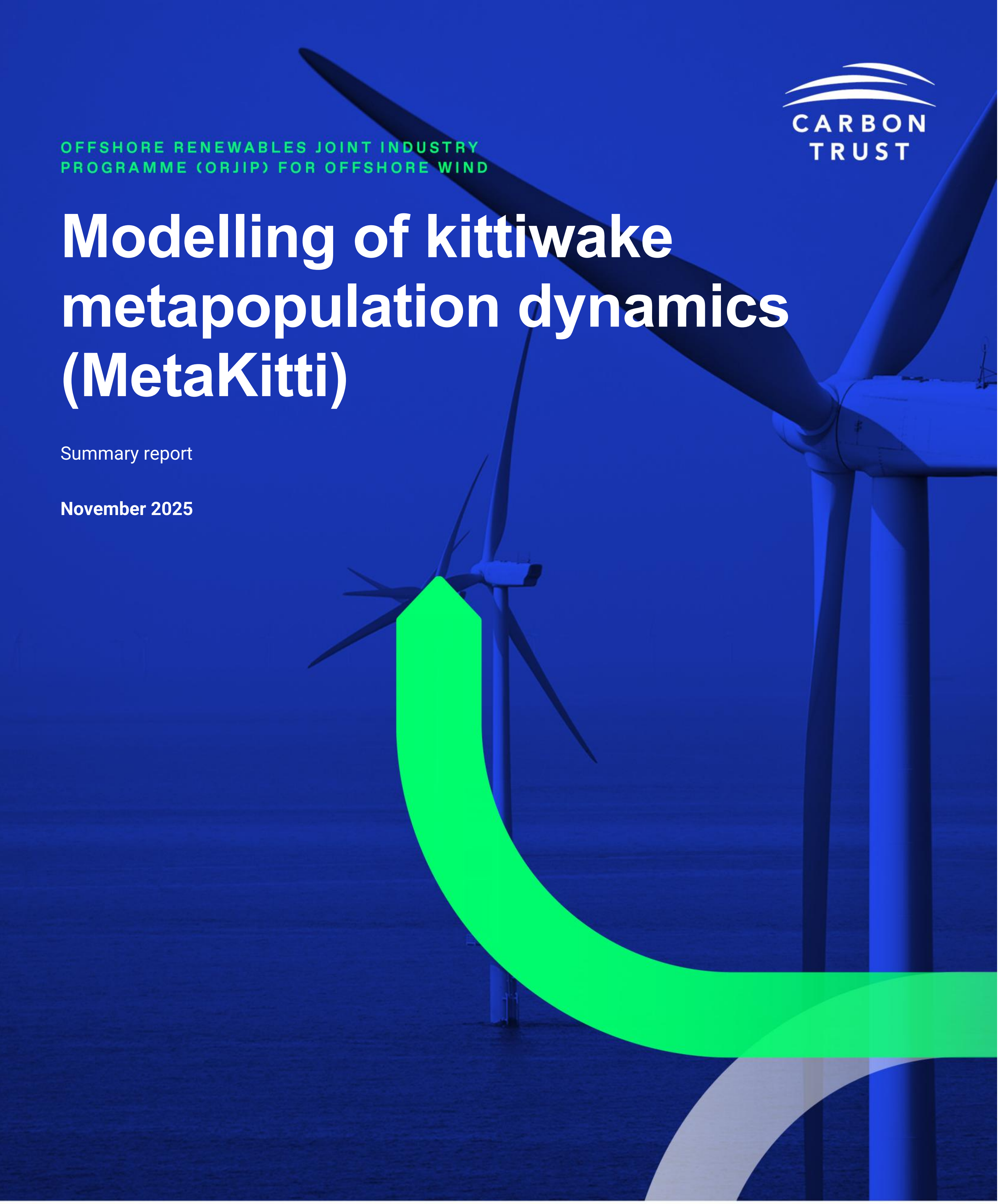

OFFSHORE RENEWABLES JOINT INDUSTRY
PROGRAMME (ORJIP) FOR OFFSHORE WIND

# Modelling of kittiwake metapopulation dynamics (MetaKitti)

Summary report

**November 2025**

working to accelerate
offshore consenting

# ORJIP Offshore Wind

The Offshore Renewables Joint Industry Programme (ORJIP) for Offshore Wind is a collaborative initiative that aims to:

- Fund research to improve our understanding of the effects of offshore wind on the marine environment.
- Reduce the risk of not getting, or delaying consent for, offshore wind developments.
- Reduce the risk of getting consent with conditions that reduce viability of the project.

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For further information regarding the ORJIP Offshore Wind programme, please refer to the Carbon Trust website, or contact Ivan Savitsky (ivan.savitsky@carbontrust.com) and Žilvinas Valantiejus (zilvinas.valantiejus@carbontrust.com).

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- Scottish Government's Marine Directorate

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# Executive summary

The spatial structure of breeding seabirds is increasingly recognised as a metapopulation—a network comprising connected subpopulations, each facing distinct risks, demographic dynamics, and environmental pressures. Yet, risk assessments conducted via population viability analysis (PVA) have typically treated these subpopulations in isolation. In addition, subpopulations have been assumed to be density independent (i.e., insensitive to the effects of sparsity or crowding). These assumptions are made for simplicity and as a precaution. However, both connectivity and density dependence are common in nature, and ignoring these mechanisms may lead to biased assessments.

This issue is particularly important for the black-legged kittiwake (Rissa tridactyla, hereafter kittiwake), a UK red-listed species in decline. Conservation efforts have focused on individual Special Protection Areas (SPAs), but the broader network of kittiwake colonies—including non-SPA sites—remains poorly understood. Key questions include how colonies are connected, whether non-SPA sites support or deplete SPA colonies, and how the system as a whole responds to disturbance.

We developed the first seabird metapopulation model that integrates connectivity, three forms of density dependence, and floater birds that could buffer population shocks. Our goals were to: 1) fit this advanced model to all available UK and Irish kittiwake data, 2) produce a next-generation metapopulation PVA tool for seabirds, 3) assess the roles of connectivity and density dependence, and 4) explore both local and system-wide mitigation or compensation options.

We compiled a comprehensive dataset on kittiwake populations in Britain and Ireland, including both SPA and non-SPA colonies. The data span the period 1985–2023 and include population counts, breeding success, survival of adults and immatures, and dispersal based on bird ringing data.

We tested three versions of our broad modelling framework: Model 1 allowed each colony independent demographic time series; Model 2 grouped demographic rates into six UK regions; and Model 3 added time trends to Model 2. All models showed a consistent decline in the metapopulation, with only some persistence in central and eastern Britain.

Using the most parsimonious Model 2, we forecast trends for the next 50 years, in the absence of any environmental drivers. All colonies are predicted to decline towards extinction, with no consistent geographic pattern in the rate of decline. In this situation, connectivity had limited impact because the entire metapopulation functions as a collection of sink populations.

We explored what improvements in demographic rates could reverse these trends, testing combinations of increases and decreases in breeding success, adult survival, pre-breeder survival, and floater survival. Adult survival emerged as the most critical factor. We also examined the potential of artificial nesting structures (ANS) as a compensation tool, offering a practical framework for evaluating their placement and impact.

Ultimately, for a declining metapopulation composed entirely of sink colonies, widespread and drastic improvements are needed to reverse the downward trends predicted by this modelling. Nonetheless, understanding connectivity and density dependence—particularly Allee effects in small colonies—is essential for evaluating and designing effective conservation strategies, when these are undertaken.

Despite the unprecedented realism and computational feasibility of this framework considerable validation and development work lies ahead. We outline priority areas for future work that will improve the realism of the model and extend its reliability and predictive ability. Chief among them is the inclusion of environmental covariates that will connect our predictions to processes such as climate and ocean change, and the connection of particular mitigation and compensatory measures to the quantitative population improvements they may confer.

# 1. Background

Many seabird colonies form stable, distinct networks during the breeding season, making them well-suited to being studied as metapopulations — networks of connected subpopulations whose overall dynamics depend on the movement of individuals between colonies [1–5]. In seabirds, this connectivity is driven mainly by young birds that travel widely while searching for places to breed [6–8].

Tracking these movements requires intensive mark-recapture studies, that are often impractical [9]. As a result, current conservation policies often assume that colonies, especially those within Special Protection Areas (SPAs), are "closed"—meaning they don't receive or send birds to other colonies. This assumption may be neither precautionary, nor biologically realistic.

In fact, bird numbers in any given colony may be influenced by immigration or emigration, which can mask or mimic the effects of other factors like food availability or crowding. Some colonies, called source populations, produce more birds than they lose and can support others. Sink populations, that cannot sustain themselves without incoming birds, may appear stable or even growing simply due to these outside contributions [10]. Assessed in isolation, measured impacts on individual colonies may not map correctly to (i.e., overestimate or underestimate) the importance of their causes, hence leading to incorrect assessment of population persistence or vulnerability under additional anthropogenic pressure.

Understanding which colonies are sources or sinks, and how birds move between them, is key to predicting how seabird populations respond to disturbance. Yet, few studies have used full metapopulation models for seabirds, and even fewer have applied them to real-world data (see examples in Miller et al. 2019, Jeglinski et al. 2023).

Our aim in this project was to address this gap by using data on movement, demography and population size within a realistic and practical model of population dynamics for a declining species, the black legged kittiwake (*Rissa tridactyla*, hereafter kittiwake) to improve how we manage and protect this species within UK and Irish sea waters.

In addition to connectivity, dependence on density is lacking from Population Viability Analyses (PVAs). Density dependence accounts for how the size of a population affects its growth but this is often left out of PVAs, either because it is difficult to measure or because its inclusion is a-priori assumed to be less precautionary. However, connectivity and density dependence, acting together can seriously mislead risk assessments. For example, a large colony may supply young birds to several smaller colonies. If this network is disturbed, say by a known reduction in breeding output, the anticipated impact on the smaller colonies may be underestimated, because not only will they be producing less, but they will also be receiving fewer donations from the source colony, whose previously surplus individuals will be able to recruit locally.

Density dependence also works at different scales and in different ways [12]. Some colonies are limited by space—there are only so many suitable nest sites. Others are limited by regional food supply, with nearby colonies competing for the same fish. These effects can vary across the seabird network and over time.

Another important but often overlooked form of density-dependence is the Allee effect [13]. This happens when very small populations grow more slowly—or not at all—because they lack a "critical mass" to thrive, making it hard for new colonies to become established and raising the risk that declining ones could disappear entirely. Despite its importance, especially for vulnerable seabird species, the Allee effect is rarely included in PVA models.

Another simplification of existing PVAs is that they exclude the effects of population buffering by non-breeding adults (floaters) a group that includes pre-breeders nearing maturity and older birds not breeding in a given year (sabbaticals) [14]. They are excluded from standard breeding surveys and are difficult to quantify, yet they may play a critical role in population dynamics by buffering colonies against disturbances, aiding in the founding of new sites, and enhancing resilience.

Because floaters cannot be directly counted, their effects must be inferred from patterns in breeding colony growth. Their distinct survival and recruitment traits must be explicitly included in models as a latent class to improve population forecasts and conservation planning.

Environmental variables determine the size and variability of population regulation, whether by demography or by redistribution. The primary focus of this work was to recreate and examine trajectories in kittiwake populations across the UK, so consideration of environmental variables was considered out of scope for now, but it should be noted that the framework has the capacity to quantify the impact of and gain predictive accuracy from both natural and anthropogenic variables.

In this project, for the first time, we extended classic PVA models to include connectivity, density dependence (Allee effects, crowding at the colony, competition for prey at sea) and floaters. The resulting model was fitted statistically and holistically to the combination of different data-types available for kittiwakes. This ensured that all of the model's features were simultaneously tuned to the entire body of evidence, and therefore that its predictions are as precise as the available data will permit.

# 2. Project objectives

**Incorporate into model connectivity, density dependence, floaters:** We developed a model capturing direct (immature dispersal) and indirect (adult competition) density dependence, colony connectivity and the effect of floaters. We fitted within an integrated Bayesian statistical framework to comprehensive kittiwake data across colonies.

**Develop advanced population viability analysis:** We recast this fully fitted model into a fast and compact simulation model for stochastic population viability analysis. This PVA model forecast population and demographic trends for individual colonies, regions and the whole metapopulation.

**Examine closed vs. open systems:** We compared population predictions with and without connectivity to understand source-sink roles in the kittiwake network.

**Investigate impact of mitigation/compensatory measures:** We quantified effects on breeding success and the survival of different groups, and evaluated benefits of nationwide as well as local interventions like artificial nesting structures (ANS).

**Issue recommendations:** Guidance is provided on disturbance tolerance and future data inclusion and additional collection priorities for improved forecasting. We discuss candidate covariates as explanatory tools for the decline and the exploration of future intervention actions.

# 3. Data availability and collation

The project was based on a wide diversity of data that were critically collated and organised for this purpose from various sources. Here, we summarise the key data sources, leaving other evidence categories for the detailed technical report.

### Colony census counts

Kittiwake colony census data are available online from the JNCC Seabird Monitoring Programme (SMP) database. This database is particularly focused on the SPA suite for breeding seabirds, which makes locating census data for SPA populations relatively straightforward. The SMP data start from 1986, which requires use of other sources for older counts. Temporally sparse non-SPA estimates were derived from the national census data for 1998-2002 (Seabird 2000) and for 1985-87 (Seabird Colony Register).

### Breeding success

Kittiwake breeding success is monitored at many colonies throughout Britain and Ireland [15]. We used data in the JNCC SMP database on kittiwake productivity at SPA colonies. Whereas the JNCC SMP database provides data from 1986 to 2023, there are some time series of kittiwake breeding success over longer and earlier periods. Localised data (North Shields, Marsden, Foula) for various time periods were also collated.

### Adult survival

Adult survival can be estimated from analysis of ring recovery data, or from annual resightings (or recaptures) of individually marked breeding adults at study colonies. Several studies have published estimates of kittiwake adult survival, from a range of different study colonies [16–21]. The British Trust for Ornithology (BTO) runs the Retrapping Adults for Survival (RAS) scheme, which has included several studies of individually ringed breeding kittiwakes, at a range of colonies around the UK. Annual estimates of adult kittiwake mortality were taken from studies in Tyne, Skomer and Foula.

### Immature (pre-breeder) survival

From ring recovery data, [22] pre-breeder survival is estimated to be 0.79, up to the age of one. This is the only published estimate for first year survival of NE Atlantic kittiwakes. It is to be expected that first year survival is lower than that of adults. However, it is less clear whether survival in the second and third year of life, when many kittiwakes are not closely associated with the competitive environment at breeding sites, is lower or higher than survival of breeding adults.

### Natal dispersal

BTO ring recovery data includes all recoveries of kittiwakes ringed in Britain and Ireland, and recoveries in Britain and Ireland of kittiwakes ringed abroad. We updated previous analyses by [23,24] to determine the pattern of natal dispersal. We updated these analyses held by the BTO were requested.

# 4. Modelling approach

## 4.1. Bayesian integrated metapopulation modelling

We prioritised the development of an approach leading, more broadly, to the next generation of Population Viability Analyses for seabirds. The three overarching advancements required to achieve this approach were:

**A biologically realistic representation of demography.** We identified three forms of density dependence that have never previously been examined simultaneously in population models and, certainly never individually been incorporated into seabird risk assessments: 1) The Allee effect, representing the difficulty faced by nascent colonies to increase in size [25], 2) Crowding, experienced by birds attempting to settle at established colonies, and 3) Scramble competition between birds from multiple colonies, for marine resources, potentially leading to reductions in breeding success.

**A metapopulation structure of sufficient detail.** For biologically realistic connectivity estimates, the spatial scale over which different forms of density dependence operate must be informed by data, from both direct (e.g., ring-resighting data) and indirect (e.g., net colony growth) evidence. It is important therefore to represent the network with sufficient resolution and spatial extent, while paying due attention to the computational costs of doing so.

**Integrated use of multiple sources of data.** Integrated analysis of diverse available evidence was implemented and wherever this was not possible or practicable, we developed informative priors for the integrated model fitting.

The metapopulation model was fitted to the multiplicity of available data directly, within a Bayesian state-space modelling (SSM) framework. A state-space framework [26,27] is a time-series modelling approach that couples a biological process model with an observation process (the link to the data). In the present context, the process model captures demography, density dependence and connectivity, while the observation model captures the biases, imprecisions and intermittencies in the available data. The ability of SSMs to simultaneously account for biological and observation processes means that they are the best modelling framework for teasing apart the main processes of interest from nuisance or confounding processes.

## 4.2. Treatment of space and time

Our approach was spatially implicit, working on a network of 89 breeding colonies. Of those, 33 were designated SPAs and their positions were provided. The remaining 56 were approximate locations with associated population counts placed at approximate positions along the coast, aimed to represent aggregations of smaller colonies (Fig. 1).

To enable the investigation of spatial patterns across the metapopulation's range, we opted to subdivide space into a small number of regions, corresponding to six compass points (Region 1-NW, 2-NE, 3-W, 4-E, 5-SW, 6-SE, see Fig. 1). This subdivision was arbitrary but also quite non-interventionist, in the sense that it split space into approximately equal-sized areas and was not driven by prior-perceptions about sub-population or regional status.

The model operates at annual time units, focusing solely on the breeding season, as the time of the year during which much of the adult population is countable, and when crucial bottlenecks occur, such as recruitment of pre-breeders into the breeding population, acquisition of resources that determine breeding success and effects on the survival of the most vulnerable population classes, the fledglings.

Our data do not contain complete population or demographic time series for all colonies and time series of breeding and survival for most colonies are unavailable. Our model deals with these varying degrees of latency by treating every missing state as a model parameter, to be estimated (imputed) on the basis of the surrounding information.

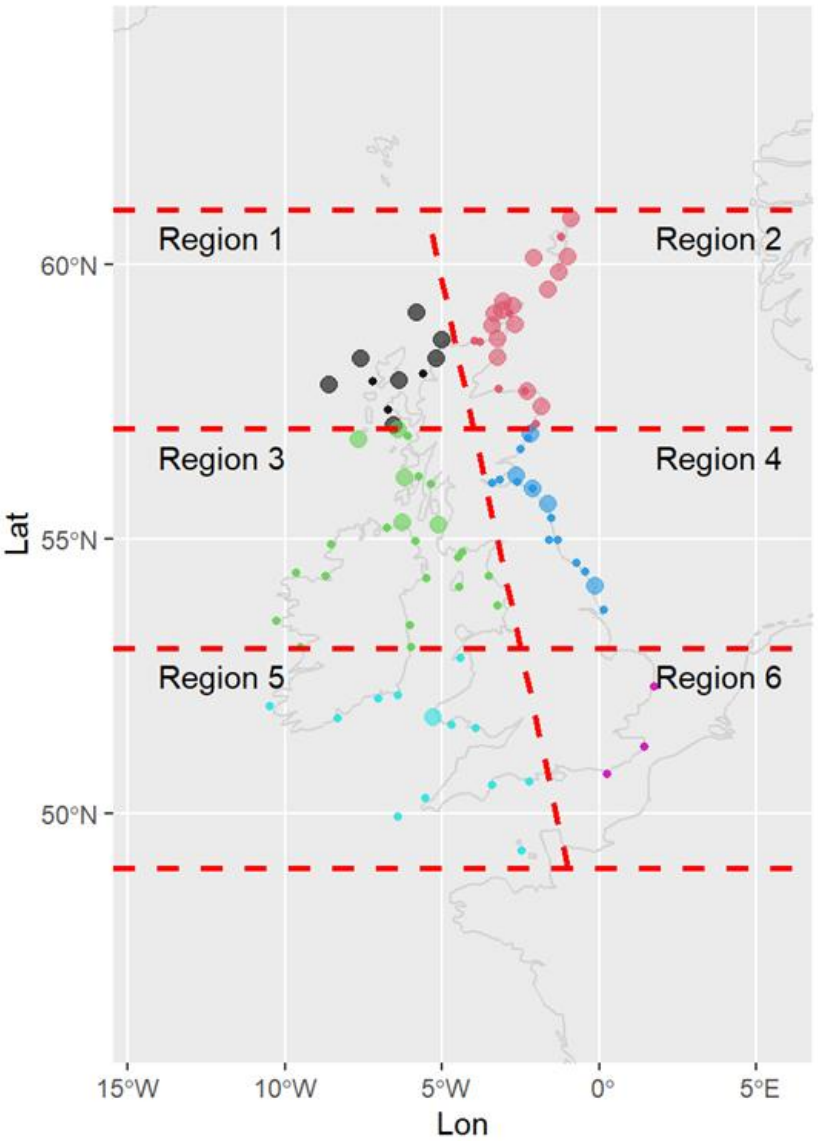

**Figure 1. The network of SPAs (large circles) and approximate management areas (small circles) corresponding to named administrative regions. The six regions defined by the dashed red lines were used for further analyses of aggregate population trends and demography.**

## 4.3. The process model

The core process is an age-structured metapopulation model, treating the breeding colonies as the nodes of a network. Purely by looking at the population trajectory of a single colony, it is impossible to separate the effects of local demography (survival and breeding success) from the behavioural processes of natal site fidelity, immature prospecting, and density-dependent recruitment. The state-structured model tracked three population classes: breeders, pre-breeders and floaters. Features of the model permitted connectivity between colonies, either through dispersal of pre-breeders, or through competition for food between adults. Recruitment into a given colony was affected by its size (i.e., if it was too small to be perceived as attractive or, so large as to suffer from crowding effects). We also built in the capability for the model to detect global or regional impact of environmental or human-induced pressures, although such environmental variables were not brought in within the scope of this project (a key area of future work).

The main model explored as part of the technical report grouped colonies into the six regions of Fig. 1 and assumed that each region had a single set of demographic trajectories, but also, that each region had its unique baseline demographic rates.

# 5. Results of model fitting

Final population outcomes by colony (see Fig. 2) indicate variable degrees of change in population size since the mid-1980s but highlight that most colonies have shrunk. Comparison of the spatial scales characterising connectivity processes indicated that competition for food is more localised than exchange of recruits. Comparisons of the aggregate population trajectories between SPA and non-SPA colonies (Fig. 3) shows a drastic decline during the millennium years, following an apparent increase during the 1970s.

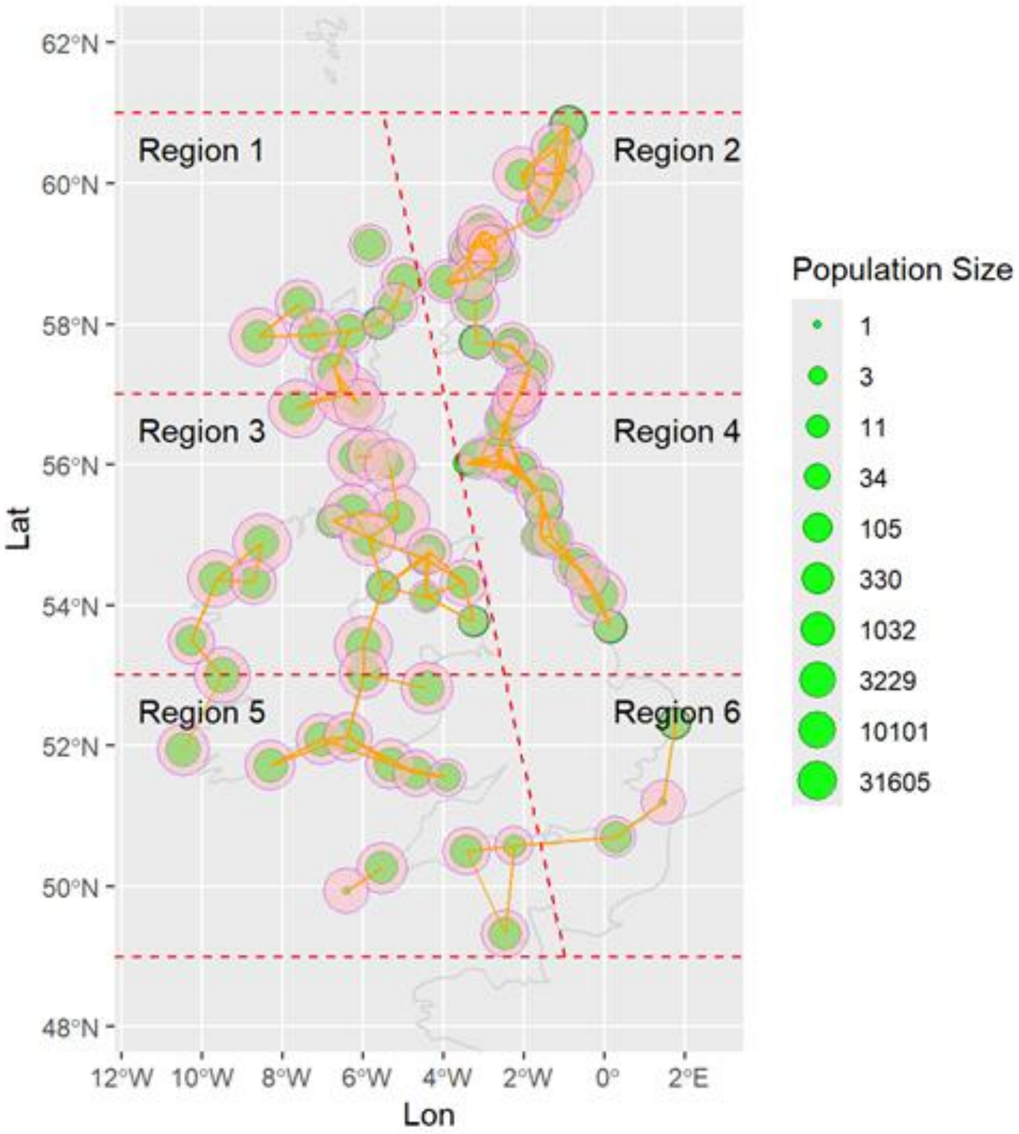

**Figure 2. Spatial representations of the metapopulation. Pink and green circles are sized according to the estimated sizes of the populations in 1985 and 2023 respectively. The orange bars indicate potential levels connectivity through recruitment. The 3% of highest connected pairs of colonies are shown by the orange links.**

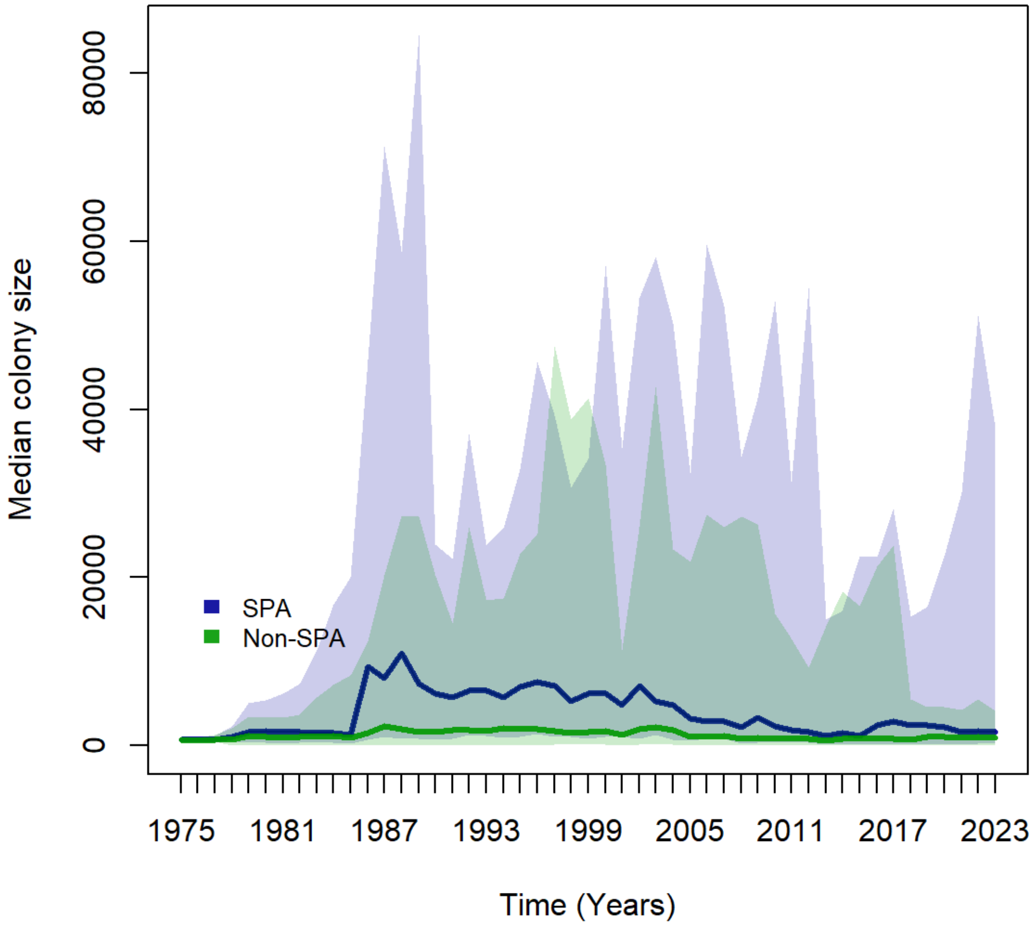

**Figure 3. Median population trajectories for populations at Special Protected Areas and the remaining population components. The 95% credible intervals represent variability between median predictions across all colonies (so they are the Bayesian equivalent of confidence intervals, rather than prediction intervals).**

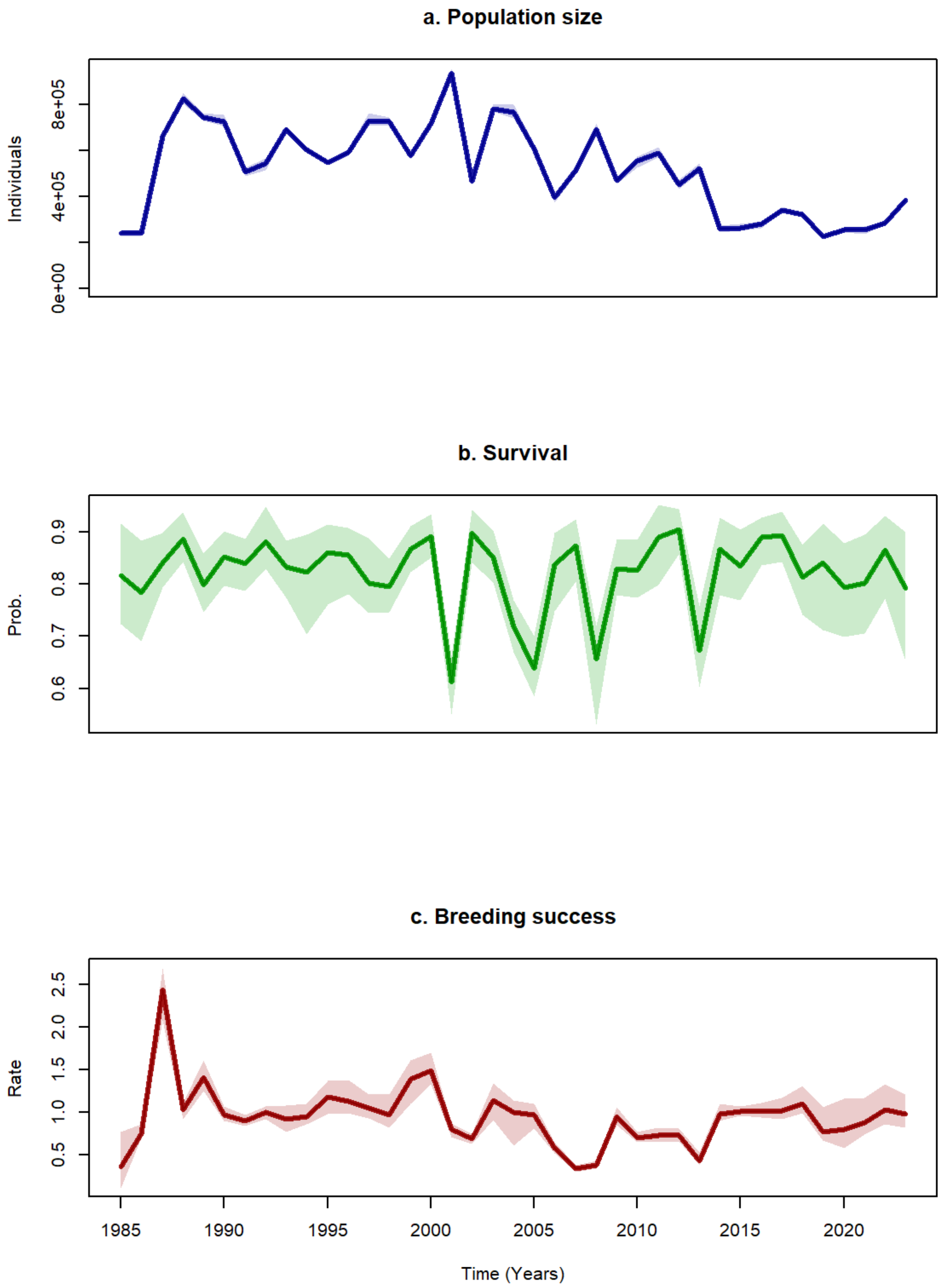

**Figure 4. Reconstructed total metapopulation size (a), aggregate adult survival, averaged across colonies (b) and aggregate breeding success, again, averaged across colonies (c).**

Plots of population size, adult survival and breeding success for each of the six regions in the model (Fig. 5) indicated predominantly declining trends for all regions (except, most recently, regions 2 - Northeast and 4 – East). There were no discernible trends in the demographic rates, but there were clear inter-regional differences in breeding success (with region 4, presenting volatile, but, on average, higher values than the other five regions).

# 6. Next-generation PVA tool for seabird metapopulations

Using the fully fitted model offers considerable PVA capability compared to any currently existing approach - such as the JNCC/Natural England PVA tool, for five reasons:

- The parameterisation of the PVA is not piecewise (i.e., it is not achieved by collating independently estimated parameter values, often without uncertainty, as is customarily the case). In contrast, it is integrated, based on all available knowledge and data.
- Connectivity is fully embedded in the projected dynamics and can be switched on/off to examine the underlying source/sink properties of particular sub-populations.
- Covariates of demographic trends may be embedded in the fitted model, and used to make covariate-driven predictions.
- Density dependent processes have been estimated and embedded into the projections as a matter of course, allowing the model to uniquely capture the numbers of surplus/available recruits. However, density dependence can be optionally switched off, to compare results with the current density independent PVA forecasts by the JNCC/Natural England PVA tool.
- Full and formal treatment of uncertainty is also captured at every stage of the modelling, allowing the PVA to associate probabilities with particular outcomes. Uncertainty exists in such complex models not only because nature is stochastic, but also because the available data are rarely enough to parameterise the models with the desirable precision. Correct representation of uncertainty was the focus of the ORJIP-funded project AssESs.

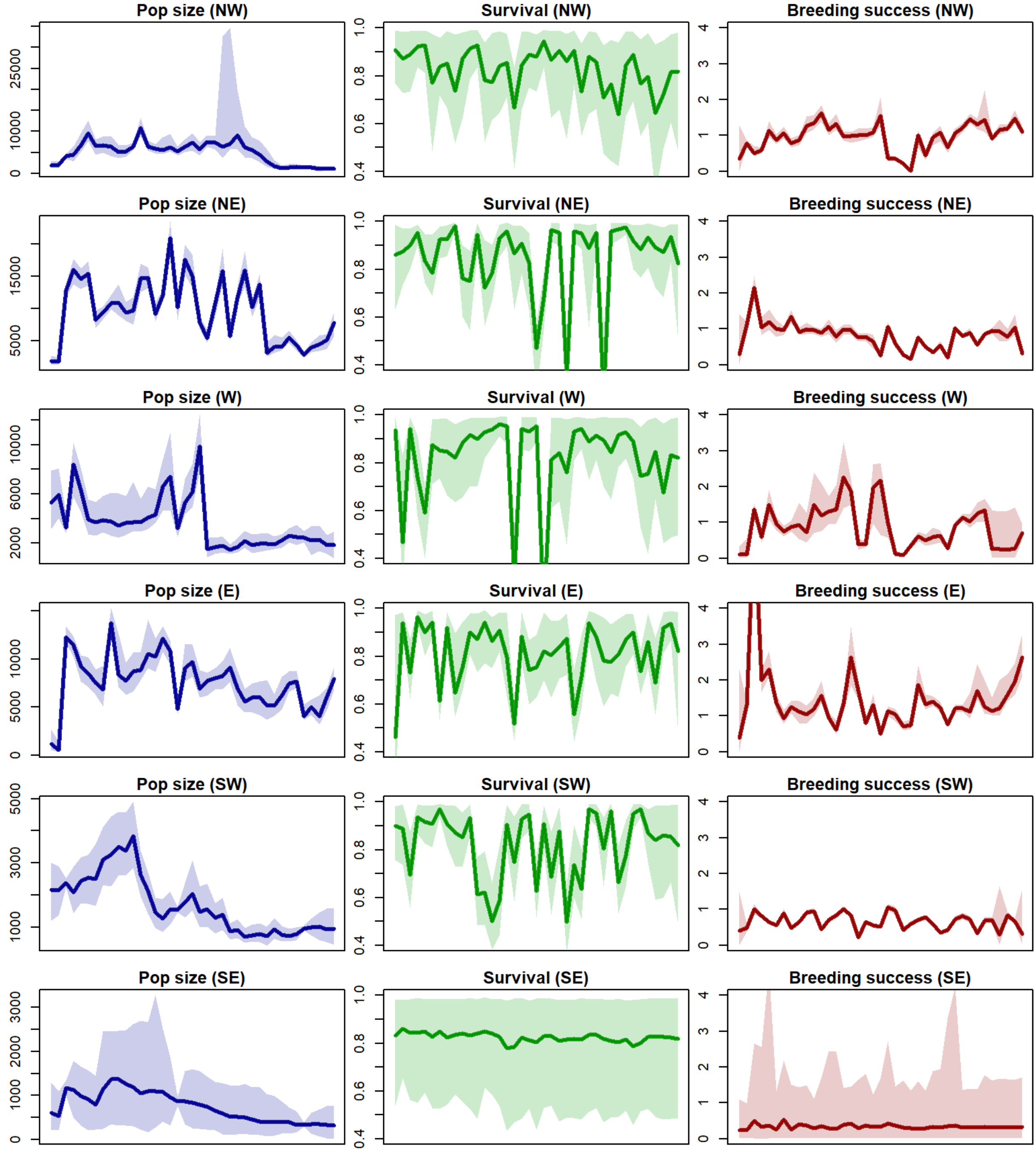

**Figure 5. Regional dynamics model. Each region (annotated by compass point shorthand) was allowed independent random effects for breeding and fecundity rates. Average colony size (a), regional adult survival (b) and regional breeding success (c).**

We used the simulation model to project the metapopulation forward for 50 years (Fig. 6). In Fig. 6a we looked at the aggregate breeding and floater populations across all colonies, with associated 96% credible intervals. In Fig. 6b we plotted the projected trajectories of all the sub-populations (coloured by SPA and non-SPA classification), on the log-scale. The key observations from these results are that:

- The kittiwake metapopulation considered here (UK and Ireland) is likely to go extinct within the 50yr projection time horizon.

- Very few colonies are likely to experience an increase in the short term.
- The pool of floater individuals is likely to be rapidly depleted as the overall population declines.
- All the larger colonies will experience concerted declines.

During the initial phase of the forecasts, the population is projected to increase (Fig. 8). This is a direct result of the recent increasing trends observed in regions 2 and 4 (Fig. 7). However, subject to model assumptions, the estimated parameters for demography and environmental stochasticity, the population is expected to decline after that. This projection would prove to be over pessimistic, if the recent years of increase in regions 2 and 4 represented a genuine change in environmental regimes that would lead to an ongoing increase in these regions, a possibility for which we cannot collect supporting evidence without the aid of covariate input (see discussion on covariates below).

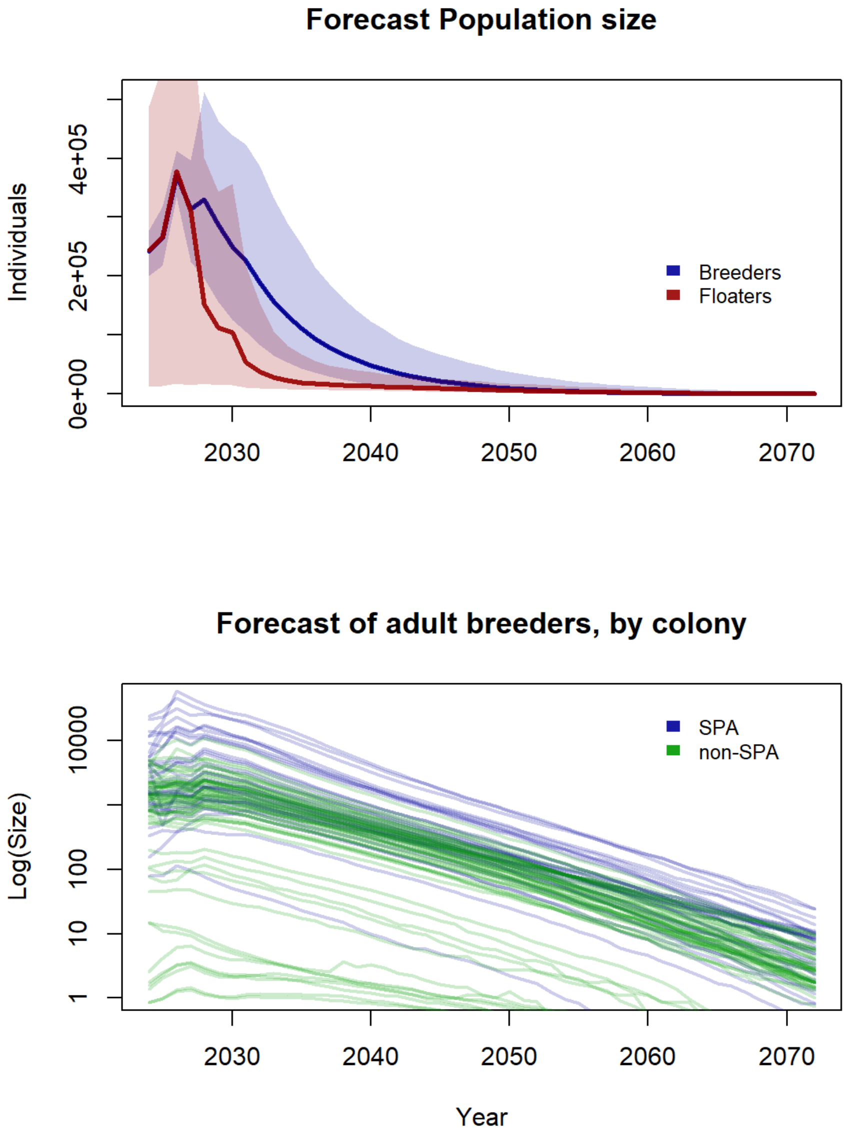

**Figure 6. a) Aggregate population sizes for the main adult components of breeders and floaters. Shaded regions indicate 95% credible intervals. b) Individual mean trajectories of breeders in different colonies coloured by spa (blue) and non-spa (green).**

# 7. Connectivity-related modelling

We investigated the effects of connectivity on the underlying sub-population dynamics of the kittiwake network. We examined two aspects of this problem. The instantaneous status of each colony as a donor or receiver of recruits (results developed and discussed in the technical report) and the ability of a colony to survive in isolation (source), or based on subsidies from other colonies (sink).

Such source/sink dynamics i.e., whether the projected impacts on open and closed populations differ, form a counterfactual that is of particular interest for policy and development. In a simulation setting this can be done by switching the estimated connectivity or density dependence on or off. For example, it is possible that in sink populations, immigration may help maintain population size despite predicted OWF mortality. Contrastingly, detrimental anthropogenic impacts on large, source populations may be felt elsewhere in the network, via the inadvertent reduction of subsidies to satellite colonies.

The finding that all the major colonies are in decline (Fig. 6) means that there are no real source populations. We nevertheless projected the aggregate and colony-specific trajectories for the next 50 years to compare what is the difference made by lack of colony connectivity in the dynamics. We found only small differences compared to the connected projections, only in the sense that some of the smaller colonies are likely to go extinct even sooner than current projections.

# 8. Compensatory measures

We explored the potential for global and regional interventions (mitigation/compensation). Global intervention would involve mechanisms of improvement likely to benefit all colonies. For instance, if fishing moratoria for prey species such as sandeels [28,29] can be shown to increase the persistence and availability of prey to the focal species, then these benefits may be felt across the metapopulation. Mitigation may therefore aim to protect prey species at critical foraging grounds, during key breeding and non-breeding stages [29,30]. Any such improvements may occur at the same time as other environmental drivers are causing global deterioration in one or more vital rates. First, we therefore considered sensitivity of the PVA outcomes across multiple combinations of improvements and deteriorations in the four vital rates of the model. Regional intervention might involve specialised interventions such as the construction of artificial nesting structures (ANS) [31,32]. We therefore then investigated an illustrative example of ANS to exemplify how such an impact could be quantified via our metapopulation PVA.

### Global interventions: Investigation of demographic sensitivity

We systematically explored combinations of increments and decrements in current values of adult/pre-breeder/floater survivals and breeding success. Our results confirmed the importance of adult survival for the viability of the population: Recovery cannot occur unless adult survival is increased by 15% of its current value. Although breeding success can play a role, this is not visible when subadult and floater survivals are low. This is because breeding success cannot benefit the breeding population if these individuals cannot survive to recruit. This result may suggest that even if measures were taken to protect food availability during the breeding season, it may be difficult to control for the effects of adverse conditions on, e.g., overwinter survival.

These outputs will need to be investigated with more thorough simulations but could ultimately be used to prioritise the measures identified in ESCARP[33] and Scottish Seabird Conservation Action Plan [34], and the Welsh strategy when it becomes available. It would also be useful in informing future compensation measures.

### Regional interventions: A PVA experiment using artificial nesting structures (ANS)

For this experiment, we positioned five hypothetical ANSs around the UK at distributed, offshore coordinates and assumed particularly favourable conditions for those birds breeding at the ANS. The ANSs were allowed to subsidise the full metapopulation via recruitment of surplus birds. Results from this experiment showed that although the artificial colonies persisted indefinitely, and they seeded the rest of the metapopulation, they were not enough to reverse the decline of the natural colonies.

# 9. Future work

This project has produced several quantitative findings that can help advise the management of kittiwakes (see conclusions, below), and, in the form of the next-generation PVA, it has established a workflow for evaluating these important questions for any other seabird species. However, several areas need to be built on.

### Considerations regarding covariates

The spatiotemporal patterns of heterogeneity in breeding success and survival revealed in Figs 4 and 5 invite explanation in terms of environmental covariates such as climate change, prey availability, human disturbance, land predators, weather events etc. Regime shifts in trending processes such as climate are likely to be reflected in the covariate data. Such detailed investigations are now methodologically possible (indeed, the model was designed from the start with this capability).

In the technical report we detail the prospects (both opportunities and challenges) of incorporating covariate information on prey availability data and oceanographic proxies, climate covariates, land predators, site availability and colony carrying capacities, offshore windfarms as well other disturbance causes. Further, we look at the potential inclusion of biotic covariates of intra- and inter-colony competition.

### Extensive validation

While the model validation protocol used during development demonstrated that the metapopulation model is computationally tractable and can recover parameters both under idealised conditions and in the case of the real data, much more can be done in the way of validation to increase confidence in its predictions.

## Modelling residual spatial and temporal patterns of variation

Even when detailed investigations of covariates are made possible by available hypotheses and data, there will always be some residual signal in the fitted model, not explained by available covariates. In our study, we have found some evidence of temporal and possibly spatial dependencies in the demographic trends. These have not been modelled explicitly, but they could, to improve model fit and short-term predictive accuracy (short-term because these patterns have limited predictive "memory").

## Improvements on the connectivity model

The prior for our natal dispersal connectivity was based on an expedient analysis of ringing data. The analysis methodology is being extended to use information from birds that were ringed but never recaptured. Additional gains in accuracy and precision can be made by, as-yet undeveloped methods integrating other types of data, such as genetics or telemetry. Our metapopulation model may also be able to incorporate  the average breeding success of target colonies as a covariate of their perceived suitability by prospecting animals [35]. Finally, our model may be extended to include a proportion of breeding dispersal [36].

## Modelling the floater class

The impact of floaters for population assessments could be quite high [14]. The model presented here is, to our knowledge, the first to estimate and use in a PVA the contribution of floaters to apparent population growth, or decline. Our modelling of floaters included assumptions about their association with colonies that may be challenged by experimental studies.

## Improvements to naïve priors

Although our model priors were motivated by data as available, there is still considerable potential to elicit expert opinion, particularly on questions of carrying capacity for different colonies. In addition, continued search for published findings stands to improve the specification of our priors.

## Artificial nesting structures

Evidence gathered to date suggests that the numbers present on offshore breeding structures could be significant [37], although it is noted that population counts are currently limited. We have demonstrated how to model the effect of these additional colonies on the metapopulation. It is important to acquire data on the location and carrying capacity of these structures, but more importantly, data on the survival and breeding success of pairs breeding there.

Use of information on ANS breeding and survival could facilitate the discussion on mitigation and support ANS as a strategic compensatory measure by the installation of purpose-built ANSs at strategic locations. The investigation of the effects of such structures would be conducted according to the methodology illustrated in this report, but more so, we could develop a methodology that could optimise the placement of such structures in order to maximise access to prey fields, but also the distance from other colonies that could benefit from surplus emigrants.

### Overwinter dynamics

The question of where any seabird species spends the winter has emerged for many of these protected species. Once such data are available, we can analyse them to reveal the connections between breeding and overwintering locations [38].

### User-friendly implementation

Gains in usability can be made by capturing this functionality into an software package containing all the functionality for fitting a metapopulation model to data files of particular specifications, but, more appropriately, it could contain regularly updated files of full parameterisations for the PVA for all species of interest. Additional functions could contain the ANS placement optimisation, as well as functions to calculate exposure and demographic impacts as a result of new proposed OWF. Such a library would increase the credibility of risk estimates and projections both for the whole metapopulation, but also for parts of it.

# 10. Conclusions

1. Analysis of the BTO ringing data indicated strong natal site fidelity. Approx 50% of young birds were found to be philopatric. The half-distance of dispersers was approx. 200km. Both numbers were confirmed by the metapopulation model-fitting.
2. In contrast to connectivity via dispersal, the spatial scale of foraging competition at sea was barely 30km. Hence, adults have a more proximate effect onto other colonies, compared to sub-adults.
3. Fitted population trajectories quantify the gradual decline of aggregate numbers since the 1980s. This decline seems to be more pronounced in SPA colonies. The aggregate trends in breeding and survival are very small, so it appears that the decline is due to overall low levels of adult survival and breeding. Examination of regional trends indicates that the east and northeastern parts of the metapopulation have been performing comparatively better.
4. Investigation of alternative models for spatiotemporal trends (i.e. allowing colonies rather than regions to have independent fluctuations and incorporating explicit temporal trends in breeding and survival) does not lead to radically different conclusions.
5. Forward projections of the population using the next-gen PVA predict a continued decline and likely extinction within the next century. In particular, all extant colonies are expected to drop below 100 breeding pairs by the year 2060.
6. It is currently not scientifically productive to explore source-sink dynamics, since all colonies have a decreasing rate. The model estimates some emigration however, which allows us to examine net-donors and net-receivers. In comparative terms, the locations of net-donor colonies have not changed much in the last 30 years, but a smaller proportion of colonies are now net donors (from 32% in 1993 to 21% in 2023).
7. We explored compensatory measures, first at a global scale. Of the four baseline vital rates, adult survival is by far more important than the survivals of pre-breeders and floaters, but also, the baseline breeding success. We estimate that recovery scenarios are only possible if adult survival can be increased by 15% of its current baseline value (from its currently estimated baseline value of 0.82, to 0.95.
8. Regional compensatory measures were explored via the example of artificial nesting structures. Our investigation was not exhaustive, rather serving as a proof-of-concept, however, we believe that it shows that even under ideal conditions of proximity, and improvements in adult survival and breeding, ANSs can serve as refuges, rather than sources, and would not prevent the broader metapopulation decline.
9. We discuss the potential for incorporating different types of covariates in future analyses. We prioritise climate covariates, especially if they can reliably predict prey availability and the exposure to OWFs.
10. Future extensions of this work should aim at covariate exploration, user-friendliness in the use of the next generation PVA, improvements to connectivity model and detailed information on the effect of overwinter performance.

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