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An overview and exploratory analysis

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Summary

Although there is evidence that density-dependence operates in seabirds populations, population models used for assessment of ecological effects of offshore wind farms (OWF) often lack density-dependent processes for precautionary reasons, and because it remains challenging to specify the form and strength of density dependence. The choice of not including density dependence might, however, unnecessarily hinder OWF developments, and has been criticized to be overly prohibitive.

Here we review the current state of knowledge regarding density-dependent effects in seabird populations and explore to what extent density-dependent processes are accounted for in assessments of offshore wind farm impacts in other countries. Furthermore, we analyze the possible consequences of including density-dependent processes in the population models as used within the Dutch KEC (*"Kader Ecologie en Cumulatie"*) assessment for seabirds. In addition, we review and analyze the consequences of the recent epidemic of high-pathogenic avian influenza (HPAI) virus, that led to mass mortality and widespread breeding failure in several seabird species in 2021-2022. Effects of HPAI will likely interact with density-dependent processes and are therefore treated in the same study.

We find that, although density dependence is common in seabird populations, there is no single form of density-dependence that can be applied to all species and populations. Density dependence can act to compensate additional losses from a population if there is a negative response population growth rate with population abundance (negative regulation), or aggravate additional mortality (depensation) if this response is positive. Compensatory responses are reported mainly at larger population sizes, while depensatory responses operate mostly in depleted population or endangered species. Impact assessments into offshore wind farm effects performed in other countries around the North Sea can only consider density dependence if supported by robust evidence and a strong justification of the density-dependent terms used. It is likely that compensatory density-dependent responses occur at larger population sizes and will therefore be most relevant for the KEC, because of the large spatial scale of this assessment. Depensatory responses will be relevant for species that breed in several small colonies that are vulnerable to predation.

Density dependence can have a considerable compensatory effect on OWF-induced mortality, as exemplified by our analysis for the northern gannet. Although the shape of density dependence matters, the KEC outcome was relatively insensitive to the carrying capacity level assumed, except when the carrying capacity was substantially larger than current levels and the modelled population could growth exponentially. Interestingly, mass mortality and breeding failure due to a simulated HPAI virus outbreak did not change the assessment outcome when using density-independent models, but increased the relative impact of OWF-induced mortality on population size when using density-dependent models.

Although realistic models should be used to inform cumulative assessments of OWF impacts, the potentially strong compensatory effect of density dependence requires a solid evidence-base on how density dependence operates on the scale of the KEC assessment. In addition, the use of density-dependent models within the KEC also requires more knowledge on other processes that can affect population dynamics, such as HPAI outbreaks. We conclude that the evidence base is currently insufficient to solely base the KEC assessment on density-dependent population models. We therefore recommend to further study how density-dependent processes operate on the scale on the DCS, which is the most relevant scale of the KEC. Considering the risk of mis-specifying the strength of density dependence, we also recommend to host an expert discussion session to investigate for which species enough information is available to warrant use of density-dependent models in the KEC assessment. We further recommend to continue the simultaneous monitoring of demographic rates and population sizes, in combination with more advanced population modelling that utilize population census data to unravel the processes that are driving seabird population dynamics.

1 Introduction

Within the KEC assessment for seabirds, population models are used to estimate the impact of additional mortality from offshore wind energy developments on seabird populations (Soudijn et al. 2025; IJntema et al. 2025). These population models lack any form of density dependence, which implies that the modelled population grows or declines exponentially. Although there is sufficient evidence that density dependence operates in seabirds populations, and unhindered population growth is considered unrealistic, population models used for OWF assessments often lack density-dependent processes for precautionary reasons, and because it remains challenging to specify the form and strength of density dependence (Horswill et al. 2017; Green et al. 2016; Miller et al. 2019; Searle et al. 2020; 2019). The choice of not including density dependence might, however, unnecessarily hinder OWF developments, and has been criticized to be overly prohibitive (Merrall et al. 2024; Miller et al. 2019).

This memo explores the possibility of including density-dependent processes in the population models as used within the KEC assessment for seabirds. We review the current state of knowledge regarding density-dependent effects in seabird populations and discuss if and how ecological assessments of offshore wind energy developments performed in other countries account for density-dependent processes. We furthermore present a case study that quantifies the potential effects of density dependence on the outcome of the KEC assessment. We conclude with advice on the requirements of including density dependence in the KEC population models.

The study into density dependence is combined with a review and analysis on the consequences of the recent outbreak of high-pathogenic avian influenza (HPAI) virus, that led to mass mortality and widespread breeding failure in several seabird species in 2021-2022. Effects of HPAI outbreaks are currently not considered in the population models as used within the KEC. Based on this analysis an advice is given on whether time-restricted mass-mortality events, like the recent HPAI epidemic, should be included in the future. Effects of HPAI will likely interact with density-dependent processes and are therefore treated here together in the same study.

2 Assignment

In this memo we explore the possibility of including density-dependent processes in the KEC population models. In addition, we describe the recent outbreak of high pathogenic avian influenza (HPAI) virus that led to mass mortality and breeding failure among several seabird species assessed in the KEC, and the possibility and effects of accounting for such events in the KEC population modelling.

This memo includes the following components:
- A non-exhaustive review of density dependence in seabirds.
- An exploration of how density dependence is accounted for in other international assessments of the effects of offshore wind farm developments.
- An analysis of the potential effects of density dependence on the KEC outcome for a single species (the northern gannet).
- A short review of the recent outbreak of HPAI virus.
- A short analysis of the effect of a single HPAI outbreak that induces mass-mortality and breeding failure on the KEC outcomes.
- Discussion and conclusion.

3 Density dependence in seabird populations

3.1 Review

3.1.1 Compensatory and depensatory density dependence

According to Horswill et al. (2017), density dependence operates if the rates of demographic processes – such as growth, survival, reproduction, and recruitment – change as a function of the density or number of individuals in a population. Density-dependent responses of demographic processes result in a population growth rate that either increases or decreases as a function of population density. Density-dependent processes are compensatory if the resulting population growth rate decreases with population density. The resulting negative feedback leads to population numbers that stabilize around a long-term average value, which is referred to as the carrying capacity of a population. Compensatory density dependence can act to compensate additional losses from a population, for example from OWF-induced mortality. The lowered population abundance as a result of the additional mortality then increases demographic performance of the remaining individuals.

Conversely, demographic processes operate in a depensatory manner if the population growth rate increases with population density (Horswill et al. 2017). In this case there is a positive feedback between population growth and population density, which can destabilize population dynamics. Depensatory responses often play a role in depleted populations and may exacerbate disturbances or hinder population recovery.

Depensatory and compensatory responses may act on the same population, but at different densities. For example, with increasing population density breeding success might increase at low population densities through the benefits of increased anti-predator vigilance or colonial defence, but decrease again at higher densities when effects of local prey competition become apparent. Horswill et al. (2017) reported intraspecific variation in the direction of density dependence for skuas, large gulls and terns.

3.1.2 Evidence of density dependence

Horswill et al (2017) reviewed the empirical evidence on density dependence in seabird populations and, at that time, identified 11 studies (seven species) with empirical examples of depensation that was attributed to increased predation at lower population densities. Depensation was most prevalent among terns and small gulls, while it was also reported for larger species such as Arctic skua and herring gull. For a few even larger species (Northern gannet, Great skua and Great black-backed gull), egg or chick predation is likely of far lesser importance. Horswill et al (2017) conclude that considering depensation will be important for depleted populations and endangered species.

Regarding compensatory responses, the most prevalent evidence for density-dependence was the relationship between recruitment and availability of resources (Horswill et al 2017). Horswill et al (2017) found similar support for compensatory regulation among studies that considered population growth, survival, dispersal and productivity (breeding success). However, there were an equal amount of studies in which productivity rates were unrelated to colony size, compared to studies that found a compensatory response of productivity. The outbreak of HPAIV in 2021-2022 among seabirds has provided further evidence of density dependence in recruitment rates in northern gannets, Sandwich terns and roseate terns, resulting in buffering part of the loss of adults from the breeding population (see section 4.1 - The High Pathogenic Avian Influenza epidemic).

Horswill et al (2017) concluded that there was substantial evidence that populations of seabirds exhibit compensatory density-dependent regulation on survival, productivity, recruitment and dispersal processes.

There was also clear evidence that density-dependent regulation operates on productivity in specific species and populations. Depensation was reported exclusively for productivity rates and dominated by studies on small gulls and terns.

Although density-dependence is thus widespread among seabird populations, the exact strength and form of the relationships of demographic rates with density are often poorly understood. This is partly due to the difficulties of estimating these relationships from existing data – or collecting these data in the first place.

In seabirds, density-dependence has mostly been approached from studies at breeding sites, where estimation of demographic parameter is feasible. Usually, these studies have contrasted colonies with different breeding densities or the same colonies across a time of increase or decrease. However, density-dependence can also occur at larger spatial scales (Jeglinski et al. 2023).

In other groups than seabirds, ranging from small passerines to waders and ducks, density-dependence has also been identified in several demographic parameters (reviewed in Newton 1998). Hence, migratory landbird species that are treated within the KEC are also likely to experience density-dependence in demographic parameters such as productivity, survival and recruitment. As most of these species are non-colonial breeders, the mechanisms of depensatory density-dependent in these species will likely not be related to anti-predator benefits of higher densities. Instead, mechanisms such as the ability to find partners may be at play.

Merrall et al. (2024) also found mixed evidence on the type of population regulation, with both negative and positive regulation of breeding success for seabirds breeding in the UK and Ireland. Based on the Seabird Monitoring Programme (SMP 2025) database and additional information from Skomer Island and Isle of May, they found 31 populations from nine species with concurrent time series on breeding success and population counts that each covered more than 10 years. This was only a relatively small subset of the 599 populations (25 species) with time series on breeding success and 480 populations (25 species) with time series on population counts (number of breeding pairs), indicating the challenges in data collection to properly address the existence of density-dependent processes. Among the 31 data sets, Merrall et al. (2024) found strong evidence of a positive density-dependent response of breeding success in three populations (10%), and weak evidence of a generalized density-dependent response in a further five populations (16%; two positive and three negative responses). Interestingly, the positive responses of breeding success to number of breeding pairs (BPs) were found mainly for low number of BPs (shag: max. 450 BP at Sumburgh Head; kittiwake: max. 400 BPs at Elegug Stacks and max. 1,200 BPs at Dunmore East; northern fulmar: max. 700 BPs at Canna & Sanday), or seem to rely on a single outlier value (guillemot at Sumburgh Head). The negative responses were found for guillemot at max. 25,000 BPs at Skomer and max. 20,000 BPs at Isle of May, and for razorbill at max. 4,000 BPs at Isle of May (Figure 4 in Merrall et al. 2024). This is consistent with the idea that positive population regulation operates at low population sizes, while negative population operates at high population sizes (Horswill et al. 2017). The density-dependent effect on breeding success for colonial breeding guillemots at Isle of May was described also by Bennett et al. (2022). As population size increases, high quality breeding sites become occupied and an increasing proportion of the breeding population breeds at low quality sites, which reduces overall breeding success (Bennett et al. 2022). This is a common mechanism of density dependence in colonial breeding seabirds, and has also been described in other species (Gill et al. 2001, Nelson 2002).

The observed responses of breeding success to number of BPs were then used by Merrall et al. (2024) to parameterize models for Population Viability Analysis (PVA: Searle et al. 2019; Butler et al. 2021; 2020). Including the observed negative responses of breeding success to number of BPs improved the ability of the PVA to recreate observed population dynamics when compared with a density-independent PVA (Merrall et al. 2024). For positive responses, density-dependent model variants performed equally well as density independent model variants, although all formulations underestimated population declines (Merrall et al. 2024). Merrall et al. (2024) also studied the effect of additional mortality on the relative population abundance, and showed that population responses to a reduction of adult survival by 1% were larger for density-independent models when compared to population models with negative population regulation.

For some species, density dependence likely operates through a limited number of breeding sites combined with a large floater population. Bryan Nelson's (2002) classic study of gannets emphasises that colonies harbour a substantial cohort of sexually-mature but non-breeding adults (floater individuals) that perform prospecting and social roles essential to colony formation and expansion. In this way, in case of density dependence, floaters act as an important demographic reservoir, facilitating immigration into vacant territories and buffering colonies against episodic adult losses. For conservation and impact assessment, for example for OWF developments, population models that omit density dependence and a floater class are prone to two errors: (1) unrealistic exponential forecasts under favourable conditions, and (2) overestimation of the long-term effect of increased adult mortality or dramatic events like the avian influenza, because of the lack of a buffering effect of a floater population (Ainley et al. 2024, Penteriani et al. 2011).

3.1.3 Spatial scale

Density dependence can operate at multiple spatial scales and models used for conservation should consider the relevant processes at the relevant spatial scales (Jeglinski et al. 2023). Jeglinski et al. (2023) fit Bayesian state-space models to more than a century of census data from gannet colonies to compare increasingly complex scenarios of metapopulation regulation and immigration. With these scenarios they compared local, colony-specific density dependence to regional density dependence, and investigated whether immigration rates were related to the size of the receiving colony. They show that including conspecific attraction and both local and regional density dependence increase model fit, as opposed to models with equal partition of immigrants, and without regional density dependence. Interestingly, models that only include local density dependence predict a metapopulation carrying capacity that is more than twice as high than models including regional density dependence. The results by Jeglinski et al. (2023) have considerably implications for conservation and management as they show that ignoring density dependence, or mis-specifying the relevant spatial scale, can lead to underestimating future population sizes. A failure to detect density dependence that operates on a regional scale will also underestimate the strength of density dependence, and therefore underestimate that compensatory effect that density dependence may have in case of additional sources of mortality.

3.2 Use of density dependence within OWF impact assessments in other countries

This section focuses on whether assessment into OWF impacts as performed in other countries consider density-dependent processes in population modelling. For this we contacted colleagues working in several countries around the North Sea to inform about the assessment process of ecological effects of OWFs and, specifically, the use of density dependence in that.

In the UK it is common practice to perform a PVA to assess impacts of proposed offshore renewable energy developments on seabird populations (often individual colonies or Special Protection Areas). A PVA tool[1] has been tailor-made to perform such analysis (Butler et al. 2021; Searle et al. 2019; Butler et al. 2020). It was developed by Biomathematics and Statistics Scotland (BioSS) and UK Centre for Ecology and Hydrology (UKCEH) under contracts for Natural England and JNCC. It contains five possible ways of including density dependence, namely (after Butler et al. 2021):

- Density independence (i.e. no density dependence)
- Linear dependence of demographic rates on population size
- Linear dependence of demographic rates on log10 of population size
- A Weibull function, which contains a linear and an exponential term to model dependence of demographic rates on population size
- A threshold function, in which density dependence is linearly proportional to population size above the threshold, and independent of population size below the threshold.

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[1] The "nepva" R package: https://github.com/naturalengland/Seabird_PVA_Tool

There are also clear policy guideline for the use of PVA that are set out by Natural England, Natural Resources Wales and NatureScot[2]. The best practises guideline from Natural England states that, from Parker et al. (2025):

> "*Density dependent processes are likely to operate on seabird populations. If there is clear evidence of the form and strength of density dependence operating on the focal population (colony), then it may be possible to include density dependence within the population model.*
>
> *However, empirical evidence of mechanisms of density dependent population regulation are lacking for most seabird populations. Assuming that a population is capable of exhibiting a compensatory density dependent response in the absence of empirical evidence at the relevant population scale has the potential to underestimate the potential impact of a proposed development on the focal seabird population.*
>
> *If a density dependent model is proposed, it should be supported by robust evidence, a strong justification of the density dependent terms used, and presentation of a range of outputs in including metrics from density independent models.*
>
> *In the absence of robust evidence to support the form and strength of density dependence to add to a model, it is not possible to determine whether the predictions from a density dependent model are robust or accurate. Therefore, where there is limited information on population regulation for the focal population, it is recommended that a density independent model is used instead. By definition such a model will always predict that an impacted population will have a lower growth rate and smaller final size than an unimpacted population."*

The policy guideline for NatureScot[2] requires using the 'nepva' tool, but does not mention whether density dependence should be considered. The guidelines of Natural Resources Wales tend to be closely aligned with the Natural England guidelines (A. Robertson, *personal communication*).

Germany and Denmark have well-developed and expanding OWF plans. However, population-level models for seabirds, let alone including density dependence, are not used to predict long-term impacts. In both countries, extensive monitoring programmes do exist, including aerial and ship-based surveys as well as studies using tagged birds, but assessments still rely on site-based information rather than tools that forecast population changes far into the future (pers. com. Volker Dierschke, Dachverbands Deutscher Avifaunisten; Jesper Kyed Larsen, Vattenfall).

For the complete Danish Exclusive Economic Zone the current cumulative risk analysis is based on predefined protection targets; a habitat protection level (expressed as the proportion of a species' range), a target protection level for the expected number of displaced birds, and a target protection level for mortality due to collisions (expressed as the proportion of the estimated abundance within the EEZ). To determine the acceptable level of mortality, the Potential Biological Removal (PBR) calculation is used. This approach assumes that species with high adult survival and a late age of first reproduction exhibit lower population growth rates and are therefore less capable of compensating for additional mortality (pers. com. Ib Krag Petersen, Aarhus University).

In Sweden there is still a limited offshore wind development, comprising only five OWFs, of which just one is large-scale. Assessments of future developments remain restricted to the specific sites rather than predictive demographic analyses on a larger scale (pers. com. Fredrik Haas, Svensk fågeltaxering, University of Lund).

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[2] https://www.nature.scot/doc/guidance-note-11-guidance-support-offshore-wind-applications-marine-ornithology-recommendations

3.3 Effect of density dependence in KEC population models

In this section we analyse the consequences of including density dependent population growth for the KEC seabird assessment. This analysis is performed for a single species – the northern gannet (*Morus bassanus*; hereafter referred to as gannet) – using a modified version of the gannet population model as used within the KEC (Hin et al., 2025; Soudijn et al. 2022; 2025).

3.3.1 Implementation of density dependence

The gannet population model as used within KEC was modified to include three forms of density dependence (Table 1). Two of these forms regulate breeding success as a function of the number of adults, while the third form assumes that survival of each life stage declines with the total number of individuals in the population (Desaint 2025). Specifically, the following three different forms of density dependence were considered:

1. Exponential decay in breeding success with number of breeding adults
2. Limited number of breeding sites (floater population model)
3. Exponential decay in survival probability with total number of birds

The first form assumes that the breeding success parameter in the summer matrix (F_A) declines exponentially with the number of breeding adults (N_{AB}), *i.e.* $\frac{F_A}{2}e^{-\rho_i N_{AB}}(1-P_F)$ (Table 1). Here, the strength of density dependence is governed by parameter ρ. The same function is used in the third form to model the effect of total population abundance on stage-specific survival, *i.e.* $S_k e^{-\delta_i N}$ for stage k (Table 1). Here, parameter δ scales the strength of density-dependence. The second form assumes that a maximum number of adults (B) is able to breed, for example through a limited number of breeding sites. Hence, the breeding success parameter is multiplied with the fraction of adults that manage to breed, which is given by:

$$\frac{\min(B, N_{AB})}{N_{AB}}$$

Note that this formulation replaces the fixed probability of not breeding (parameter P_F) that was included in the original KEC model. We analyse each variant of density dependence separately and ignore the possibility that multiple types of density dependence might affect population growth simultaneously.

***Table 1**: Density-dependent variants of the gannet population model. Each model consists of a summer matrix* ($\mathrm{A_S}$) and a winter matrix ($\mathrm{A_W}$) which are matrix-multiplied to obtain the annual projection matrix (APM).

Model type	**Summer matrix ($\mathrm{A_S}$)**	**Winter matrix ($\mathrm{A_W}$)**
Exponential decay model (forms 1 and 3)	$\begin{pmatrix} 1 & 0 & 0 & 0 & 0 & \frac{F_A}{2}e^{-\rho_i N_{AB}}(1-P_F) \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$	$\begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ S_0 e^{-\delta_i N} & 0 & 0 & 0 & 0 & 0 \\ 0 & S_1 e^{-\delta_i N} & 0 & 0 & 0 & 0 \\ 0 & 0 & S_2 e^{-\delta_i N} & 0 & 0 & 0 \\ 0 & 0 & 0 & S_3 e^{-\delta_i N} & 0 & 0 \\ 0 & 0 & 0 & 0 & S_A e^{-\delta_i N} & S_A e^{-\delta_i N} \end{pmatrix}$
Floater population model (form 2)	$\begin{pmatrix} 1 & 0 & 0 & 0 & 0 & \frac{F_A}{2}\frac{\min(N_{AB}, B_i)}{N_{AB}} \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$	$\begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ S_0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_2 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_3 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_A & S_A \end{pmatrix}$

Table 2: *Baseline parameters for the density-dependent gannet population model. SD = standard deviation.*

Parameter	Symbol	Mean	SD	Distribution	Source
Breeding success	F_A	0.8 or 0.437	0.094	beta	See text
Probability floater	P_F	0.05	0.125	beta	(Soudijn et al. 2025)
Survival age 0	S_0	0.481	0.0853	beta	(Soudijn et al. 2025)
Survival age 1	S_1	0.816	0.0393	beta	(Soudijn et al. 2025)
Survival age 2	S_2	0.884	0.0293	beta	(Soudijn et al. 2025)
Survival age 3	S_3	0.887	0.0301	beta	(Soudijn et al. 2025)
Adult survival	S_A	0.940	0.0483	beta	(Lane et al. 2024)
Strength of density-dependent reproduction	ρ	Table 3	0	-	See text
Strength of density-dependent survival	δ	Table 3	0	-	See text
Number of breeding sites	B	Table 3	0	-	See text

To include density dependence in the KEC population models required a computational approach that differed from the implementation as used in Soudijn et al. (2025). Until now, random annual projection matrices (APMs) were generated first, and then passed to a function that performed the population projection. This implementation allowed to use a single set of baseline parameters for use in unimpacted and OWF-impacted projections, as recommended by Hin et al. (2024). This approach is also computationally more efficient compared to resampling parameters for each individual projection. However, this approach only works for density independent population models. With density dependence, the elements of the APM are not known *a priori*, because – by definition – these elements depend on population abundance, which is calculated during the projection. Therefore, a new function was written that evaluates the APMs during the population projection, depending on a list of input parameters and stage-specific population abundances. This function, called “*DDPopProjection*”, was included in the KECpopmodels R-package (Hin 2025).

3.3.2 Estimating strength of density dependence

The strength of density dependence (DD) is governed by the parameters ρ (DD reproduction), δ (DD survival) and B (DD floaters; Tables 1 and 2). These parameters implicitly determine the carrying capacity of the population, which is the long-term equilibrium population abundance. In the current analysis we focus on the Dutch part of the gannet population, which we define as the number of gannets present on the Dutch part of the North Sea (DCS) in August-September, which is the time of year when gannet abundance on the DCS is usually highest. Because the carrying capacity of this “gannet population” is unknown, we consider two scenarios:

1. The carrying capacity for the “Dutch gannet population” is equal to the number of gannets on the Dutch Continental Shelf
2. The carrying capacity for the “Dutch gannet population” is 50% higher than the number of gannets on the Dutch Continental Shelf

We estimate the number of gannets on the Dutch part of the North Sea (DCS) as the mean number of birds from the August-September bird distribution maps as used within KEC 5 (Soudijn et al. 2025). This gives as estimate of 6,649 gannets. Note that this number is much lower than the estimated August-November migration maximum of 17,200 – 44,500 gannets as reported by Sovon[3], but falls well within the range of the estimated winter maximum of 3,600-12,000. We furthermore assume that 73% of those are adults (Potiek et al. 2019), which leads to a ‘Dutch population’ of approximately 5,000 adult gannets under scenario 1. Under scenario 2, the carrying capacity is 7,500 adult gannets.

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[3] https://stats.sovon.nl/stats/soort/710

Note that the assumptions above are likely false, but workable for the purpose of the current study. We know that the number of gannets breeding in the UK was increasing, at least until the HPAIV epidemic hit (Lane et al. 2024). It is therefore unlikely that the number of gannets on the DCS is above or at its carrying capacity. As a lower estimate of the carrying capacity, we therefore take the number of gannets on the DCS (assumption 1 above). We take assumption 2 as an upper bound of the carrying capacity. Although assumption 2 might still underestimate the true carrying capacity, with an even larger carrying capacity our modelled population will grow exponentially, which defeats the purpose of our analysis as density-dependent effects will have much smaller impacts on population growth rates.

We now calculate the values of ρ, δ and B for both scenarios. To calculate ρ we solve for the value of F_A that leads to a stable population. Note that the long-term population growth rate is given by λ: the dominant eigenvalue of annual projection matrix (Caswell 2001). We used a numerical root solving routine in R (R Core Team 2024) to calculate the value of F_A that results in $\lambda = 1$, which we denote by F_A^*. Using the exponential decay population model (Table 1) with $\rho = 0$, $\delta = 0$ and other parameters at default values (Table 2), this results in $F_A^* = 0.437$. Hence, the strength of density dependence should be such that it depresses the breeding success parameter to 0.437 at either $N_{AB}^1 = 5{,}000$ breeding gannets (scenario 1), or $N_{AB}^2 = 7{,}500$ breeding gannets (scenario 2). The value of ρ is then given by:

$$F_A^* = F_A e^{-\rho N_{AB}}$$

$$\rho = -\frac{\ln(F_A^*/F_A)}{N_{AB}}$$

Using a baseline breeding success of 80% ($F_A = 0.8$; Table 3) this results in $\rho_1 = 1.2111 \cdot 10^{-4}$ and $\rho_2 = 8.0737 \cdot 10^{-5}$ (Table 3) for, respectively, $N_{AB}^1 = 5{,}000$ and $N_{AB}^2 = 7{,}500$. To derive the value of δ we used a similar approach, but now using a scalar value for the stage-specific survival probabilities (S_i). This resulted, however, in a population that declined in the first carrying-capacity scenario (5,000 adult birds). The calibrated values of δ were therefore adjusted such that this population trajectory remained approximately constant. This resulted in the values of δ_1 and δ_2 that are associated with, respectively, scenarios 1 and 2 above (Table 3).

The number of available breeding sites was derived by calculating the fraction of breeders that would lead to a stable population ($\lambda = 1$) for the floater population model, in which the parameter P_F is replaced by the fraction of adults that have managed to obtain a breeding site (Table 1). For this variant, the breeding success that leads to a stable population equals $F_A^* = 0.4148$. The required value then follows from $B = \frac{F_A^*}{F_A} N_{AB}$. Using the values of $N_{AB}^1 = 5{,}000$ and $N_{AB}^2 = 7{,}500$ results in $B_1 = 2{,}592$ and $B_2 = 3{,}889$. For the floater population model, we additionally investigate an extreme variant with a very high number of breeders ($B_3 = 10{,}000$).

Taken together, we have a total of seven combinations that include some form and strength of density dependence (Table 3). We compare the density-dependent models with two density-independent variants. One that has a stable population ($\lambda \sim 1$ and $F_A = 0.437$) and one with an exponentially growing population ($\lambda \sim 1.036$ and $F_A = 0.8$). An overview of all combinations is given in Table 3. The resulting demographic functions are plotted as a function of the number of adults in Figure 1.

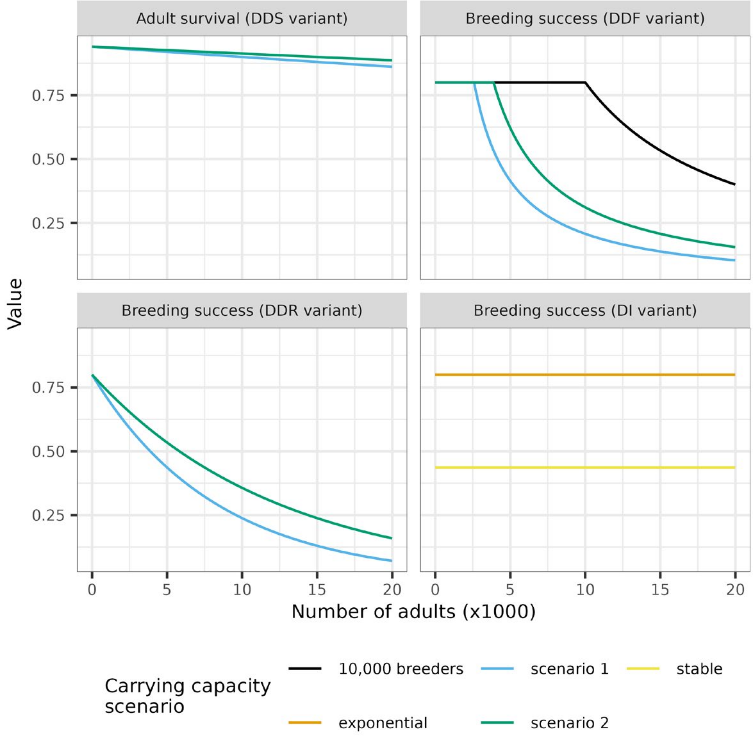

***Figure 1**: Density dependent effect on adult survival for the DDS model variants (top left panel) and on breeding success for the DDF and DDR model variants. Scenario 1 and 2 correspond to a carrying capacity of, respectively, 5,000 and 7,500 adult gannets on the DCS. The density-independent (DI variant) levels of breeding success are plotted for reference in the bottom-right panel.*

***Table 3**: Variants of density-dependence considered in this study. The model type refers to the population model used (Table 1). Pop. = population, expo. = exponential.*

Variant	**Description**	**Carrying capacity (adults)**	**Model type**	F_A	ρ	δ	B
DIstable	Stable population (density independent)	No carrying capacity	Expo. decay	0.437	0	0	-
DIexpo	Exponential growth (density independent)	No carrying capacity	Expo. decay	0.8	0	0	-
DDR1	Density-dependent reproduction	5,000	Expo. decay	0.8	1.2111e-4	0	-
DDR2	Density-dependent reproduction	7,500	Expo. decay	0.8	8.0737e-5	0	-
DDS1	Density-dependent survival	5,000	Expo. decay	0.8	0	4.382226e-06	-
DDS2	Density-dependent survival	7,500	Expo. decay	0.8	0	2.921484e-06	-
DDF1	Density-dependent floater population	5,000	Floater pop.	0.8	-	-	2,592
DDF2	Density-dependent floater population	7,500	Floater pop.	0.8	-	-	3,889
DDF3	Density-dependent floater population		Floater pop.	0.8	-	-	10,000

3.3.3 Simulations

We ran 1,000 stochastic population projections for all nine model variants in Table 3. To ensure comparability between simulations we generated three sets of baseline parameters. One set was generated for the exponential decay model (Table 1) with $F_A = 0.8$. This set was used to run model variants 'DIexpo', 'DDR' and 'DDS'. A separate parameter set was generated for the exponential decay model (Table 1) with $F_A = 0.437$. This set was used to run model variant 'DIstable' (no density dependence). A third parameter set was generated for the floater population model (Table 1), which was used to run the DDF model variants.

To mimic either collisions or habitat loss effects from offshore wind farm (OWFs), each parameter set was modified to include additional mortality. By default, we assumed that OWF-induced annual mortality followed a normal distribution with a mean of 0.01 (1% mortality) and a coefficient of variation (CV) of 20% (standard deviation = 0.002). We also investigated the effect of lower (0.5%) and higher (1.5%) mean annual mortality values, also with a CV of 20%. Note that, the mean annual mortality caused by habitat loss estimated for gannets in the most severe OWF scenario of the last KEC (Total scenario with a 10% mortality level; (Soudijn et al. 2025)) was 0.126%.

Population trajectories were projected for 50 time steps (t in years) using an initial population of 6,649 birds at the stable stage distribution. Total population abundance at t = 40 years were extracted to calculate the relative difference in population abundance between unimpacted and OWF-impacted projections. This is the measure that is used within the Acceptable Levels of Impact (ALI) methodology (Hin et al. 2024) to compare against the ALI X threshold value.

Population growth factors were calculated from projection outputs as the ratio between the population abundance in the current (N_t) and previous time step (N_{t-1}), i.e. N_t / N_{t-1}. For each model variant, summary statistics (mean, median, geometric mean, standard deviation, 5% and 95% quantile values) were calculated across the 1,000 replicate simulations and used to plot changes in population abundance and population growth factors.

3.3.4 Results

Population size projections with the model variants parameterized for a carrying capacity of 5,000 adult birds (DDF1, DDR1 & DDS1) remained approximately stable or showed a slight decrease. Mean population abundance after 50 simulated years was 6,423 birds for variant DDR1, 6,293 for DDS1 and 6,559 for DDF1, compared to an initial value of 6,649 gannets.

The population size in projections with the density-dependent model variants parameterized for a carrying capacity of 7,500 adult birds (DDF2, DDR2 & DDS2) all increased beyond their initial values (6,649 gannets; Figure 2). The approach to carrying capacity was slower for the variants with exponentially decaying vital rates (DDR2 and DDS2), compared to the floater population model (DDF2). Mean population abundance after 50 simulated years was 8,818 for DDR2, 8,714 for DDS2 and 9,696 for DDF2.

Population abundance increased to a mean of 37,861 birds in the density-independent variant DIexpo (a geometric mean growth rate of ~3.54% per year) and the density-independent variant DIstable showed a slight decline to around 6,470 birds at t = 50 years. The variant DDF3 with 10,000 breeding adults showed a rapid increase in population abundance initially, which then levelled off to a mean of 23,396 birds (Figure 2).

For all model variants, the mortality impact from OWFs reduced mean population abundance below the mean population abundance without OWF impacts (Figure 3). For the model variants in which population abundance remained approximately stable (DDF1, DDR1, DDS1 and DIstable), the mortality from OWFs led to population declines. The model variants that were based on a carrying capacity of 7,500 birds showed positive growth without OWF mortality (DDF2, DDR2 and DDS2) and mixed responses when including OWF mortality. The mean population trajectory with OWF impact was still increasing for the floater population model (DDF2) and remained approximately stable for the model with density-dependent reproduction (DDR2) and density-dependent survival (DDS2; Figure 3). The exponentially growing population model (DIexpo) and the floater model with 10,000 breeding adults (DDF3) were still growing under the modelled OWF impacts (Figure 3).

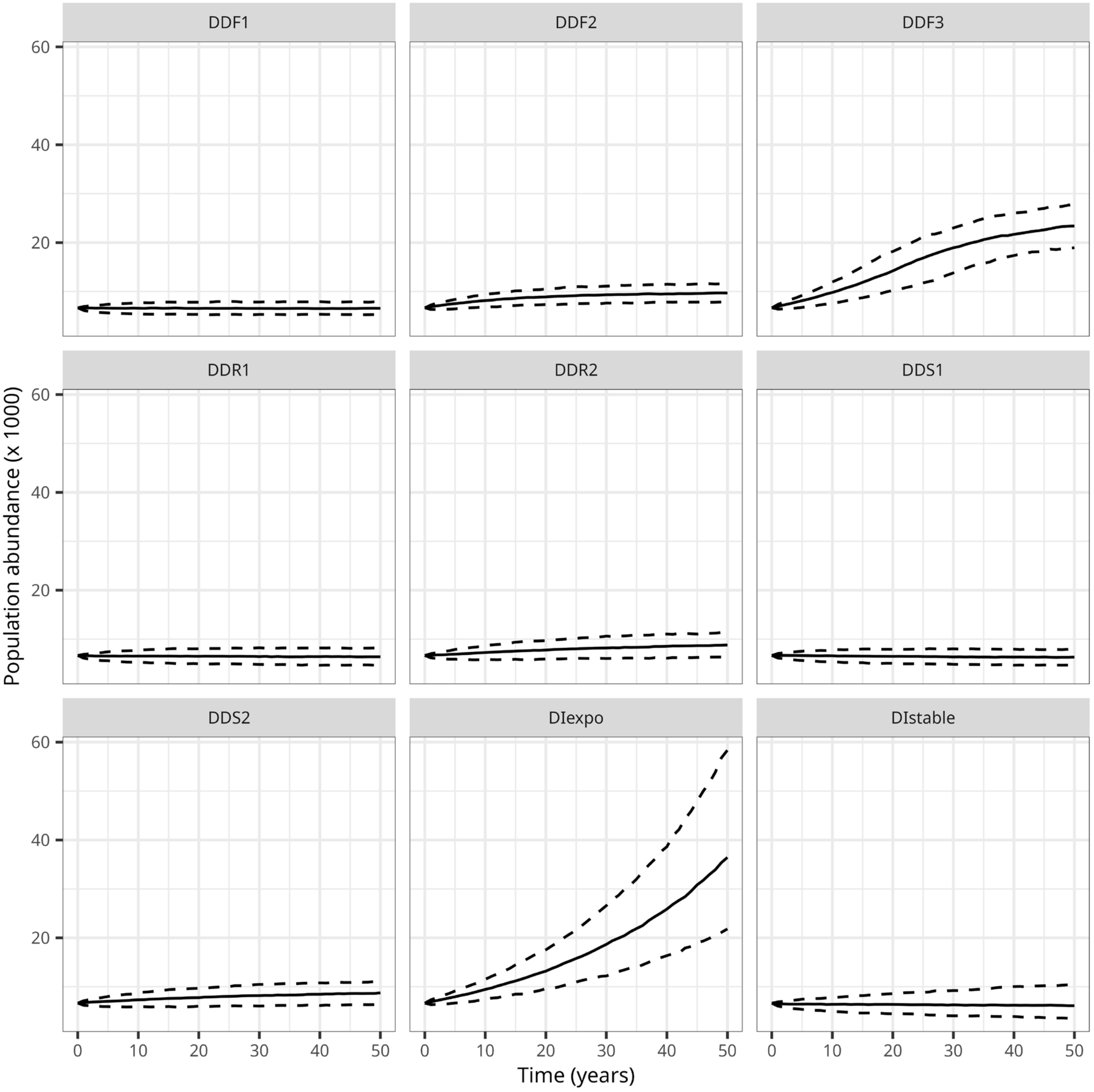

***Figure 2**: Timeseries for the different model variants (Table 3) showing median population abundance across 1,000 replicates projections (solid lines), and 5% and 95% quantile values (dashed lines).*

Density dependence compensated the impact that OWF mortality had on the population growth rate. For the density-independent variants (DIexpo and DIstable), the mean OWF mortality rate of 0.01 led to an 0.01 reduction in population growth rate irrespective of population abundance (Figure 3). However, with density dependence, the difference in population growth rate between unimpacted and impacted projections declined throughout the timeseries (Figure 3). This was solely the effect of population abundance on the population growth rate. Compensatory density dependence, which is modelled here, led to a reduction in the population growth rate at higher population abundances. OWF-induced mortality led to a lower population abundance and therefore reduced the negative effect of density dependence on the population growth rate. For the DDF3 variant, the mortality effect of OWFs led to a slightly higher population growth rate in the second half of the timeseries (Figure 3).

For all model variants in which density dependence operated on breeding success / productivity (DDF and DDR), the mean breeding success of the OWF-impacted projections was higher than its counterpart in the unimpacted projections (Figure 3; top panels). For these model variants, the compensatory response of density dependence on the population growth rate was driven by elevated breeding success. For the model variants where density dependence operated on survival (DDS), the compensatory response was driven by a reduction of the negative survival effect of OWF-induced mortality (Figure 3; second row panels).

The compensatory response of density dependence, either through survival or reproduction, had a significant effect on the relative difference in population abundance between unimpacted and impacted projections at $t = 40$ years (Figure 4 and Table 4). Without density dependence, this relative difference was approximately 33%, irrespective of the growth rate of the unimpacted population (DIstable or DIexpo). Density dependence through the floater population model (DDF variants) resulted in the lowest relative difference in population abundance, with median differences between 12.6% (DDF2) and 15.7% (DDF3). Note, however, that the DDF3 model variant has a more right-skewed distribution (longer right tail), with a 95% quantile value (29.9%) that is almost double that of the other DDF variants, and larger than the 95% quantiles of the DDR and DDS variants. The large variation in the DDF3 variant is likely due to the initial phase of exponential growth that amplifies the variability between replicate simulations. Density dependence modelled as an exponential decay function (DDR & DDS variants) all had similar outcomes; a median difference around 21% (20.6% - 22.0%).

Table 4: *Median, 5% and 95% quantiles of the percentage difference between unimpacted and OWF impacted population abundance after 40 years.*

Model variant	median	5% quantile	95% quantile
DIstable	33.1	24.1	41.6
DIexpo	32.9	23.8	41.3
DDR1	20.6	14.2	27.1
DDR2	22.0	15.2	28.9
DDS1	19.6	13.4	26.0
DDS2	21.1	14.6	27.9
DDF1	13.1	9.0	17.4
DDF2	12.6	8.6	16.7
DDF3	15.7	9.8	29.9

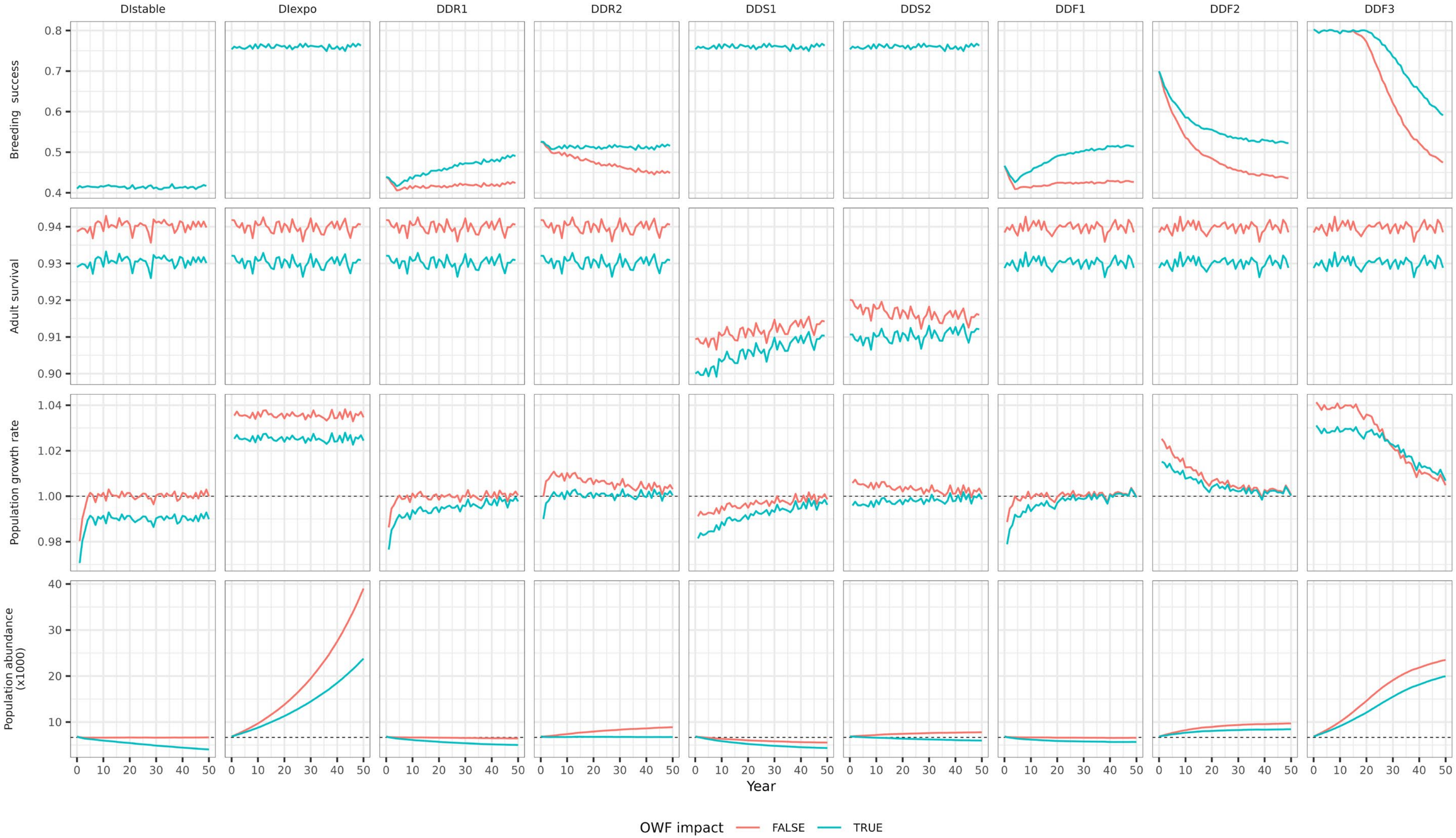

Figure 3: *Changes in breeding success, adult survival, population growth rate and abundance over time for the unimpacted (red lines) and OWF-impacted projections (blue lines). Lines depict the mean values over 1,000 replicate simulations. Different column panels show the nine model variants as summarized in Table 3.*

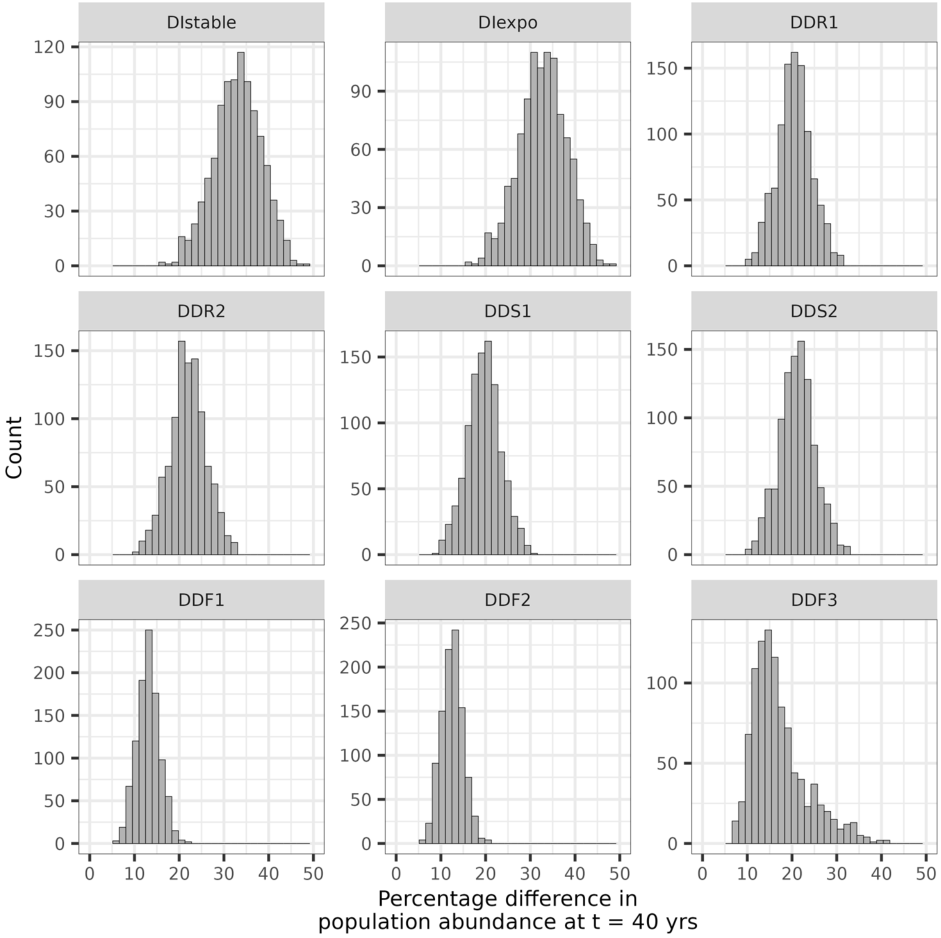

Figure 4: *Distribution of the percentage difference in population abundance between unimpacted and OWF-impacted projections for each model variant.*

The assumed level of OWF-induced mortality did not alter the impact of density dependence on the relative differences between impacted and unimpacted projections (Figure 5). For all three levels of mortality considered (0.5%, 1% and 1.5%), the variants with the floater population resulted in the lowest median population impact and the impacts of the DDS and DDR variants were comparable in magnitude. However, the Acceptable Level of Impact methodology considers the 95% quantile values of the relative difference in population abundance, as opposed to the median values. The 95% quantiles associated with the DDF3 variant exceeds that of the DDR and DDS variants (Figure 5).

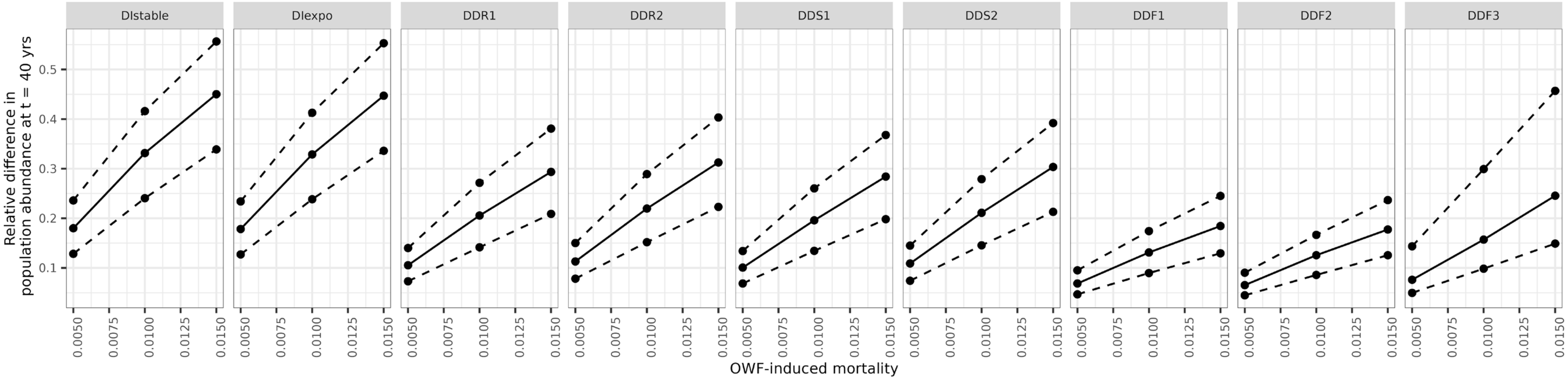

Figure 5: *The median (solid lines), 5% and 95% quantile values (dashed lines) of the relative difference in population abundance between unimpacted and OWF-impacted projections, for different levels of OWF-induced mortality (0.5%, 1% and 1.5%).*

4 Avian influenza

4.1 The High Pathogenic Avian Influenza epidemic

Avian influenza, and most notably, highly pathogenic avian influenza (HPAI) has become endemic in wild birds in western Europe in recent years. Some species, particularly several waterfowl species, carry the virus without showing clinical signs of sickness, and spread the virus widely (EFSA et al. 2025). Affected poultry farms get a lot of attention (with millions of birds culled in attempts to keep the virus in check), but wild birds have also been hit hard. HPAI (H5N1) viruses still dominate under the various strain of the virus, with new sub-lineages evolving constantly. While bird species that were affected severely in earlier years may now show signs of herd immunity, or even individual immunity (wildfowl), "new" species, or populations that escaped until recently (such as the common cranes in western Europe in the Autumn of 2025), can be hit hard, suddenly. With the virus evolving constantly, there is no guarantee that populations that have been hit before, will be safe. More than one strain of H5N1 was found simultaneously in HPAI-affected colonies of Sandwich terns in the Netherlands (Rijks et al. 2022). Moreover, another strain of the virus (H5N5) has been found in several seabirds in NW Europe, such as the northern fulmar (Caliendo et al. 2025).

Colonial seabirds have been hit particularly hard by HPAI-H5. In dense seabird colonies, the virus spreads readily from bird to bird and whole colonies can be wiped out within weeks (Rijks et al. 2022). The virus may also infect seabirds at communal roosting/preening sites (Camphuysen et al. 2022) or even at sea, possibly during feeding frenzies (Caliendo et al. 2025). Worrying for seabirds is that individuals from infected colonies may tend to shy away from such colonies and visit other colonies, often at large distances, thus spreading the virus from colony to colony (Careen et al. 2024; Lane et al. 2024). The largest colonies, in the centre of the distribution ranges of metapopulations, are most at risk by this connectivity (Spaans et al. 2021; Knief et al. 2024; 2025). And finally, the virus may disproportionally kill more older, experienced and productive individuals (Courtens et al. 2025). Colonial seabirds with relatively small global populations and few colonies are probably most at risk, such as great skuas and Sandwich terns, while species with very large numbers of colonies and a large breeding range, while suffering massive, local mortality events, may be safer at the population level (Bouwhuis 2025; Indykiewicz et al. 2025). However, HPAI-induced mortality is not restricted to the breeding sites, but may also occur at sea, on foraging trips or during migration, or in the wintering quarters, far away from the breeding colonies (e.g. Jatta et al. 2025), and thus largely unseen. Typical K-strategists among seabirds, i.e., long-lived species with slow reproduction, may take many decades to recover from massive mortality among breeders (Slaterus et al. 2022).

Species most affected by avian influenza in Europe are great skua (Tremlett et al. 2024), northern gannet (Lane et al. 2024) and Sandwich tern (Knief et al. 2024; 2025), but most European seabird species have known casualties. As many seabirds have both large populations and large distributions, population effects are still poorly understood (Tremlett et al. 2024). Within-colony mortalities were, in several studied cases, much larger than the subsequent declines in local breeding numbers, suggesting that floaters and/or younger than usual individuals supplemented the established breeders (‘compensatory recruitment'; Birkhead and Hatchwell 2025; Knief et al. 2025). This means, that simply assessing (remaining) population sizes through colony counts will be insufficient: these counts give a biased (optimistic) measure of the true population size. However, counting breeding numbers is relatively easy, at least in not too remote colonies, while assessing mortality, both on land (e.g., Tyndall et al. 2024) and at sea (e.g., Giralt Paradell et al. 2023), let alone the assessment of surviving numbers at sea, across the full range of populations is much more difficult. Yet, at the local scale, e.g. for (Dutch or international) waters within the North Sea, this is probably the best way forward to assess the true impact of HPAI at the population level of affected seabirds.

4.2 Analysis of effects of HPAIV on outcome of KEC assessment

4.2.1 Methodology

Here we study the effect of a single HPAIV epidemic on population development and the population response to OWF-impacts under different density-dependent scenarios. We used the various model variants for the density-dependent population model for the northern gannet as described in section 3.3 – “Effect of density dependence in KEC population models” with 1,000 replicate simulations per model variant and an hypothetical OWF-impact level of 1%.

The HPAIV epidemic was simulated as a single, two-year perturbation of adult survival (S_A) and breeding success (F_A). Notably, the modelled effect of the epidemic was applied to the baseline parameter sets before OWF impacts were applied. Hence, the HPAIV effect is present in both OWF-impacted and OWF-unimpacted projections. Baseline parameters were modified for projection years 4 and 5 by multiplying the sampled value for breeding success (F_A) and adult survival (S_A) by, respectively, the breeding success multiplier and adult survival multiplier for that year (see Table 5 & Figure 6).

***Table 5**: Assumed breeding success and adult survival multiplier values used to simulate a two-year HPAIV epidemic.*

Projection year	Breeding success multiplier	Adult survival multiplier
4	0.1	0.5
5	0.3	0.7

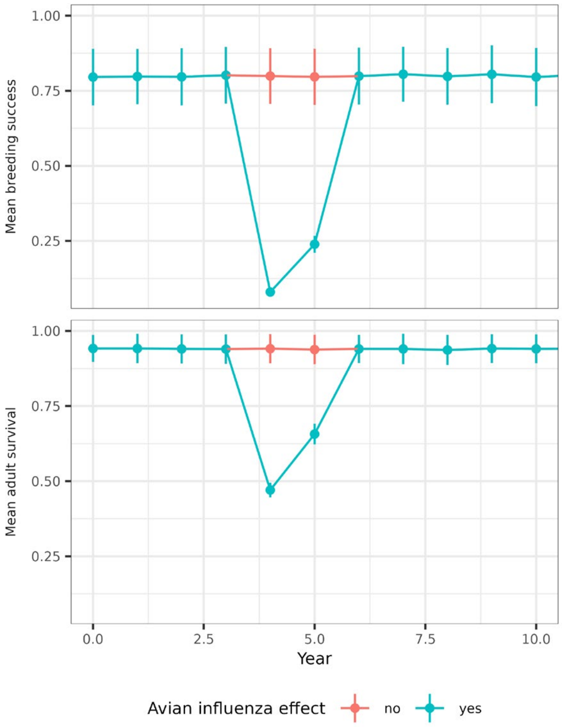

***Figure 6**: The breeding success and adult survival parameters to model the effect of HPAIV. Points are mean values and line ranges indicate parameter standard deviations. The HPAIV epidemic was assumed to be slightly more severe in its first year (Table 5).*

4.2.2 Results

The modelled HPAIV epidemic had a substantial effect on the projected timeseries, especially in absence of density dependence (Figure 7). As a result of the HPAIV epidemic, projected mean population abundance at t = 50 years declined by 60% for the DIstable model variant (from 6,470 to 2,614), and by 57% for the DIexpo model variant (from 37,861 to 16,308).

Density dependence greatly reduced the impact of the HPAIV epidemic. For the floater population model variant (DDF), the relative effect of the HPAIV epidemic on population abundance at the end of the timeseries (t = 50 years) was 4.75% (DDF1), 5.8% (DDF2) and 25% (DDF3). For the other model variants (DDR & DDS), the relative effect of the epidemic was in between 21% and 28%. With density dependence, the reduction in population abundance as a result of the epidemic lead to an increase in the population growth rate, which enabled the depleted population to catch up once the epidemic was due (Figure 7).

With density dependence, the HPAIV epidemic altered the direction of population change in response to OWF-impacts. For the model variants based on a carrying capacity of 5,000 adult birds (DDF1, DDR1, DDS1), the OWF-impacted trajectories all showed a decline towards a lower carrying capacity in absence of the HPAIV epidemic. The epidemic reduced population abundance below this new carrying capacity level, which resulted in an increase of the population in the presence of OWF effects (compare solid green and dashed green lines in Figure 7).

The modelled HPAIV epidemic increased the impact of OWFs on population abundance, but only in the presence of density dependence (Figure 8 & Table 6). Without density dependence (DIexpo & DIstable), the relative difference in population abundance between OWF-unimpacted and OWF-impacted projections was unaltered by the occurrence of the epidemic (Figure 8). For model variants DDR and DDS, the relative difference in population abundance at *t = 40* years was slightly higher in the presence of the epidemic. The effect of the epidemic was approximately equal between these model variants. This was not the case for the floater population model (DDF). Here, the model variant with 10,000 breeding adult (DDF3) resulted in a distribution comparable to the density-independent variants. This implies that the HPAIV epidemic reduced the population abundance so far below the carrying capacity, that the subsequent population growth was approximately exponential (Figure 7). For the other two DDF variants (DDF1 & DDF2) the epidemic hardly had any effect. Indeed, there was a strong compensatory response following the epidemic and the endpoints in mean population abundance were quite similar between presence and absence of the HPAIV epidemic.

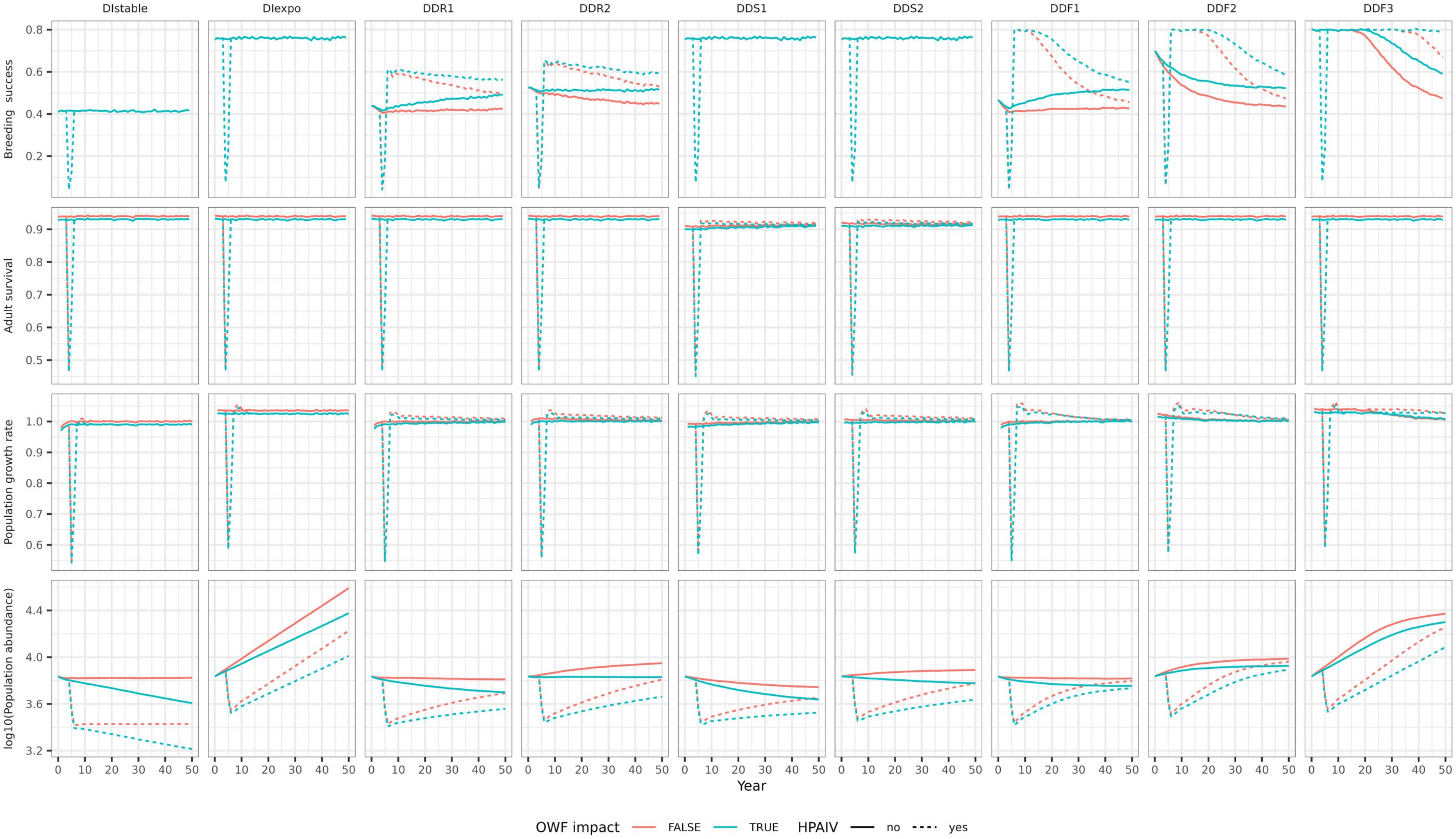

Figure 7: *Changes in breeding success, adult survival, population growth rate and abundance over time for the unimpacted (red lines) and OWF-impacted (blue lines) projections, both without (solid lines) and with the modelled HPAIV epidemic (dashed lines). Lines depict the mean values over 1,000 replicate simulations. Different column panels show the nine model variants as summarized in Table 3. This figure is a HPAIV epidemic-enriched version of Figure 3. Note the log10 scaling of the y-axis applied in the bottom panel.*

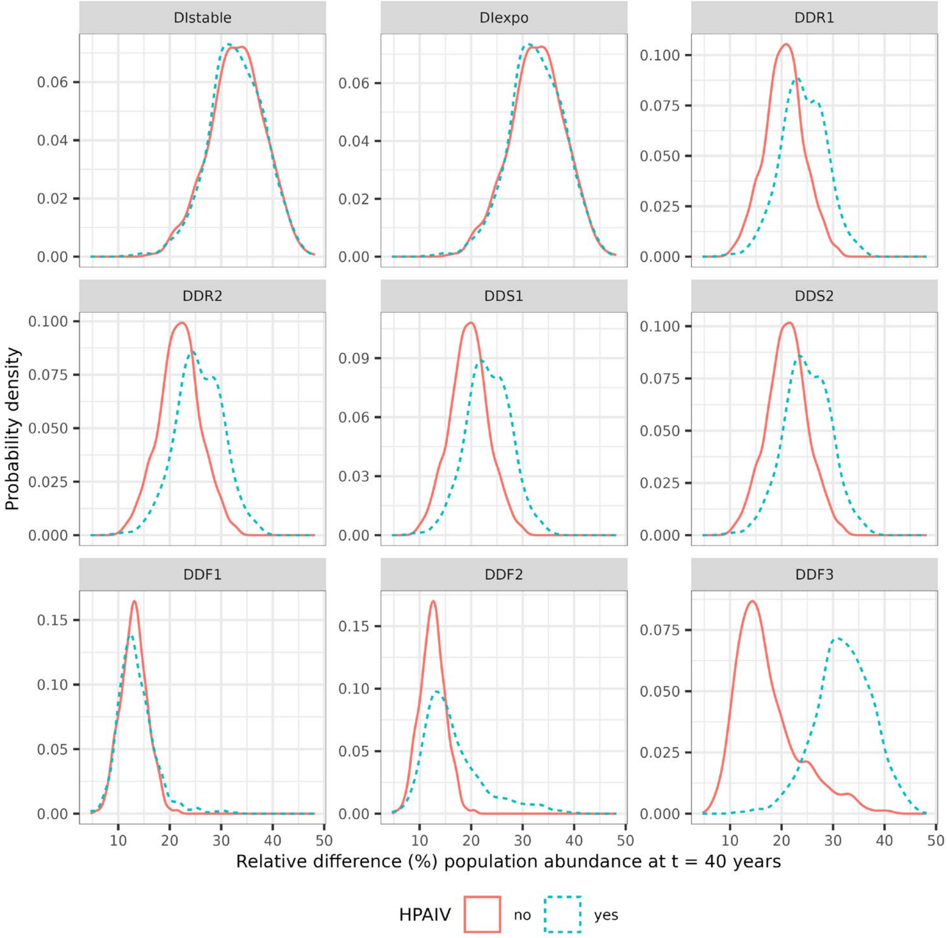

__Figure 8__: Density distributions of relative difference in percentage between OWF impacted and unimpacted population abundance at t = 40 years with (red lines) and without (blue lines) the HPAIV epidemic

__Table 6__: Median, 5% and 95% quantiles of the relative difference between unimpacted and OWF impacted population abundance at t = 40 years

projection	HPAIV	median	5% quantile	95% quantile
DIstable	no	33.1	24.1	41.6
DIstable	yes	32.8	24.0	41.7
DIexpo	no	32.9	23.8	41.3
DIexpo	yes	32.5	23.8	41.4
DDR1	no	20.6	14.2	27.1
DDR1	yes	24.0	17.0	31.3
DDR2	no	22.0	15.2	28.9
DDR2	yes	25.5	18.2	33.0
DDS1	no	19.6	13.4	26.0
DDS1	yes	23.2	16.3	30.3
DDS2	no	21.1	14.6	27.9
DDS2	yes	24.8	17.5	32.3
DDF1	no	13.1	9.0	17.4
DDF1	yes	13.0	8.8	19.6
DDF2	no	12.6	8.6	16.7
DDF2	yes	15.1	9.7	29.5
DDF3	no	15.7	9.8	29.9
DDF3	yes	32.1	22.6	41.1

5 Conclusions

Density dependence is common in seabird populations and operates through various mechanisms resulting in either compensatory (negative regulation) or depensatory (positive regulation) responses of population growth to population abundance. There is no single form of density-dependence that can be applied to all species and populations, and the direction of density dependence may even change as a function of population size (Horswill et al. 2017).

It is likely, and even inevitable, that at larger population sizes density dependence acts in a compensatory manner. On a meta-population level, most individuals will therefore experience negative population regulation. Because of the large spatial scale considered in the KEC, compensatory responses to population size will be most relevant for the KEC. Depensatory responses will be relevant for species that breed in several, small colonies that are vulnerable to predation, such as the Sandwich tern (*Thalasseus sandvicensis*).

In the UK, assessments into offshore wind farm effects that perform PVAs can only consider density dependence if supported by robust evidence and a strong justification of the density-dependent terms used. Note that these impact assessment are performed at the scale of individual colonies or Special Protection Areas, which is a much smaller scale than used in the KEC assessment.

In our analysis for the gannet, we showed that density dependence can have a considerable compensatory effect of OWF-induced mortality. In addition, the shape of density-dependence matters, with the floater population model having the greatest compensatory effect. The effects of an exponential decline of breeding success or survival with population size result in similar compensatory effects. The ALI outcome was relatively insensitive to the carrying capacity level assumed, except when the carrying capacity was substantially larger than current levels and the modelled population could growth exponentially.

Interestingly, mass-mortality and breeding failure due to a simulated HPAI virus outbreak did not change the ALI outcome when using density-independent models. However, with density dependence, the relative impact of OWF-induced mortality on population size was larger with HPAI virus outbreaks than without. In other words, the strong population decline induced by HPAI reduced the capacity of density-dependent regulation to buffer the impact of OWF. This analysis shows that the outcomes of density-dependent population models are sensitive to other processes that operate on the population, as opposed to the density-independent models currently used in the KEC.

5.1.1 Recommendation for use of density-dependent population models within KEC

Horswill & Robinson (2015) highlight that: "*there is not a simple mechanism of density-dependence that can be applied uncritically in all situations (…) and the dynamics of a colony should be evaluated if density-dependence is to be realistically incorporated within population models that evaluate the impacts of wind-farm developments*". Accordingly, the recommendation by Natural England is to only use density dependence in PVAs if there is strong evidence on the form and strength of the density-dependent processes operating at a specific colony or SPA.

The KEC assessment is a cumulative assessment over a large spatial scale, focusing on either the Dutch Continental Shelf (DCS) for national OWF scenarios, or the Southern and Central North Sea for the international scenario. If we translate the recommendation by Natural England to the KEC assessment, this implies that there should be strong evidence of the strength and shape of density dependence on the scale of the DCS, or the Southern and Central North Sea. There are currently very few studies that look into density dependence at such large spatial scales. The exception is the study of Jeglinski et al. (2023), which shows that the predicted metapopulation carrying capacity of gannets changes tremendously when including regional-scale density-dependent processes. This implies that even if we have enough information on how density dependence acts on the scale of a single colony or SPA, we are still unsure on how density dependence operates on a larger spatial scale.

Although realistic models should be used to inform cumulative assessments of OWF impacts, the potentially strong compensatory effect of density dependence requires a solid evidence-base on how density-dependence operates on the scale of the KEC assessment. While including density dependence might increase realism of the cumulative impact assessments, for many species it still remains unclear which demographic processes are controlled most strongly by density dependence and which carrying capacity levels should then be adopted for spatial scale that is relevant to the assessment. Therefore, there is still a considerably risk of mis-specifying the form and strength of density-dependence, and this might lead to impact assessments that underestimate the risk of additional mortality. In addition, the use of density-dependent models within the KEC also requires more knowledge on other processes that can affect population dynamics, such as the impact of HPAI outbreaks. We therefore conclude that the evidence base is currently insufficient to solely base the KEC assessment on density-dependent population models. We recommend to further study how density-dependent processes operate on the scale on the DCS, which is the most relevant scale of the KEC. Considering the risk of mis-specifying the strength of density dependence, we also recommend to host an expert discussion session to investigate for which species enough information is available to warrant use of density-dependent models in the KEC assessment.

5.1.2 Recommendations for future research

To increase the evidence base for using density-dependent population models in the KEC, some recommendation for future research can be made. Merrall et al. (2024) showed that despite the large number of populations monitored through the Seabird Monitoring Program (SMP 2025), there only a few concurrent time series of breeding success and population counts long enough to measure density-dependent response of breeding success (Merrall et al. 2024). Monitoring should therefore focus on measuring breeding success and population counts simultaneously and over a long period, preferable of populations or colonies that are growing or declining. The impact of the recent HPAI outbreak among several seabird species provides a natural opportunity to do so. If density-dependence operates, the reduction in population size following the HPAI outbreak will lead to changes in demographic rates. These rates should therefore be monitored alongside with the census of population counts (number of breeding pairs). Alongside measuring breeding success, other demographic variables such as immature and adult survival and age at first breeding can also display density-dependent responses, and different density-dependent processes may act simultaneously on the same population.

For some species, like gannets, density dependence might operate through a large adult floater population. Following the loss of large numbers of breeding adults due to the HPAI outbreak, these floater individuals now get the opportunity to breed for the first time. Future research should attempt to measure the size of floater populations and monitor breeding success and age of first-time breeders.

Population modelling can also be used to elucidate the potential ways in which density-dependence operates. Matrix population models, as used within many PVAs and also within the KEC, generally have a poor ability to predict future population development, because they don’t make use of population census information (Searle et al. 2020). More sophisticated frameworks, like Integrated Population Models, or Bayesian State-Space models are able to integrate various data streams to estimate the processes that govern population dynamics, including density dependence. Because they utilize the information embedded in population census data, these models perform much better at forecasting population sizes (Jitlal 2017; Miller et al. 2019; Searle et al. 2020) and can be used to estimate whether density dependence operates at local versus regional scales (Jeglinski et al. 2023). More advanced population modelling frameworks will also be required to make best use of the monitoring data collected.

Quality Assurance

Wageningen Marine Research utilises an ISO 9001:2015 certified quality management system. The organisation has been certified since 27 February 2001. The certification was issued by DNV.

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Justification

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The scientific quality of this report has been peer reviewed by a colleague scientist and a member of the Management Team of Wageningen Marine Research

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