in adult survival rate and/or breeding success per annum, where breeding success is the number of chicks fledged per nest divided by maximum brood size. These metrics are in accordance with input parameters for the 'nePVA' R package (Butler et al., 2020) for conducting seabird PVA. As impacts are expressed as absolute measures, some reductions in breeding success therefore represent absolute breeding failure, for example, common loon (*Gaviidae*, *Gavia immer*) (Burgess & Meyer, 2008) and common guillemot (*Alcidae*, *Uria aalge*) (Piatt et al., 2020; Schoen et al., 2022). Species are reported at the level of Family. Only two studies suitable for inclusion recorded impacts to both survival and breeding success. Further detail and a full list of references are available in Table S1.

pressures, spanning from just 1 year up to 25 years. Regardless of duration of impact, all PVA projections were run over 25 years to account for the longer term population consequences of chronic impacts from marine industries, including recovery potential associated with impact mitigation.

2.2 | Assessing PVA outcomes

Our modelling generated 108,750 individual PVA outcomes, constituting a vast yet valuable resource for making comparative predictions around species-specific responses to impact under different scenarios. For brevity, we therefore present summary outcomes (Figure 3), where the number of PVA simulations resulting in each of six defined categories of population change is aggregated across scenarios with impact intensities ranging from −0.1 to 0.5 impacted scenarios to the survival and breeding success, and confine the full results to the Supporting Information (Figures S2–S6). We present model outcomes as 'heatmaps' at four different scales, to facilitate interrogation at a range of intervals as may be useful to practitioners. These include three scales standardised between species for ease of interspecific comparison: Scale (1) a relatively coarse scale spanning a wide range of impact to survival and breeding success; Scale (2) compares breeding success and survival at an order of magnitude difference; and Scale (3) allows both demographic rates to span a small range of impact degrees at a finer scale. Finally, Scale 4 is a species-specific bespoke version, where intervals span the full range of possible impacts modelled for that species. For fulmar, gannet and guillemot, scales are curtailed where the minimum or maximum impact exceeds plausible species demographic rates.

We present a range of comparative metrics based on categories of population decline to address our three comparative aims. These enable us to highlight the benefits of including factors known to drive seabird population trajectories and effectively summarise the breadth of results generated across our many PVA scenarios. Firstly, we examine the overall population trends for each species at small and large population sizes, and their sensitivity to degree of impact to adult survival and breeding success. We do this by comparing the baseline trajectories for each population in an unimpacted, density-independent scenario. For each impact scenario, we calculate the final impacted median population size as the proportion of the initial population size remaining after 25 years (Miller et al., 2019). We then classify outcomes into six categories of change: (1) 'Population increase' (a population increase of >1% relative to initial population size); (2) 'No change': a proportional change of <0.01; (3) 'Moderate decline': 0.99–0.8 remaining (decline <20%); (4) 'Moderately severe decline': 0.8–0.5 remaining (decline of 20%–50%); (5) 'Severe decline': 0.5–0.1 remaining (decline of 50%–90%); (6) 'Catastrophic decline': <0.1 remaining (decline >90%). To increase the useability of our supplementary heatmaps, we further divide 'moderate decline' into three finer intervals: 0.99–0.95, 0.95–0.90 and 0.9–0.8. These thresholds were selected based on established conservation criteria (IUCN, 2012) and guidelines for minimum effective population sizes (Frankham et al., 2014).

To fulfil our second comparative aim, we examine the effect of density dependence on population trajectories across species and impact durations by comparing the categories described above under density-independent and density-dependent regulation. For the third comparative aim, we examine the effect of impact duration at different degrees of impact to survival and breeding success across species. We do this by specifically comparing the effects of high impact scenarios with short (1 year) impact durations (simulating 'acute' impact), against scenarios of low, incremental impacts over long (25 years) impact durations (simulating 'chronic' impact). Here 'high' impact is defined as an absolute reduction of 0.5 (except fulmar, where the maximum possible reduction in breeding success is 0.4), and 'low' is an impact of 0.05, in both survival and breeding success. This is designed to reflect the contrasting demographic effects of real-world acute disturbances (e.g. an oil spill or avian influenza HPAI) versus chronic stressors (e.g. long-term heavy metal contamination or ongoing disturbance from licenced activities). All figures were produced in R Studio (Posit team, 2025) using package ggplot2 (Wickham, 2025), and some code was debugged and streamlined using Microsoft Copilot (Microsoft, 2025).

3 | RESULTS

3.1 | Population responses to impacted demographic rates

Under a baseline PVA scenario (i.e. no additional impact to survival or breeding success and density-independent regulation of breeding success), two of the five focal species were projected to decline over a 25-year period (Figure 2): kittiwake (Figure 2a) and fulmar (Figure 2j). Kittiwake experienced the most pronounced decline, with a median reduction of approximately 90% by the end of the projection period (Figure 2f). By contrast, guillemot populations remained stable (Figure 2d), while populations of shag and gannet were projected to increase. Specifically, shag populations more than tripled over the 25-year period, although the large confidence intervals around the median trajectory encompassed the possibility of no net change (Figure 2g). Gannet populations demonstrated a projected 50% increase in median size over the same timeframe (Figure 2m). Under baseline conditions, population trajectories were qualitatively consistent across small and large initial colony sizes for all species (Figure S6).

We found that across the extensive range of impact scenarios explored for each species, population responses were broadly similar between small and large populations under density-independent conditions (Figure S7), although declines tended to be more severe in small populations under high impact scenarios (Figures S2–S6). For brevity, the full range of outcomes across all impact intensities and durations is not presented here but is available in the Supporting Information (Figures S2–S6).

As expected, species-specific population trajectories varied in response to demographic impacts, reflecting differences in baseline demographic rates. Under density-independent regulation of breeding success, kittiwake populations experienced severe declines (defined as more than 50% loss of the initial population after 25 years) under all scenarios where impact ceased after one year (Figure 3a), and catastrophic decline (defined as more than 90% loss) in most scenarios with impacts persisting for 10 years or more (Figure 3p,u). Kittiwake population increases were only projected when both survival and breeding success improved continuously over the 25-year period (Figure S2A, (v)). Similarly, fulmar populations declined under the majority of impact scenarios, with 20%–50% loss after 25 years in most one-year impact scenarios (Figure 3d), and more than 90% loss in the majority of 25-year impact scenarios (Figure 3x). However, in contrast to kittiwake, fulmar populations were projected to increase under scenarios where survival improved by more than 0.05, even with an almost complete loss of breeding success (Figure S5, page 1A(v)).

Although guillemot populations remained stable under baseline conditions, they declined under the majority of impact scenarios across all durations (Figure 3b). A one-year reduction in survival exceeding 0.25 resulted in more than 20% population loss over 25 years (Figure S3: 1A(i)), while a continuous reduction in survival greater than 0.1 over the full simulation period led to more than a

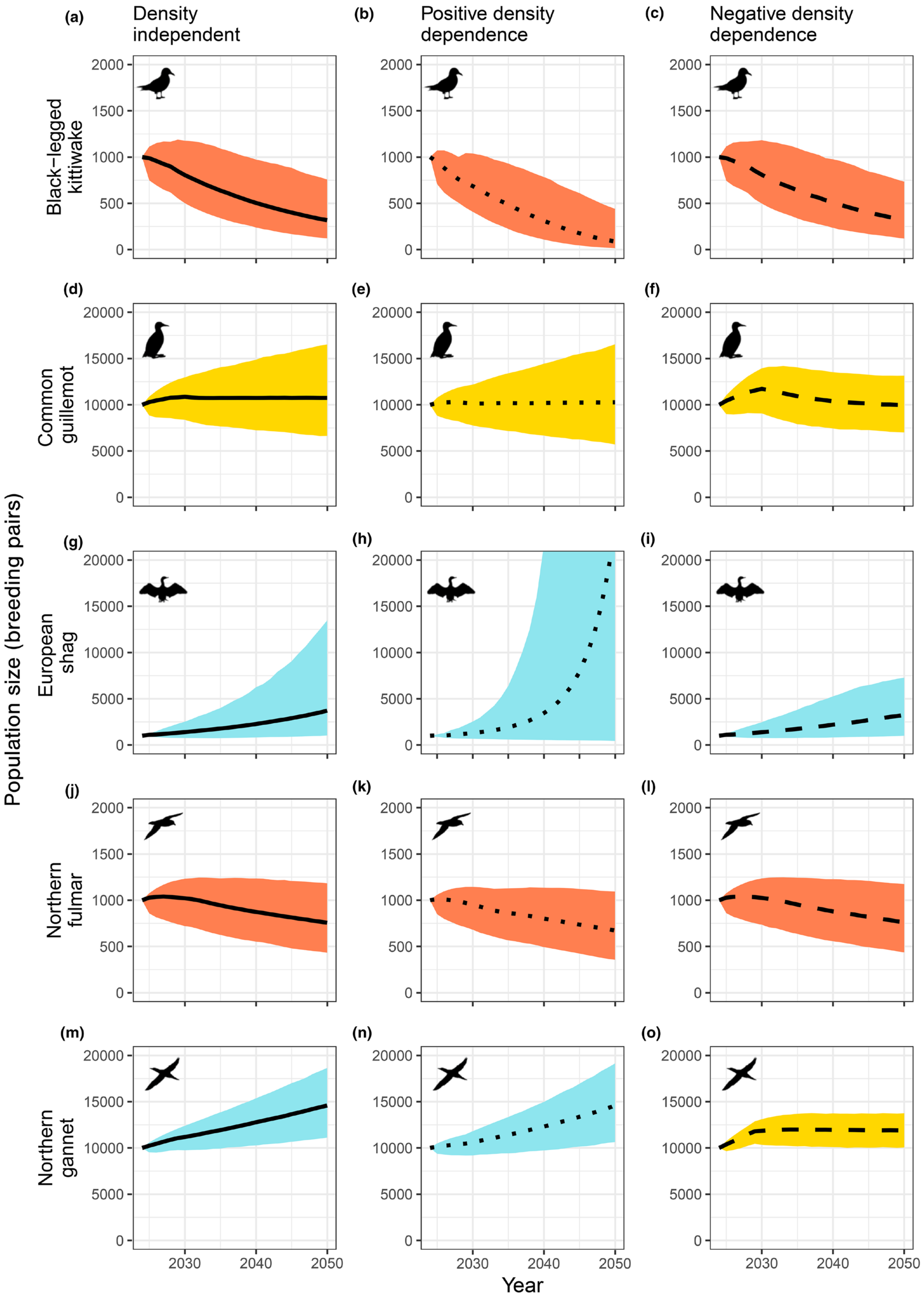

FIGURE 2 Panels (a) to (e) show baseline trajectories of theoretical populations of five seabird species modelled over a 25-year period, using population viability analysis (PVA). We examined population trajectories under density-independent (solid line), positive (dotted line) and negative (dashed line) regulation of breeding success. Lines denote median population size per annum, and coloured ribbons represent confidence intervals at 2.5% and 97.5%. Colours highlight population trends (red = decreasing, yellow = stable and blue = increasing). Initial population size for all species is ‘large’ (population size trajectories are compared in Figure S7).

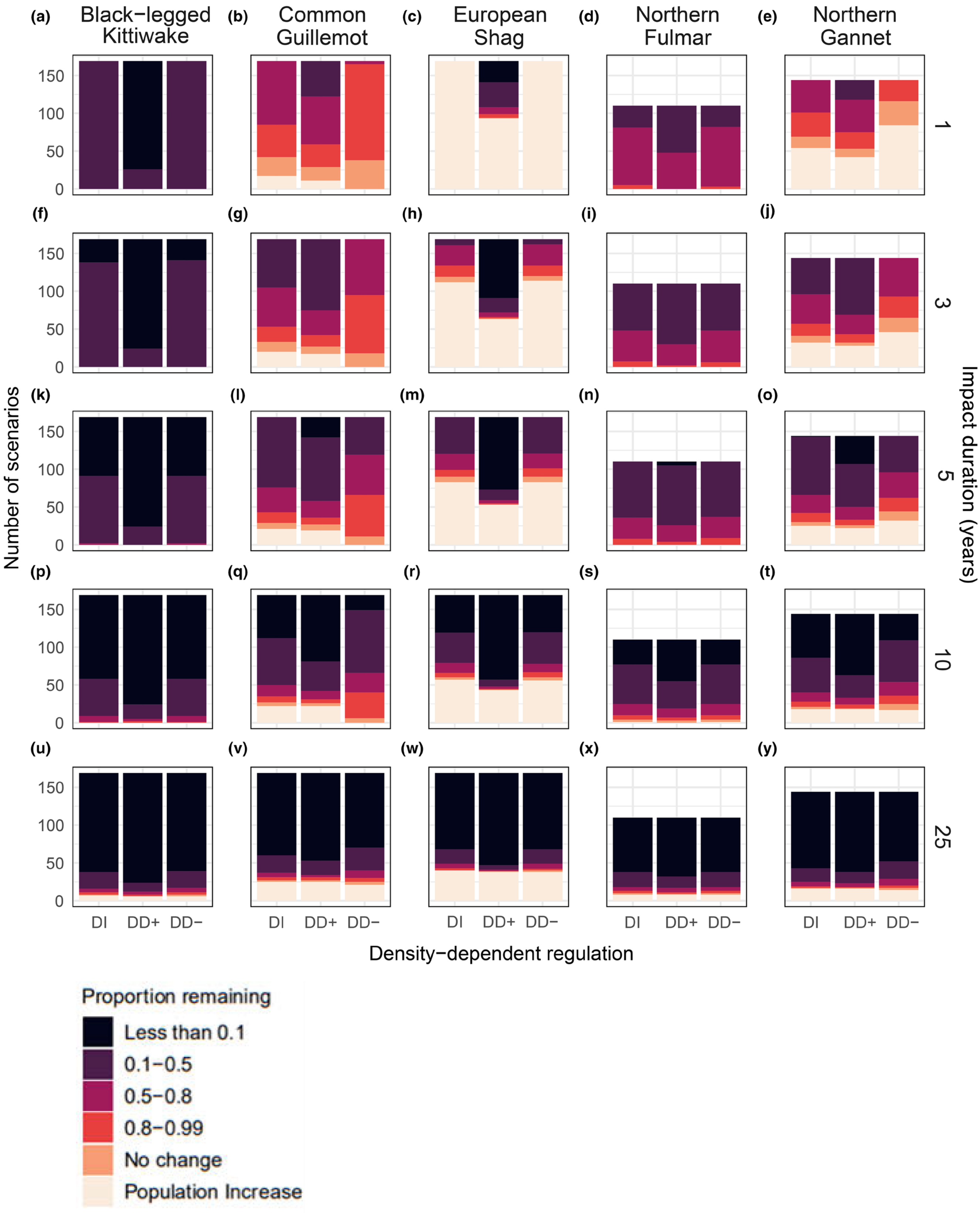

FIGURE 3 Number of modelled PVA scenarios where the proportion of the population remaining after 25 years is examined against six categories of population change. Panels a to y show species sensitivity to pooled reductions in adult survival and breeding success at one of five impact durations, and under density-independent ('DI'), positive ('DD+') and negative ('DD−') regulation of breeding success. Impact scenarios range from an impact of −0.1 to 0.5 to breeding success and survival (scale 1: Figures S2–S6, 1A–F), excepting fulmar and gannet (see main text for details). Initial population sizes are 'large' (see main text) for all species.

50% decline years (Figure S3: 1A(v)). Shag populations were generally resilient. Under all one-year impact scenarios, including high-magnitude reductions in survival and breeding success, population trajectories were positive (Figure 3c). In simulations where survival was unaffected, breeding success reductions alone did not result in population decline across any duration (Figure S6: 1A(i–v)). At 10-year durations of impact, only survival reductions greater than 0.1 produced population declines over 25 years (Figure S4: 1A(iv)); however, when impact continued for 25-years, most scenarios resulted in catastrophic decline (Figure 3w). Gannet populations were projected to increase or remain stable under all one-year impact scenarios with survival reductions less than 0.25 (Figure S6: 1A(i)). However, scenarios involving survival reductions above 0.05 over durations more than 10 years, particularly when combined with reduced or unchanged breeding success, resulted in severe or catastrophic population declines (Figure S6: 1A(iv–v)).

3.2 | Population responses under density-dependent regulation

Species varied in their projected response to positive and negative density-dependent regulation, both in terms of their baseline trajectories and population responses to impact (Figures 2 and 3). For the two species projected to decline under baseline conditions (kittiwake and fulmar), positive density-dependent regulation resulted in steeper declines relative to density-independent scenarios, with kittiwake projections approaching complete population collapse (Figure 2b,k). In contrast, projections under negative density-dependent regulation produced outcomes comparable to those under density-independence (Figure 2a,c,j,l). In guillemot, population trajectories remained stable under positive density-dependent regulation (Figure 2e). However, under negative density-dependent regulation, population growth was slightly suppressed at large initial population sizes (Figure 2f; Figure S7L). For gannet, which demonstrated positive growth under baseline conditions, the incorporation of positive density dependence produced results nearly identical to those under density-independent regulation (Figure 2m,n). Conversely, negative density dependence reduced projected growth rates, leading to a stable trajectory in the large population (Figure 2o, Figure S7D). In shag, another species with increasing baseline trajectories, projections under density-independent and negative density-dependent regulation yielded similar growth patterns (Figure 2g,l). However, under positive density-dependent regulation, population trajectories exhibited unrealistically rapid exponential growth (Figure 2h). Notably, confidence intervals for all density-regulation scenarios in shag were broad, encompassing both stable and declining trajectories as well as extreme growth projections. Across species, positive density-dependent trajectories were consistent between small and large populations (Figure S7).

Species also varied in their sensitivity to demographic impacts under different density dependence assumptions. In general, all species demonstrated heightened sensitivity under positive density-dependent regulation compared to negative or density-independent scenarios (Figure 3). This sensitivity was most apparent under shorter impact durations and moderate levels of impact, while differences across density-regulation types diminished with prolonged or severe impacts. At 25 years of continuous impact, distinctions between regulation types were minimal at the coarse impact scale examined (Figure 3u–y). The effect of positive density dependence was particularly pronounced in shag. Under density-independent and negative regulation, the majority of impact scenarios resulted in continued population growth. However, the addition of positive density dependence led to widespread projected declines: at durations exceeding 3 years, a majority of impact scenarios resulted in severe (>50%) or catastrophic (>90%) reductions (Figure 3h,m,r,w). In kittiwake, even a one-year impact under positive density-dependent regulation resulted in catastrophic declines in the majority of scenarios (Figure 3a), underscoring the compounded vulnerability of already declining populations when subject to Allee effects (Allee, 1931) or related positive feedbacks in demographic regulation.

3.3 | Interactions between duration and degree of impact

Species exhibited relatively little variation in their responses to impact duration across both low and high levels of demographic impact (Figure 4). Under a density-independent model, population trajectories were broadly similar between scenarios simulating low-magnitude impact over 25 years (chronic impact) and high-magnitude impact occurring over a single year (acute impact), for both adult survival and breeding success (although low-magnitude impact to survival over 25 years produced slightly worse outcomes than high-magnitude impact for just 1 year in all species). Across all species, sensitivity to impact duration was minimal in scenarios involving low-level reductions in breeding success, as demonstrated by the minimal difference in population outcome between the low-magnitude impacts to breeding success for all five impact durations (Figure 4). In contrast, species appeared more sensitive to impact duration when survival was reduced, even at low-magnitude impacts a.k.a. there were stark differences in all species between population outcomes after 1 year of impact and after 25 where survival was the impacted demographic rate. Recovery following one-year impacts was generally consistent across species and impact types, except in scenarios involving high-magnitude reductions in survival, which frequently precipitated long-term declines. In particular, guillemot, fulmar and gannet maintained population stability under scenarios of sustained high-magnitude impacts to breeding success, provided survival remained unaffected (Figure 4d,j,m).

When density dependence was incorporated, these patterns remained largely consistent. An exception was observed in shag, where positive regulation of breeding success resulted in unrealistic exponential population growth across nearly all scenarios, with the exception of high-magnitude impacts to survival (Figure 4h).

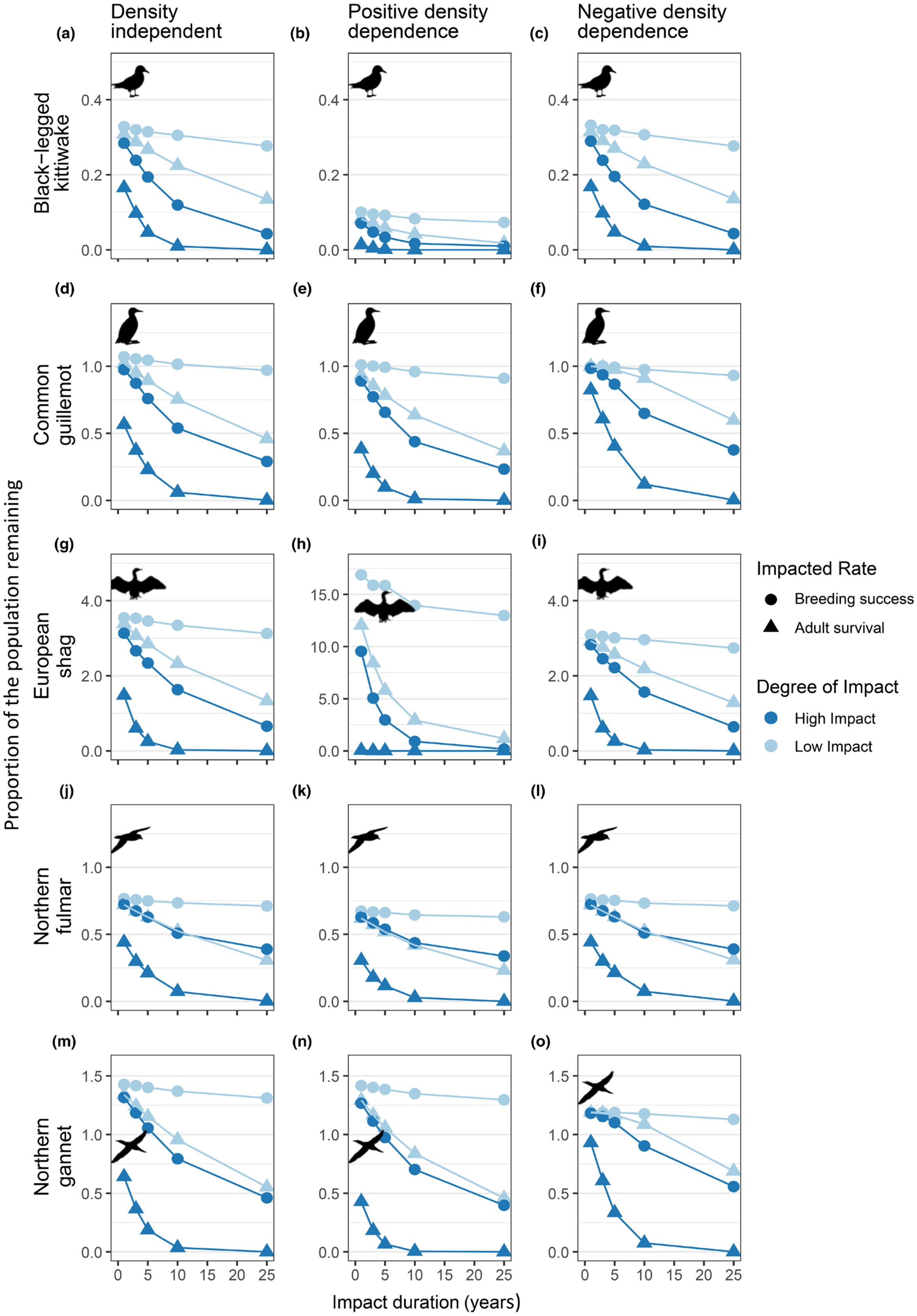

FIGURE 4 Proportion of initial population remaining after 25 years at different durations and degrees of impact. Panels a to e show the relationship between impact duration and population decline in response to two different degrees of impact to either adult survival or breeding success for each species, to explore whether species differ in their sensitivity to acute reductions in their vital rates in contrast with longer lasting chronic reductions. Population responses are modelled under density-independent, positive and negative regulation of breeding success. The 'High' and 'Low' impact scenarios plotted here are 0.05 and 0.5 reductions in breeding success and survival, respectively (with the exception of fulmar—see main text for details). Initial population sizes are 'large' (see main text) for all species.

In most cases, impacts to breeding success over long durations (25 years) produced outcomes comparable to those of short-term (1-year) impacts to survival. For example, in fulmar, projections 25 years of low-magnitude impacts to breeding success and 1 year of low-magnitude impacts to survival both resulted in a proportion of around 0.75 of the population remaining, while 25 years of high-magnitude impact to breeding success and 1 year of high-magnitude impact to survival resulted in around 0.5 of the population remaining (Figure 4j,l). These losses were greater under a scenario of positive density dependence.

4 | DISCUSSION

For decision-makers and practitioners to advise on the impacts of human activities and design of mitigation or compensatory measures, understanding of how impacts to key demographic rates influence population dynamics and trajectories across different species is essential. Here we show how population viability analysis (PVA) can be leveraged to generate an accessible library of comparable modelled outcomes that can aid practitioner decision making around conservation prioritisation and consenting of activities, while still allowing critical influences on population trajectories to be incorporated. This is in light of the precipitous declines that many species of seabird are experiencing as a consequence of anthropogenic activities. In showcasing this approach, we provide a resource that has immediate use for practitioners in making judgements around the plausible population consequences of a wide range of demographic impact scenarios in five highly protected species of UK seabird. This resource will allow practitioners to consider quantitative comparisons of impact for meaningful and realistic scenarios without having to necessarily undergo detailed quantitative population modelling that takes into account critical processes such as density dependence.

Evolutionary theory predicts that slow life-history strategies of high survival and low productivity over a long lifespan are likely to be favoured in highly variable environments such as marine habitats, where reproductive success will vary greatly with variation in food resources. Seabird life histories typically follow this pattern (Hamer et al., 2002; Sæther & Bakke, 2000). However, in the Anthropocene, human activities such as fishing, energy generation and the spreading of pathogenic disease and non-indigenous species has caused severe reductions in seabird survival at acute and chronic levels (as summarised in Table S1). Our findings reflect expectations from life-history theory: All species were highly sensitive to impacted survival, and all were projected to severely or catastrophically decline when survival was reduced by more than an additional 20% per year for 3 years or more, regardless of their baseline trajectories. Such impacts could be caused by repeated bouts of HPAI (Falchieri et al., 2022); or possibly the continued effects of extreme weather or food shortages caused by climate change (Frederiksen et al., 2008; Mitchell et al., 2020). The library we provide here can be used effectively to make preliminary assessments of the scale of interventions required to aid struggling populations, by establishing the positive demographic impacts required to alleviate population decline (Figures S2–S6). Compensatory measures might offer a promising avenue into improved outcomes for impacted species by establishing additional conservation efforts (Furness & Furness, 2025; McGregor et al., 2022), however, as shown here, for species such as kittiwake and fulmar, unless they seek to change the current background of pressures on demographic rates, these measures would need to boost survival continuously to sustain populations, and this may be unrealistic in reality.

While density dependence is well evidenced in seabirds (Horswill et al., 2017; Horswill & Robinson, 2015), straightforward guidance for its inclusion in non-population-specific PVA is still lacking, even in popular tools such as nePVA (Howells et al., 2023). This is partly because despite the existence of extensive seabird time-series data relative to other taxonomic groups, relatively few incorporate the required concurrent estimates of population size and breeding success (or another relevant demographic rate) across multiple years (Horswill et al., 2021), even in well studied locations such as the UK (Merrall et al., 2024). For this reason, specifying density-dependent coefficients within practitioner population models is still a challenge. Here we not only demonstrate the effective use of median density-dependent coefficients taken from quantified relationships between population size and breeding success (Merrall et al., 2024) but also the impact of their inclusion in our library of population outcomes. This provides practitioners with an effective way of making preliminary assessments of the plausible range of population change in response to impact where density dependence could be acting on population dynamics.

Of the five species examined in this study, two were projected to decline under a density-independent, unimpacted scenario (kittiwake and fulmar), while two species appeared to be increasing in number over time (shag and gannet), and guillemot remained roughly stable. The rapid decline of kittiwake populations across the United Kingdom is well documented (Burnell et al., 2023), and this species has received a great deal of conservation attention over the last decade (Ruffino et al., 2020). However, the projected trends shown here, particularly that of accelerated extreme decline with the addition of positive density-dependent regulation of breeding success, are still very troubling. The majority of seabird impact assessments carried out in the United Kingdom do not include density-dependent regulation on the assumption that this will maintain a precautionary approach (Green et al., 2016; Horswill et al., 2017). However, this assumes that density dependence is negative and will therefore be compensatory, whereas in small declining populations, the opposite is likely true (Allee, 1931; Merrall et al., 2024). We find that under negative regulation, large stable and increasing populations (guillemot and gannet) are maintained at a suppressed but stable population trajectory, while small declining populations (kittiwake and fulmar) under positive density-dependent regulation are projected accelerating rates of decline.

The variation we find between population trajectories under different formulations of density dependence is coherent with what we would expect from biologically plausible relationships between population size and breeding success (Allee, 1931; Horswill et al., 2017; Merrall et al., 2024). This is with the notable exception of shag, where growth is uncurtailed by negative regulation and accelerated under positive regulation. One plausible explanation for this disparity is that the generic distributions or coefficients describing density-dependent regulation we selected are too far removed from shag population dynamics to recreate a realistic trajectory. The addition of a negative density-dependent regulation in large populations (10,000 breeding pairs) of guillemot and gannet resulted in lower projected population sizes compared with a density-independent formulation: in gannet, population growth was repressed, resulting in a stable trajectory as opposed to one of increase; and in guillemot, the population was projected to remain stable at a slightly depressed size. In densely populated colonial species such as these, we would expect to find negative relationships between breeding success and population density when they are at their environmental carrying capacity (Horswill et al., 2017). However, although gannet populations were projected to be relatively insensitive compared with guillemots to short impact durations, both species were projected to experience catastrophic population decline following all chronic impact scenarios.

While population projections with PVA are not necessarily accurate, they can still effectively inform comparative judgements about species sensitivity to change in demographic rates (Cook & Robinson, 2016). For example, we projected the median population size for shag to more than double over the next 25 years; however, the broad confidence intervals around median trajectories, coupled with the population decline recorded nationally for shag between the most recent seabird censuses (although the last 4 years have seen an upturn) (Burnell et al., 2023), make these projections seem unlikely. Shags have a relatively short/fast life-history strategy for a seabird (Hamer et al., 2002), and more visibly stochastic demography following boom/bust cycles (Frederiksen et al., 2008), making their population dynamics harder to capture. However, these projections still provide information on the relative sensitivity of shag populations to impact: shag trajectories were highly sensitive to longer term impacted demographic rates (positive or negative), and despite their increasing baseline population trajectory on current trends, were projected catastrophic decline if subjected to continuously reduced survival greater than an additional 10% reduction per annum (Figure S5: 1A(v)–C(v)). We conclude therefore that shag populations may fluctuate unpredictably, which is a valuable outcome beyond the absolute population sizes.

Absolute projections generated using PVA reflect the quality of the demographic data available (Horswill et al., 2021; Jitlal et al., 2017; Reed et al., 2002). For UK seabirds, these data are some of the best in the world, collected from hundreds of colonies across numerous species by a mixture of scientists and citizens every year—and it is still inevitably full of uncertainties and unknowns (e.g. no updated survival estimate has been recorded for UK fulmar since 2005, Grosbois & Thompson, 2005, which pre-dates significant changes to fisheries discards policy likely to affect fulmar, Bicknell et al., 2013). The national mean estimates for demographic rates used here are unlikely to capture population-specific dynamics where rates fall at the extremes of recorded ranges, and our projections also do not account for impacted mortality in juveniles and immatures, metapopulation dynamics or estimates of the correlations between breeding success and survival, which may play crucial roles in population dynamics (Genovart et al., 2018; Miller et al., 2019). However, the library that we create here provides practitioners with a quantitative evidence-base that can aid them in making comparative assessments of seabird response to impact. Where demographic rates are unavailable or highly uncertain for a population, practitioners could use the impact increments shown on the heatmaps provided to explore a plausible range of impacts by looking at population outcomes for a range of impacts.

As an example of how we anticipate this work might be used in practice, consider a pressure from a planned activity occurring within a three-month period which overlaps with the flightless moult period for common guillemot. The activity involves vessel transits and seismic survey within an area of medium to high densities, within 50 km of a large breeding colony. Pressures include noise and visual disturbance. We might assume no impact on breeding success given the activity is planned for outside the breeding season, but survival may be impacted. We would anticipate this impact being very small given the limited extent and duration of activities over a relatively large area. If the population is stable or increasing, it is reasonable based on size to assume that breeding success will not be positively regulated. The resource produced here could be used to quickly examine possible population consequences of a range of small incremental changes in survival for a large population for 1 year of impact, using plots (Figure S3: 3D(i)) (density-independent) and (S2: 3F(i)) (negative regulation). We can immediately see that in a density-independent scenario, a 1-year impact to survival up to 0.05 will still result in population increase after 25 years, but an impact greater than 0.08 will cause decline. While under negative regulation, the population will remain stable up to an impact of 0.1. How practitioners might settle on likely impacts to demographic rates is a separate process worthy of further exploration.

While seabirds are more extensively studied than most marine predator species, UK conservation bodies still highlight the need for more information in order to effectively prioritise conservation and make precautionary choices relating to offshore development consenting (Ruffino et al., 2020). We show how it is possible to create an accessible library of pre-modelled population trajectories based on tools and data currently available. Practitioners will be able to use such libraries to make comparative judgements of population vulnerability to a range of multi-dimensional impacts that could plausibly arise from activity and pressure combinations, especially where their precise impacts have not been quantified. For our five showcase species, such judgements can be made with our resource right away. We have made use of the publicly available nePVA R package (Butler et al., 2020) rather than developing bespoke models, because tools of this type are often used by conservation and EIA practitioners when investigating impact. While the package contains extensive functionality around the incorporation of processes such as density dependence, rate correlations and metapopulation dynamics, it is still challenging for conservation practitioners to know how to quantify and incorporate these processes. It remains the case that population-specific PVA using time-series data will be the best option when investigating the potential quantitative impacts or trends of a given population of seabirds (Horswill et al., 2021, 2022, 2022). However, our work provides an accessible and powerful alternative where resources to undertake bespoke analysis are lacking, or as a first step to highlighting where there may be significant risk of population collapse and further investigation is warranted. By using PVA to generate a quantitative resource of pre-modelled population trajectories, we provide a valuable new tool for practitioners making complex seabird conservation decisions in the UK and beyond.

AUTHOR CONTRIBUTIONS

Jonathan A. Green, Catharine Horswill, Leonie A. Robinson, Julie Black, Francis Daunt and Eve Merrall conceived the study and designed the methodology; Eve Merrall executed modelling and conducted analysis with assistance from Catharine Horswill, Adam Butler and Jonathan A. Green. Eve Merrall led the writing of the manuscript with guidance from Jonathan A. Green, Catharine Horswill, Leonie A. Robinson, Julie Black and Francis Daunt. All authors provided editorial advice and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.70202.

DATA AVAILABILITY STATEMENT

Population viability analysis outcome summary data is accessible via Zenodo at https://doi.org/10.5281/zenodo.17622372, along with code for the replication of the heatmap library provided in the Supporting Information. PVA was carried out using the nePVA R package (Butler et al., 2020; available on Github at https://github.com/naturalengland/Seabird_PVA_Tool).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Schematic showing all modelled PVA scenarios. Input combinations totalled 30 constructed PVAs for each species and 841 scenarios of impact degree for each PVA. Impact degree and duration scenarios attempt to cover a large range of plausible values and timespans in accordance with the diversity of pressures faced by UK seabirds (Figure 1; Table S1), as well as possible positive changes that could arise from mitigation interventions. Density-dependent slope coefficients are the median estimates recorded across eight species from Merrall et al. 2024 for the density-dependent regulation of productivity. Survival is modelled at smaller increments (a fine scale) at lower degrees of impact, and larger increments (a coarse scale) at higher degrees of impact, to allow the exploration of small impacts over long time periods (chronic effects) without causing model proliferation. Not all scenarios are plausible for all species (i.e. some impacts exceed the existing population's modelled breeding success or survival), however in order to simplify the modelling process, these scenarios have been filtered out at the model presentation stage.

Figure S2. Heatmaps showing the effect of impacted adult survival and breeding success on projected outcomes for theoretical populations of black-legged kittiwakes at population sizes of 100 (A–C) and 1000 (D–F) breeding pairs.

Figure S3. Heatmaps showing the effect of impacted adult survival and breeding success on projected outcomes for theoretical populations of common guillemots at population sizes of 1000 (A–C) and 10,000 (D–F) breeding pairs.

Figure S4. Heatmaps showing the effect of impacted adult survival and breeding success on projected outcomes for theoretical populations of European shags at population sizes of 100 (A–C) and 1000 (D–F) breeding pairs.

Figure S5. Heatmaps showing the effect of impacted adult survival and breeding success on projected outcomes for theoretical population of northern fulmar at population sizes of 100 (A–C) and 1000 (D–F) breeding pairs.

Figure S6. Heatmaps showing the effect of impacted adult survival and breeding success on projected outcomes for theoretical population of northern gannet at population sizes of 1000 (A–C) and 10,000 (D–F) breeding pairs.

Figure S7. Trajectories of two sizes of theoretical populations of five key seabird species, modelled using population viability analysis (PVA) over a 25-year period. Demographic rates are based on nationally recorded averages (Tyler et al., in review, updated from Horswill and Robinson, 2015). Black lines represent the median population size per annum, and shaded grey ribbons represent confidence intervals at 2.5% and 97.5%. We examined population trajectories under density independent, positive and negative regulation of breeding success (highlighted by solid, dotted, and dashed lines respectively). Silhouettes highlight different species. All PVA were conducted using the 'nePVA' R package from Natural England (Butler et al., 2020).

Table S1. A list of studies from a course literature search demonstrating quantified impact on seabird and other aquatic species by anthropogenic activity. Studies span a range of locations and activities, including efforts to increase species demographic rates via conservation measures. Impacts are recorded as absolute reductions in survival rate and/or breeding success per annum, where breeding success is the number of chicks fledged per nest divided by maximum brood size.

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