

RESEARCH ARTICLE

Incorporating density-dependent regulation into impact assessments for seabirds

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Handling Editor: Richard Sherley**Abstract**

1. Many industries are required to perform population viability analysis (PVA) during the consenting process for new developments to establish potential impacts on protected populations. However, these assessments rarely account for density-dependent regulation of demographic rates. Excluding density-dependent regulation from PVA-based impact assessments is often assumed to provide a maximum estimate of impact and therefore offer a precautionary approach to assessment. However, there is also concern that this practice may unnecessarily impede the development of important industries, such as offshore renewable energy.
2. In this study, we assess density-dependent regulation of breeding success in 31 populations of seabird. We then quantify the strength and form of this regulation using eight different formulations. Finally, we use PVA to examine how each formulation influences the recreation of observed dynamics (i.e. model validation), as well as the predicted absolute and relative population response to an extrinsic threat (i.e. model projection).
3. We found evidence of both negative ($n=3$) and positive ($n=5$) regulation of seabird breeding success. In populations exhibiting negative regulation, excluding density-dependent regulation from PVA-based impact assessment allowed uncontrolled population growth, such that model outcomes became biologically implausible. By contrast, in populations exhibiting positive regulation, excluding density-dependent regulation provided an appropriate reconstruction of observed dynamics, but population decline was underestimated in some populations. We find that multiple formulations of density dependence perform comparably at the detection, validation and projection stages of analysis. However, we tentatively recommend using a log-linear or Weibull distribution to describe density-dependent regulation of seabird breeding success in impact assessments to balance accuracy with caution. Finally, we show that relative PVA metrics of

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impact assessment cannot necessarily be used to overcome PVA misspecification by assuming density independence in positively regulated populations.

4. *Synthesis and applications:* We suggest that a density-dependent approach when performing PVA-based assessments for seabird populations will prevent biologically unrealistic, unconstrained population growth and therefore ensure meaningful PVA metrics in populations experiencing negative regulation. It will also maintain a precautionary approach for populations experiencing positive regulation, crucial when estimating impacts for these more vulnerable populations. These conclusions have immediate international application within the consenting processes for marine industries.

KEYWORDS

breeding success, demography, density dependence, environmental impact assessment, offshore renewable energy, population dynamics, population viability analysis, seabird

1 | INTRODUCTION

The biosphere is constantly being altered by humans, primarily through land-use change for resource production and extraction (Balvanera et al., 2019). Extractive industries are required to perform ecological impact assessments to meet legislative criteria that exist to prevent the loss of species and habitats that are vulnerable or considered crucial for sustaining more-than-human life (e.g. EU Directive 2014/52/EU). A commonly used assessment framework for some taxa is population viability analysis (PVA; Broadbent & Nixon, 2019; Searle et al., 2020). This method uses a simplified representation of population dynamics to predict population response to changes in demographic processes, such as survival, sexual maturity and recruitment of juveniles (Maclean et al., 2007; Reed et al., 2002). However, despite widespread evidence of density-dependent regulation across these demographic processes (Horswill & Robinson, 2015; Stephens & Sutherland, 1999), PVA-based impact assessments are often modelled as density-independent (Chaudhary & Oli, 2019; Green et al., 2016; Henle et al., 2004). This approach is typically taken to reflect uncertainty regarding the strength and direction of local density-dependent regulation. Density-independent PVA models are also generally considered to provide a maximum estimate of the relative impact to mean population size, and thereby offer a precautionary approach to assessment (Chaudhary & Oli, 2019; Green et al., 2016; Maclean et al., 2007; Peer et al., 2013).

The assertion that density-independent PVA offers a precautionary approach to assessment assumes that density-dependent regulation of demographic processes is operating as compensatory (i.e. negative regulation: Horswill et al., 2017; Searle et al., 2020). Negative regulation is characterised by a negative relationship between demographic rates and population size that reflects increased intraspecific competition for resources when a population reaches carrying capacity (Beverton & Holt, 1957). Overlooking negative regulation in PVA-based impact assessments therefore could result in a threat being over-estimated (Chambert, Duriez, Deleaux,

et al., 2023; Green et al., 2016; Horswill et al., 2017; O'Brien et al., 2017). However, density-dependent regulation can also operate as depensatory (i.e. positive regulation). Here, a positive relationship between demography and population size, reflecting processes such as colonial defence, occurs when a population drops below a critical density (Allee, 1931; Stephens & Sutherland, 1999). Thus, contrary with negative regulation, not including positive density dependence when using PVA for impact assessments could result in threat being underestimated (Horswill et al., 2017; O'Brien et al., 2017).

In PVA, the population response to demographic changes associated with extrinsic threat is typically assessed by comparing predicted population trajectories under impacted and unimpacted scenarios. The difference is often quantified using relative (as opposed to absolute) metrics, including probabilistic measures and ratios (Cook & Robinson, 2016; Jitlal et al., 2017). This approach was adopted to minimise any false sense of confidence associated with absolute assessment outputs that do not readily reflect uncertainty and error in the demographic parameters and processes influencing a predicted population response (Chambert, Duriez, & Besnard, 2023; Jitlal et al., 2017). Additionally, there are also multiple types of functional response models, or formulations, of density dependence that are available for PVA (e.g. Butler et al., 2020; Tinker et al., 2022). Studies investigating the influence of these formulations on PVA are limited (but see Henle et al., 2004), and crucially, how different formulations of density dependence influence the assessment of threat using either absolute or relative metrics remains an open question.

In the UK, offshore wind energy developments are set to dramatically increase over the next decade (i.e. from 8GW installed capacity in 2020 to 50GW in 2030, HM Government, 2022). Offshore windfarms (OWFs) potentially threaten the internationally important populations of seabirds breeding in the UK, namely through collisions with turbine blades and habitat displacement (Bradbury et al., 2014; Broadbent & Nixon, 2019; Furness et al., 2013). OWF developments that may generate

significant population-level impacts to key seabird colonies in Special Protection Areas require impact assessments to be conducted (EU Birds Directive 79/409/EEC, Habitats Directive 92/43/EEC, EU Directive 2014/52/EU, European Commission, 2013). However, these impact assessments rarely incorporate density-dependent feedbacks despite widespread evidence for both negative and positive regulation of seabird demographic processes (Croll et al., 2022; Horswill et al., 2017). Best practice guidance, to determine when and how to incorporate density dependence in these models, is thus urgently required.

In this study, we investigate density-dependent regulation of seabird breeding success and test appropriate ways to incorporate it into PVA-based impact assessments. To do this, we address four key objectives: (1) collate suitable datasets for examining density-dependent regulation of seabird breeding success, (2) investigate the prevalence of density-dependent regulation of seabird breeding success and quantify its shape and direction using eight different formulations, (3) test how these different formulations influence the recreation of observed dynamics and (4) quantify how different formulations influence the absolute and relative projected population response to an extrinsic threat.

2 | MATERIALS AND METHODS

2.1 | Data collation

To assess the prevalence of density-dependent regulation of seabird breeding success, we collated population-specific data on breeding success and abundance from the Seabird Monitoring Programme (SMP), supplemented with additional data from the SMP 'key sites' of Skomer Island and the Isle of May (<https://app.bto.org/seabirds/public/index.jsp>; Newell et al., 2022; Wood, 2023). In these datasets, breeding population size is monitored using standardised species-specific methodologies, either as whole colony or subplot counts that are then extrapolated (Walsh et al., 1995). Likewise, breeding

success is consistently calculated in subplots as the average number of fledglings produced per nesting attempt. To generate the final dataset, we removed records graded as having a low degree of accuracy, and then only retained populations with at least 10 years of concurrent breeding success and abundance data between 1986 and 2021. For populations with multiple estimates of annual breeding success, we calculated annual population-specific mean values, and where population counts were subdivisions of a full census, values were summed. To minimise the effect of demographic stochasticity, we removed populations which averaged less than 40 breeding pairs.

2.2 | Quantifying density dependence

To quantify the shape and direction of density-dependent regulation in seabird breeding success, we used generalised linear mixed models (GLMMs). Here, we assume that a significant non-linear relationship between breeding success and population count provides evidence of density dependence (Miller et al., 2019; Searle et al., 2019). For each population, we considered nine GLMMs including a density-independent model and eight formulations of density dependence. The different formulations were linear, log-linear, threshold under two separate scenarios and Weibull under four separate scenarios (Figure 1). These four formulations (linear, log-linear, threshold and Weibull) are based on those included in the dedicated PVA-based software package developed for conducting seabird impact assessments for OWFs ('nePVA' package for Program R, version 4.13, Searle et al., 2019; updated Butler et al., 2020). These formulations therefore reflect those available to and currently used by stakeholders.

In the density-independent model, we assume no relationship between breeding success and population size (Figure 1). In the linear and log-linear formulations, we assume that the effect of density dependence is linearly proportional to population size and a linear function of \log_{10} population size, respectively (Figure 1). In the

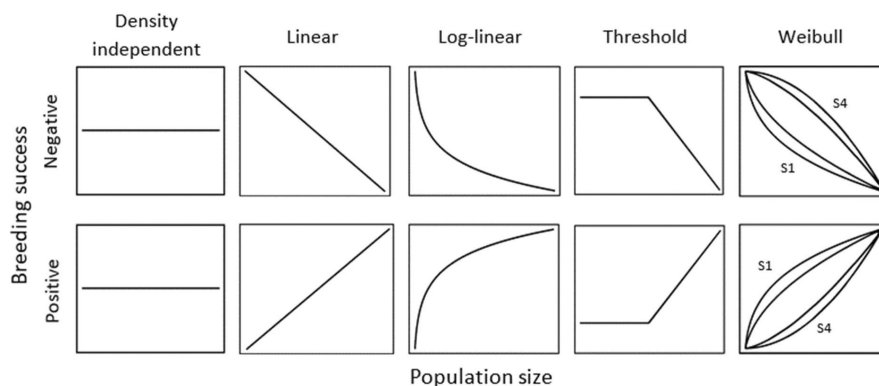


FIGURE 1 Schematic illustration of the different formulations of density dependence used in our analyses with variations for populations exhibiting negative or positive regulation. We considered four Weibull scenarios, using exponent values of 0.25, 0.5, 1.5 and 2 (S1–4, respectively). Figures made using the nePVA package (Butler et al., 2020) with an intercept of 0.8 on the logit scale and a slope of -0.002 and 0.002 for negative and positive regulation respectively.

threshold formulation, we assume that the relationship is linear but is removed below a specified (threshold) population size (Figure 1). To allow the analytical sensitivity to a specified threshold to be evaluated, we considered two thresholds for each population. These thresholds were assigned based on a colony-specific visual examination of the data to ensure local relevance. Thresholds were selected to be plausible based on observed population sizes. However, the inclusion of the threshold within the observed range of population sizes was deemed unnecessary because projection analyses have the potential to extend this range. Therefore, the specified thresholds were 5000 and 10,000 breeding pairs for common guillemots (*Uria aalge*, hereafter guillemot) from Skomer Island and the Isle of May, 1000 and 5000 breeding pairs for guillemots from Sumburgh Head, 500 and 1000 breeding pairs for razorbills (*Alca torda*) from the Isle of May, and 40 and 100 breeding pairs for all remaining (smaller) populations. Finally, in the Weibull formulation we assume that density dependence operates as a power of population size (Figure 1), and we considered four values for the exponent: 0.25, 0.5, 1.5 and 2 (note: an exponent of one is equivalent to the linear model). We specified the exponent externally as the duration of time series prevented reliable estimation of this parameter during model fitting.

We fitted all GLMMs using binomial error distributions and a logit link function. To allow the use of a binomial model for the species that produce multiple offspring annually, breeding success was scaled by multiplying the number of observed nests by a species-specific maximum brood size (Table S1). This approach follows the methodology implemented within the 'nePVA' package for Program R (Butler et al., 2020). In all GLMMs, we included population count as a fixed effect and year as a random effect, the latter allowing temporal variation to be explicitly estimated. We fitted the GLMMs using a Bayesian approach in JAGS (v.4.3.0, Plummer, 2003) via the 'jagsUI' library (v.1.5.1, Kellner, 2019) for program R (v.4.1.0, R Core Team, 2020). We assigned the intercept and coefficient terms of these models using normal prior distributions centred on zero with a low precision (i.e. a high standard deviation). We selected a precision of 0.001 to allow inference on the logit scale across a large range of values (Kery & Schaub, 2012, Figures S1 and S2). For the slope coefficient, centring the prior distribution on zero also supports an a priori null hypothesis of no statistical relationship and allows the direction (i.e. positive or negative) and strength of regulation to be determined during model fitting. We found that detecting density dependence was not influenced by increasing precision on this prior distribution (Table S2). Finally, to limit variation to biologically plausible values on the observed scale we assigned the standard deviation of the random effect for year using a uniform prior distribution bounded between zero and five. Fitting the GLMMs involved running three Monte Carlo Markov chains (MCMC) for 100,000 iterations and retaining every 100th step to minimise autocorrelation in the MCMC sampling. To confirm convergence of the chains, we used the Brooks-Gelman-Rubin diagnostic tool (all values $\hat{r} \leq 1.01$). We removed the first 5000 MCMC draws as burn-in and visually checked that convergence of the MCMC chains had occurred before this cut-off.

We determined evidence of density-dependent breeding success for each population and GLMM (i.e. formulations of density dependence) using the 95% credible interval (CRI) of the slope coefficient with population size. Populations were considered to exhibit evidence of density-dependent regulation if the 95% CRI of the slope coefficient did not straddle zero in one or more GLMM. To compare the performance of the different GLMMs within a population, we calculated the difference between the model-specific deviance information criteria (DIC) and the minimum DIC (DICmin) for that population. Formulations were considered comparable if the difference between the DIC and the DICmin (the Δ DIC) was less than two DIC units (Fordyce et al., 2011). Populations where the density-independent model was within this group were interpreted to indicate weak evidence for density dependence. Populations where it was not comparable, and the slope coefficient with population size was deemed significant, were considered to exhibit strong evidence. Finally, we investigated the relationship between the detection of density-dependent regulation and the duration of the time series analysed. To do this, we compared years of available data with the slope coefficient from the best candidate GLMM and the Δ DIC between the density-independent and density-dependent formulations (i.e. whether the density-dependent GLMM was comparable to the density-independent GLMM).

2.3 | Validation analysis using PVA

We ran a series of model validation PVAs to examine whether the different formulations of density-dependent breeding success considered in the GLMMs were able to accurately recreate observed dynamics. For each population identified as exhibiting evidence for density-dependent regulation of breeding success, we constructed nine PVAs to reflect the GLMMs: density-independent and eight different formulations of density dependence. 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). We used the earliest observed count as the starting size for each population. For all populations, the earliest population count was comparable to counts observed in following years (Figure S4), such that biases introduced from erroneous starting points are considered minimal. To propagate parameter uncertainty into the simulations, we ran each PVA for 500 iterations and for each iteration we described breeding success by randomly selecting intercept, slope and environmental stochasticity terms from the full joint posterior distribution of the respective GLMM. We selected values from the same MCMC draw of each GLMM to retain any covariance between parameters (e.g. Horswill et al., 2021). We used the library within the nePVA package to assign the remaining demographic processes (i.e. mean species-specific survival rates, environmental stochasticity in survival, age of first breeding) and applied environmental stochasticity to annual survival and breeding success events using logit-normal distributions. We estimated the initial stable age structure using the eigenvalue from a transition matrix with mean species-specific

demographic information (Table S1, Caswell, 2002) and included demographic stochasticity using binomial distributions on annual survival and breeding success probabilities. Finally, we assumed a 1:1 sex ratio in the population, with all breeding-age individuals reproducing annually.

For each population and PVA, we quantified how well the different formulations of density-dependent regulation recreated observed dynamics by calculating the sum of the squared residuals between the observed population counts and the concurrent simulated values for each iteration (e.g. Horswill et al., 2016). To compare different models, we examined the distribution of summed squared residuals within formulations (i.e. across populations), as well as between formulations (i.e. within populations). Here, higher values and greater variability in the summed squared residuals indicate that a specific formulation was less able to recreate the observed population trajectory.

2.4 | Projection analysis and PVA metrics

To examine how different formulations of density dependence may influence PVA-based impact assessments, such as those used in consenting OWFs, we constructed projection simulations for each population identified as exhibiting evidence of density dependence. We ran each projection PVA for 500 iterations and for each iteration we described breeding success by randomly selecting intercept, slope and environmental stochasticity terms from the full joint posterior distribution of the respective GLMM. We initiated each PVA with the final observed population count, and population dynamics were projected over 25 years (the average lifespan of an OWF; Miller et al., 2019).

For each population and density-dependence formulation, we constructed two PVA projection scenarios. The first, 'the unimpacted scenario', used the baseline species-specific demographic profile, as per the validation analyses. The second, 'the impacted scenario', incorporated an additional extrinsic threat that decreased annual rates of adult survival by 1%, to represent additional mortality (e.g. from collisions with wind turbine blades or displacement from favoured foraging habitat). Extrinsic factors can differentially influence groups of individuals within populations of seabirds (e.g. Searle et al., 2018; Wood et al., 2021); however, age-specific variation in collision mortality with OWFs is unknown for seabirds and therefore excluded. We selected 1% additional mortality because although this is considered an acceptable threshold of loss by the EU ORNIS Committee (EU Birds Directive 79/409/EEC), several studies demonstrate that this can still lead to population-level consequences in seabirds (Horswill, Miller, et al., 2022; Horswill, Wood, et al., 2022; Schippers et al., 2020).

We calculated absolute and relative metrics of the population response to test their influence on the detection of threat under different formulations of density dependence. To estimate the absolute population response, we calculated the summed squared residuals between the mean population trajectories predicted under

unimpacted and impacted scenarios. Here, higher values indicate greater differentiation between trajectories and a greater absolute population response to reduced rates of adult survival. To account for parameter uncertainty, we calculated the summed squared residuals for all 500 PVA iterations. To estimate the relative population response, we calculated the percentage difference between the final mean population counts for the unimpacted and impacted scenarios across all 500 PVA iterations. This value is sometimes also referred to as the counterfactual of population size (Cook & Robinson, 2017; Jitlal et al., 2017). Populations that went extinct during the validation simulations ($n=1$, Figure S4E), and populations where validation failed to recreate observed dynamics ($n=1$, Figure S4D) were excluded from this analysis.

3 | RESULTS

3.1 | Data collation

We identified 599 populations across 25 species of seabird with time series of breeding success (Figure 2). We also identified 480 populations across 25 species of seabird with time series of population counts (Figure 2). However, only 31 populations across nine species had concurrent data for both processes for a minimum of 10 years (Figure 2). These datasets were collected across the UK and Ireland (Figure 3). The range of species-specific reproductive strategies, foraging styles, population sizes and population trajectories is presented in Table S1. Species with concurrent breeding success and count data were guillemot ($n=3$), razorbill ($n=2$), black-legged kittiwake (*Rissa tridactyla*, hereafter kittiwake, $n=15$), northern fulmar (*Fulmaris glacialis*, hereafter fulmar, $n=3$), European shag (*Gulosus aristotelis*, hereafter shag, $n=4$), great cormorant (*Phalacrocorax carbo*, $n=1$), northern gannet (*Morus bassanus*, hereafter gannet, $n=1$), herring gull (*Larus argentatus*, $n=1$) and common tern (*Sterna hirundo*, $n=1$).

3.2 | Quantifying density dependence

We found strong evidence for density-dependent regulation of seabird breeding success in 10% ($n=3$) of populations, and weak evidence in a further 16% ($n=5$) of populations. These populations included guillemot (populations at Sumburgh Head, Isle of May and Skomer), kittiwake (Elegug Stacks and Dunmore East), shag (Sumburgh Head), fulmar (Canna and Sanday) and razorbill (Isle of May). The form of density dependence varied between populations, but all formulations agreed on the direction of regulation within a population. The three populations exhibiting strong evidence of density dependence all demonstrated positive regulation. In total, this form of density dependence was identified in five populations (range of median posterior slope coefficients for the linear model: 9.32×10^{-4} to 8.60×10^{-3}). The remaining three populations demonstrated negative regulation (range of median posterior

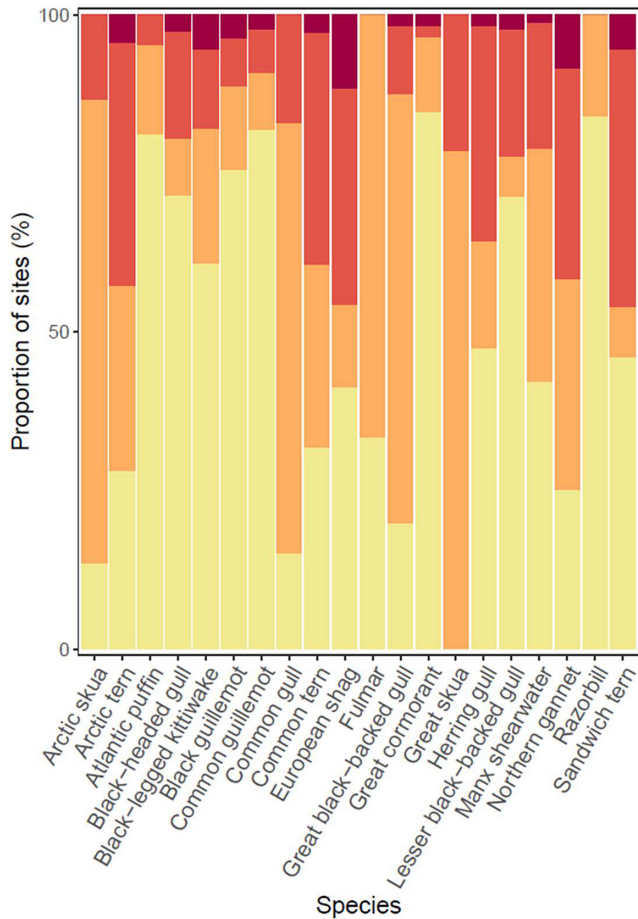


FIGURE 2 Data availability in the UK Seabird Monitoring Program database by species. The proportion of sites with at least 10 years of concurrent breeding success and population count data (dark red) is low, compared with the number of sites where data collection occurs at different times (i.e. during different phases of the annual cycle or in different years, pale red) or where only breeding success (orange) or population size (yellow) is monitored. These totals are taken prior to filtering observations based on accuracy grade, which further reduced the number of populations examined in this study.

slope coefficients for the linear model: -1.16×10^{-4} to -4.46×10^{-5} ; Figure 4).

For each population, the DIC indicated that multiple density dependence formulations achieved a comparable fit to the data (i.e. $\Delta\text{DIC} < 2$, Table S3). However, some formulations performed consistently well across populations, irrespective of the direction of regulation (Table S3). For example, the linear, log-linear model and the Weibull model with a 0.25 exponent (Weibull scenario 1) were within the best-fitting candidate models for seven out of the eight populations exhibiting evidence of density dependence. Finally, the detection and strength of evidence for density dependence may reflect the duration of data available. We found that a significant relationship between population size and breeding success is less prevalent when examined using shorter time series (Figure S3A), and that for most populations, the density-independent formulation was

not comparable to the best-fitting density-dependent formulation when examined using more than 20 years of data (Figure S3B).

3.3 | Validation analysis using PVA

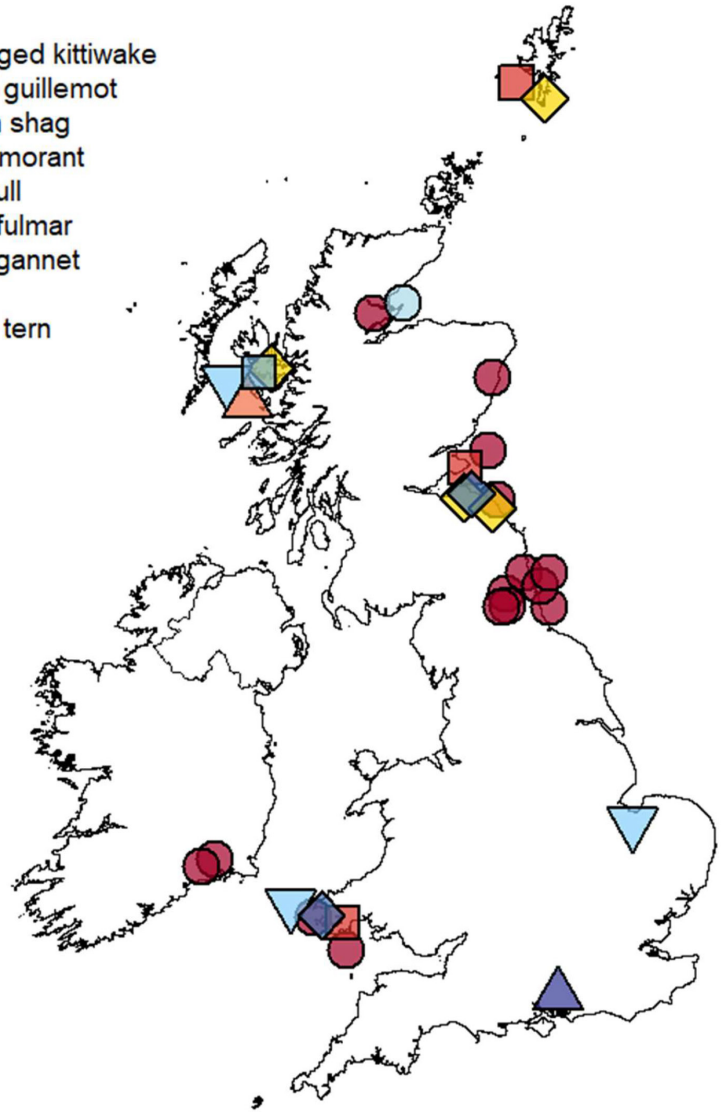
The validation PVAs indicated that across populations, the ability of the density dependence formulations to recreate observed population dynamics varied with the type of regulation operating (negative vs. positive), albeit with a small number of populations experiencing negative regulation ($n=3$; Figure 5, and see Figure S4 for projected dynamics with 95% CI). In the two guillemot populations experiencing negative regulation, all formulations performed substantially better at recreating observed population dynamics than the density-independent formulation (Figure 5a,b). However, in the razorbill population, all formulations entirely failed to recreate the observed dynamics (Figure 5c). By contrast, for populations experiencing positive regulation, the density-independent, log-linear and Weibull (exponent 0.25) formulations all performed consistently well (Figure 5d-h). However, all formulations, including the density-independent model, mostly underestimated population decline (Figure S4D,F,H). Within each population, the best formulation for describing density dependence based on the GLMM analysis and ΔDIC (Table S3) did not consistently produce the most accurate recreation of observed dynamics based on PVA (Figure 5c-h).

3.4 | Projection analysis and PVA metrics

The projection PVAs demonstrated that the estimated absolute and relative population response to reducing adult survival rate by 1% appeared to vary with the formulation of density dependence used and the type of density dependence operating (negative vs. positive), albeit with only two populations experiencing negative regulation (Figure 6, also see Figure S5 for projected dynamics with 95% CI). For the two guillemot populations experiencing negative regulation, the density-independent formulation generated a larger absolute response, compared with the density-dependent formulations (Figure 6a,b). This was generated by uncontrolled, exponential population growth in the density-independent PVA (Figure S5A,B). The absolute population response also varied amongst the different formulations of density dependence (Figure 6a,b). This variation between formulations decreased when using relative metrics, although the density-independent scenario still generated the largest response, with the highest uncertainty (Figure 6a,b). For populations experiencing positive regulation ($n=4$), the absolute and relative population response was much more consistent across the different formulations (Figure 6c-f). However, in contrast to the results for populations under negative regulation, the density-independent PVA generally projected a smaller (guillemot, kittiwake) or comparable (shag, fulmar) population response to the density-dependent formulations (Figure 6c-f, Figure S5C-F). The population outcomes were also less visibly varied between absolute and relative metrics in

FIGURE 3 Spatial representation of datasets available for examining the prevalence, strength and direction of density-dependent regulation of seabird breeding success ($n=31$). Datasets were distributed throughout the UK and Ireland and spanned nine species (see [Table S1](#) for population and species-specific information on life-history strategy and local population dynamics).

- Black-legged kittiwake
- Common guillemot
- ◆ European shag
- ▲ Great cormorant
- ▼ Herring gull
- Northern fulmar
- Northern gannet
- ◆ Razorbill
- ▲ Common tern



positively regulated populations, with the exception of the guillemot population at Sumburgh Head ([Figure S5C](#)).

4 | DISCUSSION

Population viability analysis is commonly used in impact assessments to predict how populations may respond to demographic change (Croll et al., 2022). Confidence in PVA outcomes is therefore essential for safeguarding threatened species, such as seabirds, whilst also facilitating the development of crucial industries, such as offshore renewables. Impact assessments used within consenting processes are often density-independent in the belief that this will produce precautionary assessments (Searle et al., 2020). This approach also reflects uncertainty around the prevalence, strength and direction of density-dependent regulation (Horswill et al., 2017). However, this approach faces criticism for being potentially overly prohibitive (Miller et al., 2019). Consequently, there is a pressing need to test how specific formulations of density dependence influence the

recreation of observed dynamics and the predicted absolute and relative population response to extrinsic threat.

We found strong evidence for density-dependent regulation of breeding success in three populations of seabird and weaker evidence in a further five. This represents approximately 25% of the study populations for which we had sufficient data on breeding success and population size to examine density dependence. However, we found that populations lacking evidence for density-dependent regulation typically had shorter study periods ([Figure S3](#)). Therefore, it is probable that the number of studies demonstrating evidence of density dependence is underestimated, and extending time series will likely enhance detection. This emphasises the importance of long-term monitoring projects.

We show that concurrent, site-specific data for breeding success and population counts are only available for a very small proportion of the seabird populations monitored in the UK and Ireland. The remote nature of seabird colonies means that monitoring is challenging and time consuming. Data collection across the UK relies on a small number of funded key sites, and a much larger number of colonies

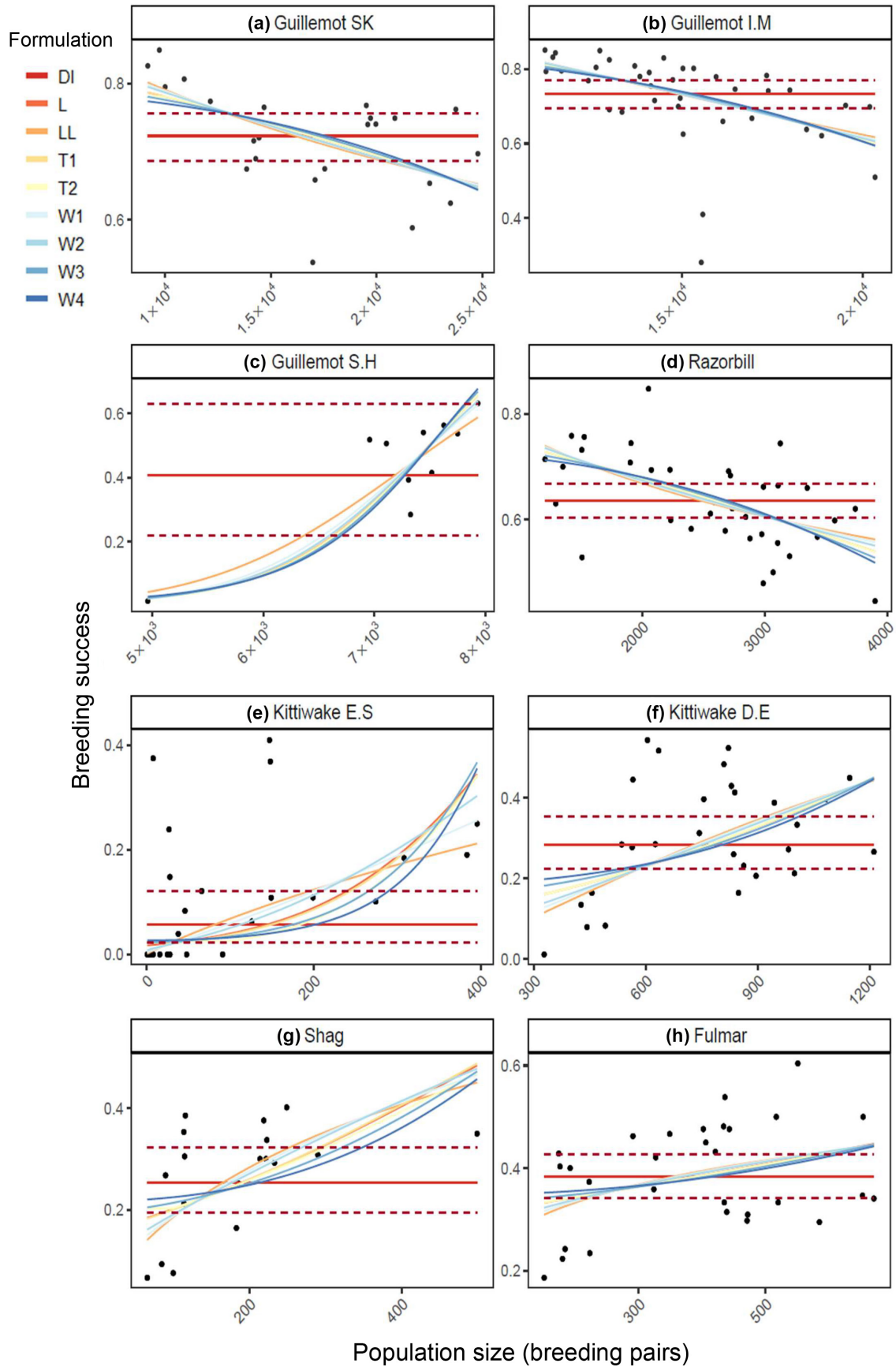
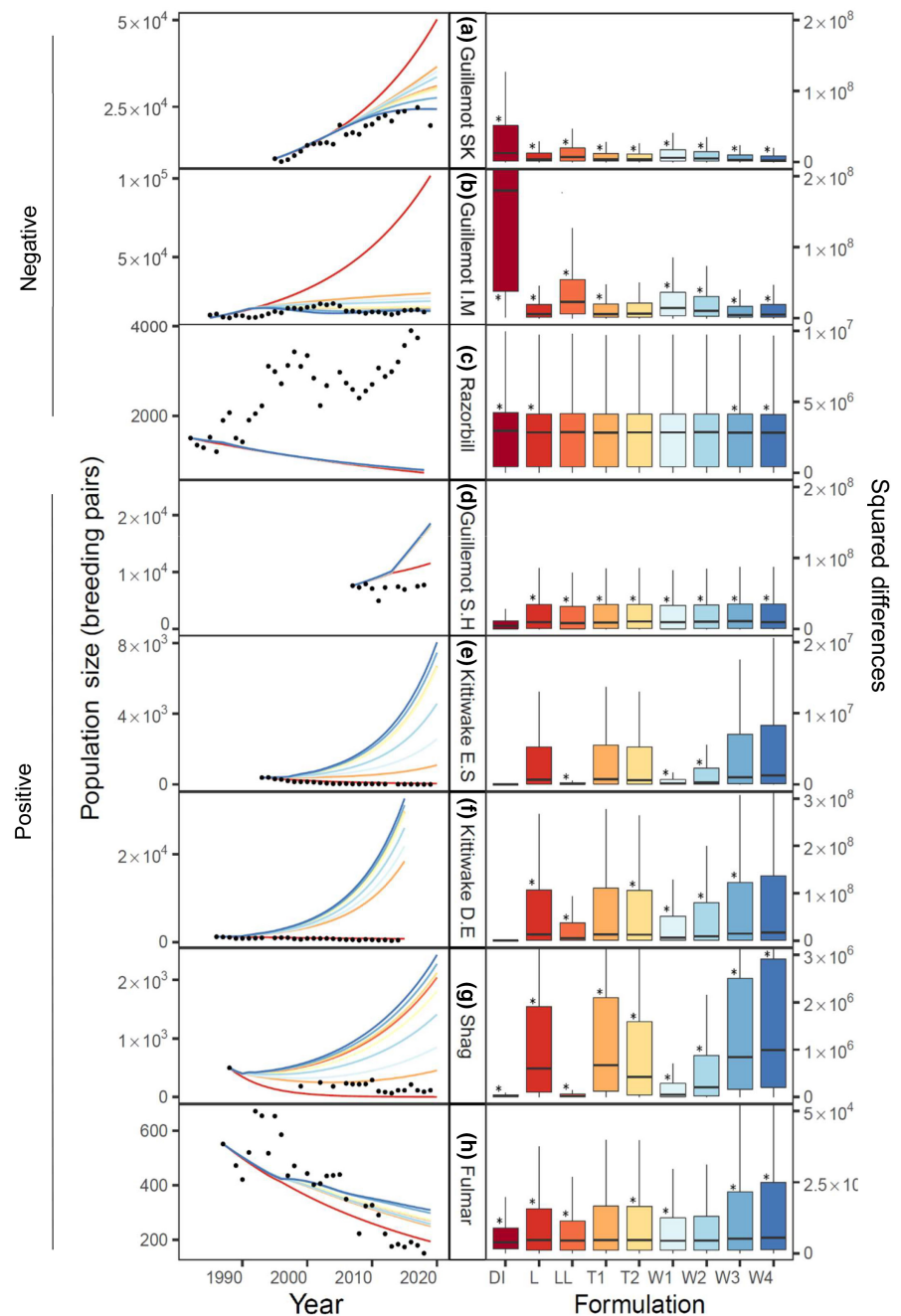


FIGURE 4 Population-specific relationships between seabird breeding success and population size. We identified significant relationships in eight populations and five species. For each population (a-h), we considered nine different generalised linear mixed models (GLMMs) including a density-independent (DI) model and eight formulations of density dependence: L=linear, LL=log-linear, T1=threshold scenario 1, T2=threshold scenario 2, W1=Weibull scenario 1, W2=Weibull scenario 2, W3=Weibull scenario 3, W4=Weibull scenario 4. Black dots show observed population-specific values of breeding success and population size, whilst coloured lines show the predicted relationships from the GLMMs. Dashed red lines show the 95% credible intervals for the density-independent model to illustrate populations with potentially weaker evidence of density dependence. Population notation: (a) common guillemot SK, Skomer; (b) common guillemot I.M, Isle of May; (c) common guillemot S.H, Sumburgh Head; (d) razorbill, Isle of May; (e) black-legged kittiwake E.S, Elegug Stacks; (f) black-legged kittiwake D.E, Dunmore East; (g) European shag, Sumburgh Head; (h) northern fulmar, Canna and Sanday.

FIGURE 5 Formulations of density dependence that most effectively recreated observed dynamics in seabird populations (a-h) differed with the type of density-dependent regulation operating. In populations experiencing negative regulation (a-c), the Weibull formulation performed consistently better; for populations experiencing positive regulation (d-h), the density-independent and log-linear formulations performed better. Panels on the left (line graphs) show the population viability analysis (PVA) predicted population trajectories compared with the observed population count data used to estimate density dependence (black points). Lines reflect the mean population trajectory from the validation PVAs. Some formulations are obscured by overlapping trajectories, for example panel (d). Panels on the right (boxplots) show variation in the squared differences between counts of observed populations when compared to predicted mean population counts from the validation PVAs. The bold central line is the median, the box reflects the interquartile range, and the whiskers are the $1.5 \times$ interquartile range. Asterisk indicates formulations providing a comparable fit based on the deviance information criteria (DIC) scores of the generalised linear mixed models (GLMMs). Outliers are excluded. The Y-axis is truncated in some instances to allow visual comparison between formulations on the same scale. Formulation, colours and population notation match Figure 4.



monitored by volunteers and citizen scientists (Burnell et al., 2023; JNCC, 2021). Focusing efforts to increase the number of sites that concurrently monitor breeding success and population counts

would facilitate a more comprehensive understanding of the factors influencing regional population dynamics, including assessments of density-dependent regulation. Consequently, we recommend

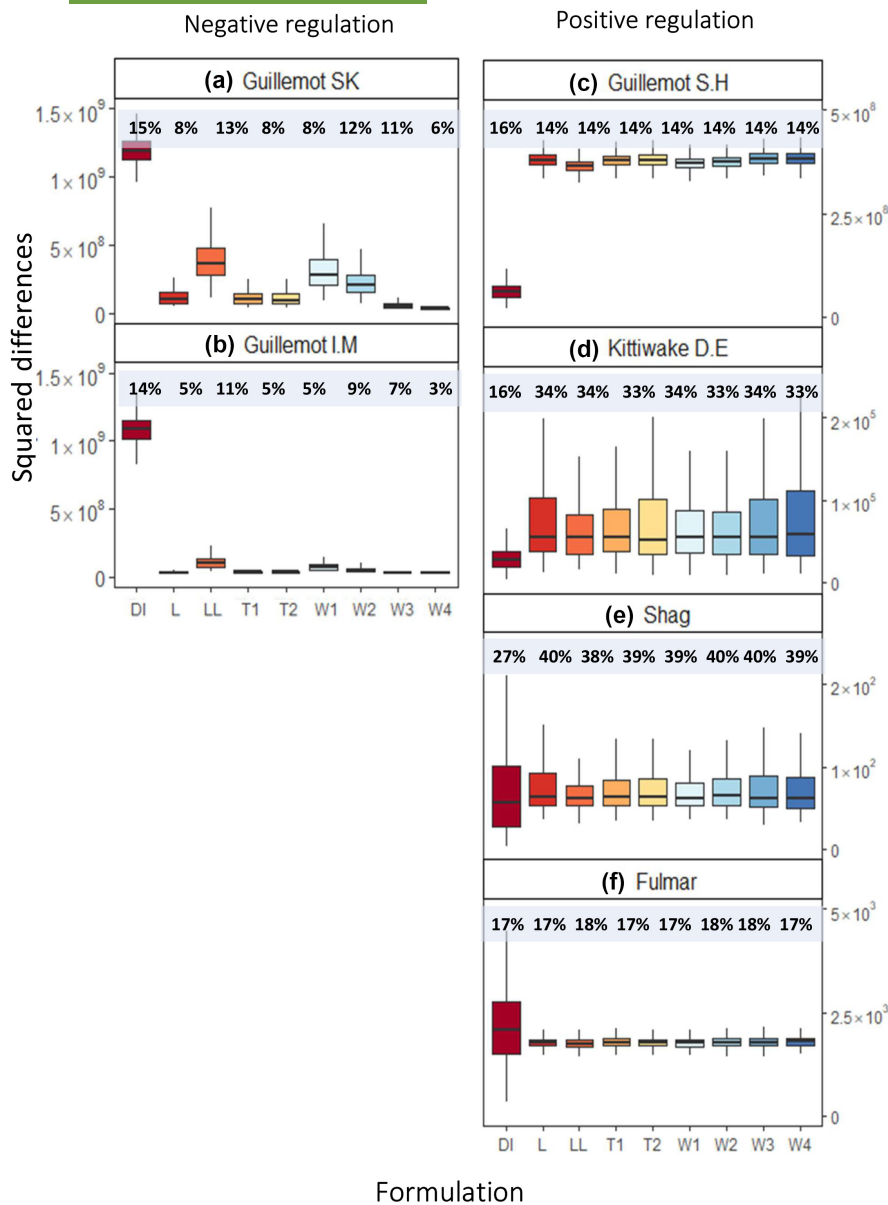


FIGURE 6 Absolute and relative projected responses of different seabird populations (a-h) to an extrinsic threat estimated using different formulations of density dependence. Boxplots show variation in the estimated absolute population response using the squared differences between the predicted mean population counts from the population viability analysis (PVA) under an impacted (where the survival rate was reduced by 1%) and unimpacted scenario. Higher median values (indicated by bold central line in each box) and greater variability (indicated by box size and whiskers) reflect a larger difference between the impacted and unimpacted PVA scenarios for each formulation and population. Percentages reflect the relative population response, represented by the counterfactual of population size. Outliers are excluded. The Y-axis is truncated in some instances to allow for visual comparison between formulations on the same scale. The population of kittiwakes from Elegug Stacks (i.e. Kittiwake E.S) is excluded because it became extinct during the validation time period, and the population of razorbills is excluded because none of the formulations were able to recreate the observed population trajectory during validation analysis. Formulation abbreviations, colours and population notation match those detailed in Figure 4.

further examination of monitoring sites to identify colonies where volunteers can be supported and incentivised (e.g. through financial assistance) to monitor both traits. This approach is likely to be the most promising avenue for maximising uptake and ensuring long-term commitment, without necessitating greater numbers of volunteers. Financial investment in monitoring from industry, such as OWF developers and regulatory bodies could also support the acquisition of these data, whilst serving to improve the consenting processes and safeguard protected populations.

We found evidence for density-dependent breeding success across all study populations for guillemot ($n=3$). The UK guillemot population is considered stable, with some local variation in population trends (Burnell et al., 2023). The three guillemot colonies identified as showing evidence of density dependence were either stable, or increasing (Table S1), such that colonies may be nest site limited or reaching regional carrying capacity. The direction of density dependence identified in these colonies differed,

and we found weak evidence of negative regulation in the two very large populations (>10,000 breeding pairs—Isle of May and Skomer). Negative density-dependent regulation of breeding success has been previously reported for guillemots on the Isle of May (Bennett et al., 2022). However, we also identified strong evidence of positive regulation in the smaller population at Sumburgh Head. Intraspecific variation in the direction of density-dependent regulation of seabirds has previously been shown in skuas, large gulls and terns (Horswill et al., 2017). By expanding this evidence, our study further emphasises the value of using population-specific data when assessing population viability (Horswill et al., 2021; Horswill, Miller, et al., 2022; Horswill, Wood, et al., 2022), rather than generalising demographic processes across species and populations.

Density-independent PVAs are generally considered to provide a precautionary approach to assessment (Chaudhary & Oli, 2019; Green et al., 2016; Maclean et al., 2007; Peer et al., 2013). Accordingly, we found that for populations under negative

regulation, a density-independent PVA projected the largest estimation of absolute and relative impact (Figures 5a–c and 6a,b). However, this formulation also provided the worst fit to the observed data. This is because without density-dependent control, the simulated populations experience unconstrained growth. Therefore, although the PVA metrics indicate a precautionary assessment for these populations by overestimating impact, the population trajectories are reaching such unrealistically large population sizes that the metrics become biologically implausible (Figure S5A,B). By contrast, for populations experiencing positive regulation of breeding success, we found that the density-independent validation PVA produced trajectories most comparable to the observed dynamics. However, in the projection analysis, the density-independent model predicted the lowest absolute and relative threat response across multiple populations. This finding is in agreement with previous expectations that density-independent PVA will not provide a precautionary assessment for seabird populations under positive regulation (Horswill et al., 2017). Given these results across both negative and positive density-dependent regulation, we conclude that a density-independent model is unlikely to provide a suitable or precautionary assessment approach.

We identified a suitable group of density-dependence formulations for each population. Whilst the composition of these groups varied across populations, some formulations were consistently favoured. We found that a log-linear or Weibull (exponent 0.25) formulation provided the best representation of density-dependent regulation of breeding success in the highest number of populations assessed (Figure 4; Table S3). These formulations also performed comparably to, or better than, the other formulations at recreating observed population dynamics under positive regulation ($n=5$, Figure 5d–h). Additionally, for populations experiencing positive regulation, the log-linear and Weibull (exponent 0.25) formulations yielded similar predictions regarding population response to extrinsic threat compared with the other formulations. This suggests that the predicted population response under positive regulation is relatively insensitive to the formulation of density dependence (Figure 6c–g). This was with the exception of a density-independent formulation, which estimated substantially lower, and therefore potentially less precautionary, population responses to extrinsic threat. We were unable to draw strong conclusions about the best formulation of density dependence for describing populations under negative regulation ($n=2$, excluding razorbill). Most formulations performed comparably, with the exception of the density-independent formulation, which was by far the worst at recreating observed dynamics (Figure 5a,b, Table S3). In terms of identifying a precautionary assessment under negative regulation, the log-linear and Weibull (exponent 0.25) formulations predicted the largest (and therefore possibly more precautionary) population response to an extrinsic threat compared with the other formulations, excluding the implausible density-independent outcome.

When making recommendations for incorporating density dependence into PVA-based impact assessment, we need to consider

that PVAs are simulation models capable of projecting populations beyond the observed range of population sizes. We must also consider that, in agreement with previous studies on seabirds (Horswill et al., 2017), we find evidence of density dependence across various species and populations. Therefore, even if populations currently exhibit no evidence of density dependence, accounting for density dependence in PVA simulation models could be vital for preventing unconstrained growth or incorporating rapid population decline in predictions. This becomes particularly relevant when evaluating long-term impact and compensation scenarios that may result in large changes in population size. Consequently, we support the investigation of density-dependent scenarios in PVA-based impact assessments, even in the absence of population-specific evidence for density-dependent regulation.

Based on our validation and projection analyses, we tentatively recommend that log-linear and Weibull (exponent 0.25) formulations may be the most appropriate for including density dependence in PVA. To implement such analyses, the parameters from the GLMMs, and the correlations between these parameters, could be used to define a joint prior distribution for a Bayesian PVA. To support this, we provide the imputed range of slope coefficients in the Supporting Information (Table S3). For populations where information on the presence and strength of density dependence are missing, we recommend examining the sensitivity of PVA results to the range of values identified for key parameters in the log-linear and Weibull (exponent 0.25) formulations as part of PVA scenario testing. Future studies may also consider comparing the performance of the log-linear and Weibull formulations for describing density dependence in PVA to other approaches (e.g. Tinker et al., 2022). Our study reaffirms the continued importance of not basing conservation and consenting decisions solely on PVA outcomes, especially where site-specific population data is lacking (Hernández-Camacho et al., 2015; Horswill et al., 2021).

We show that, for the majority of populations assessed, absolute and relative metrics estimated using density-independent PVA are different from those estimated by density-dependent PVA, in terms of the mean estimated impact. For the two guillemot populations under negative regulation, the density-independent PVA generated the highest mean absolute and relative impact, although the difference is far less pronounced in the relative metric. By contrast, for populations experiencing positive regulation ($n=4$), the density-independent PVA tended to generate the smallest population response, and similarly to the two populations experiencing negative regulation, the relative metric largely shows less pronounced differences between populations. These results indicate that whilst using relative metrics in density-independent PVA impact assessments might, to a certain extent, mitigate the minimisation (under negative regulation) and exaggeration (under positive regulation) of impacts, this approach will not overcome biases introduced by overlooking density dependence, particularly where positive density dependence is present.

Whilst the sensitivity of PVA to the misspecification of inputs can, to an extent, be mitigated using relative PVA metrics, the reliability

of PVA outputs will still reflect the quality of the inputs (Boyce, 1992; Coulson et al., 2001; Jitlal et al., 2017; Reed et al., 2002). The model validation analysis demonstrated that the formulations of density dependence that best described the relationship between breeding success and population size were often unable to recreate the observed population dynamics in PVA. This mismatch between observed and simulated trajectories, most pronounced in the razorbill population (such that we are reluctant to draw any conclusions regarding the inclusion of density dependence in PVA for razorbills; Figure 5c), highlights that density dependence is one aspect of demography that can improve PVA model performance. Additional aspects include improved estimates of demographic rates, including inter-colony movements, resolution of the relationships between demographic rates and environmental factors, and improved models of observation error (Searle et al., 2023). The inclusion of environmental features, such as climate, habitat, prey availability, metapopulations and interspecific competition, alongside additional demographic inputs, such as correlations between vital rates, may elucidate the drivers of interannual variation in population dynamics (Boyce, 1992; Miller et al., 2019; Searle et al., 2022, 2023; Wakefield et al., 2017). However, this approach is challenged both by the breadth of covariate data available for inclusion, and the methodological capacity to simultaneously include them whilst retaining the degree of simplicity desired by practitioners (Butler et al., 2020). For example, measuring marine food resources, such as fish biomass, on appropriate spatial and temporal scales is extremely difficult, such that seabirds are more commonly considered as indicators of marine productivity and the availability of forage fish (Einoder, 2009; Ramos & Furness, 2022).

In this study, we provide support for incorporating density-dependent regulation into seabird impact assessments used during the consenting process for marine industrial developments, such as offshore wind farms. For populations experiencing negative regulation of breeding success, including density dependence prevents unconstrained population growth, thereby creating a more faithful recreation of observed dynamics and producing more applicable measures of relative impact. For populations experiencing positive regulation of breeding success, a density-dependent model will prevent any underestimation of absolute population decline and thereby maintain a precautionary approach for assessing these more vulnerable populations. Our findings tentatively suggest that a log-linear or Weibull formulation of density-dependent breeding success could be most suitable for quantifying density-dependent regulation in PVA assessments. These models provided a comparable or better recreation of population dynamics than other formulations, whilst still providing more precautionary impact assessment metrics for vulnerable, positively regulated populations. The apparent link between time-series duration and detection of density dependence suggests that this process may be more prevalent than shown, and we highlight a need to maximise concurrent collection of breeding success and population count data from existing SMP sites to support the examination of spatial variation in density dependence and population dynamics. Finally, we highlight the importance of

caution in the use of PVA in consenting decisions, especially where population-specific data is lacking. More broadly, our study provides evidence that incorporating density-dependent regulation may produce more meaningful assessments of future impact on protected populations.

AUTHOR CONTRIBUTIONS

Catharine Horswill, Jonathan A. Green, Leonie A. Robinson, Julie Black, Francis Daunt and Eve Merrall conceived the study and designed the methodology. Mark A. Newell, Matt J. Wood. and Francis Daunt collected and managed data. Eve Merrall extracted data, executed modelling and conducted the analysis with assistance from Catharine Horswill and Adam Butler. Eve Merrall led the writing of the manuscript with guidance from Catharine Horswill, Jonathan A. Green, Leonie A. Robinson 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.

DATA AVAILABILITY STATEMENT

All data are available through the Seabird Monitoring Program database (SMP: <https://app.bto.org/seabirds/public/index.jsp>) and the NERC Environmental Information Data Centre (Newell et al., 2022; <https://doi.org/10.5285/3bf9b65d-727c-4b46-9db6-c0814dc5895f>). Data from Skomer used in this study are also available on request from the University of Gloucestershire Research Repository (Wood, 2023; <https://eprints.glos.ac.uk/id/eprint/12532>). Code for replicating Bayesian analyses is available on publication from Zenodo (Horswill & Merrall, 2024; <https://doi.org/10.5281/zenodo.11553113>). All population viability analysis was carried out using the nePVA tool (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. Illustration of the prior distribution used to assign the intercept term in each GLMM and the respective posterior distributions (by formulation) for all populations exhibiting evidence of density-dependent regulation.

Figure S2. Illustration of the prior distributions used to assign intercept terms in the density-dependent GLMMs.

Figure S3. (A) Populations with an insignificant relationship between population size and breeding success (blue) were more prevalent than populations with a significant relationship (red) when examined using shorter time series of data. Median posterior values shown for the slope coefficients describing density-dependent regulation of breeding success in the Weibull S1 GLMM with 95% credible intervals. (B) The density-independent formulation was mostly not comparable to the Weibull S1 formulation when more than 20 years of data was available (i.e. $\Delta\text{DIC} > 2$).

Figure S4. The model validation assessment showed that PVAs using different formulations of density dependence (coloured polygons show 95% CI and mean trajectory as black line) performed differently in their ability to recreate observed dynamics (black points).

Figure S5. The PVA projection analysis demonstrated that decreasing rates of survival by 1% (impacted scenario: red) decreased rates of

population growth (A–C) or increased rates of population decline (D–F), compared to an unimpacted scenario (blue).

Table S1. Life-history strategies, foraging styles, population sizes and population trajectories for all populations used to examine density-dependent regulation of breeding success.

Table S2. Sensitivity of density-dependent GLMMs to the precision of the normal prior distributions used to assign the intercept and slope coefficient terms.

Table S3. Performance of GLMMs using different formulations to describe density-dependent regulation of breeding success.

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